

RESEARCH ARTICLE

Age trajectories in extra-pair siring success suggest an effect of maturation or early-life experience

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Funding information

Max-Planck-Gesellschaft

Handling Editor: John Hunt

Associate Editor: Melissah Rowe

Abstract

Across birds, male age is the most consistent predictor of extra-pair siring success, yet little is known about age effects on paternity over the lifetime of individuals. Here, we use data from a 13-year study of a population of blue tits (*Cyanistes caeruleus*) to investigate how extra-pair siring success changes with age within individuals. Our results indicate that extra-pair siring success does not continuously increase with male age. Instead, siring success was related to male age in a threshold fashion, whereby yearling males were less likely to gain paternity than older males. This effect was independent of the age of the social partner, but influenced by the age of the extra-pair female: success of yearlings at siring extra-pair young (EPY) with older females was even lower. Among males that sired at least one EPY, the number of extra-pair mates and the proportion of EPY sired were unrelated to male age. We found no evidence for an influence of selective disappearance on extra-pair reproduction. Senescence, if anything, only occurs at ages blue tits rarely reach. A literature review indicates that an effect of male age on extra-pair siring success may be limited to the switch from yearling to older in many species. Thus, the generally observed age effect on male extra-pair siring success may be linked to age class rather than continuous ageing. This suggests that lack of experience or not fully completed maturation are important drivers of age patterns in extra-pair paternity.

KEYWORDS

age class, ageing, *Cyanistes*, delayed maturation, experience, extra-pair paternity, within-individual effect

1 | INTRODUCTION

Extra-pair paternity (EPP) is common in socially monogamous bird species, especially among passerines (Brouwer & Griffith, 2019; Lifjeld et al., 2019). Many studies have reported that older males in a population have a higher probability of siring extra-pair young (EPY; Akçay & Roughgarden, 2007; Cleasby & Nakagawa, 2012; Hsu et al., 2015). This result is the most consistent finding in the

EPP literature (Nakagawa et al., 2015) and it thus deserves special attention.

Higher success of older males can be explained by several, non-mutually exclusive hypotheses. First, such an effect can arise when individuals with lower success are less likely to survive to older age (effect of selective disappearance; van de Pol & Verhulst, 2006; van de Pol & Wright, 2009). Despite the conspicuous generality of an age effect on male extra-pair siring success, to date only three studies

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have separated within-individual changes with age from effects of selective disappearance (Cooper et al., 2021; Hsu et al., 2017; Raj Pant et al., 2020).

Second, older males may outperform young males because of their increased ability to convince or coerce females into extra-pair matings (Hsu et al., 2015; Westneat & Stewart, 2003). This age-dependent improvement may be an effect of (a) the incomplete maturation of younger males, which prevents them from fully expressing extra-pair behaviour, (b) the experience of older males, which increases their efficiency in pursuing extra-pair copulations (EPCs; Weatherhead & Boag, 1995) or in performing other activities (e.g. foraging, territory defence), freeing them to invest more into the pursuit of EPCs (Curio, 1983), (c) physical or social dominance of older over younger males (Morton et al., 1990), and (d) a female preference for older males as EPC partners (Brooks & Kemp, 2001; Dickinson, 2001; Kokko, 1998; Nakagawa et al., 2015).

Third, older males may be more successful at siring EPY because of an age-related improvement in their fertilization success (Girndt et al., 2018; González-Solís & Becker, 2002). Independent of their success in gaining EPCs, post-copulatory success could be higher for older than for younger males, for example, if they transfer more sperm or more competitive sperm (Cramer et al., 2020; Girndt et al., 2019; González-Solís & Becker, 2002; Laskemoen et al., 2008). Note, however, that effects of senescence can lead to a decline in sperm competitiveness with age (e.g. due to mitochondrial dysfunction or genetic disintegration, Monaghan & Metcalfe, 2019).

Depending on the underlying cause, a within-individual increase in extra-pair siring success may thus be limited to an early-age effect in a threshold manner or it may be an ongoing process, where male performance continues to increase as they get older. In addition, senescence may lead to a performance decline from a certain age onwards. To better understand the evolutionary mechanisms underlying the relationship between male age and paternity gains, it is, therefore, important to study the effect throughout the lifetime of individuals.

Most studies reporting the effect of male age on extra-pair siring success classified males as yearlings or older (Akçay & Roughgarden, 2007; Cleasby & Nakagawa, 2012; Hsu et al., 2015). Such studies cannot be used to investigate the duration of early-life improvement or age-related changes later in life. Furthermore, the combination of early-life improvement, attainment of peak performance and senescence means that age effects are not necessarily described well by modelling approaches based on a parabolic curve (Forslund & Pärt, 1995; Martin, 1995; van de Pol & Verhulst, 2006; Zipple et al., 2019; but used by, e.g., Hsu et al., 2017; Raj Pant et al., 2020), especially if threshold effects are involved (Cooper et al., 2021).

Here, we use data from a population of blue tits, *Cyanistes caeruleus*, to describe the shape of the relationship between male age and extra-pair siring success throughout the lifetime of individuals. We distinguish between effects of selective disappearance and within-individual changes with age. To investigate the importance of incomplete maturation or lack of experience, we compare models

indicating ongoing improvement with those indicating a threshold effect. We also examine senescence by testing for a decline later in life. To explore age-related changes in fertilization success, we also perform the analyses for males that sire at least one EPY while controlling for the number of extra-pair mates.

The observed EPP patterns may be male-driven, but they may also result from a female's likelihood to be involved in or actively pursue EPCs, which may in turn depend on her age (Brekke et al., 2013; Grant & Grant, 2011; Micháľková et al., 2019; Moreno et al., 2015; Raj Pant et al., 2020; Stutchbury et al., 1997). For example, a study on barn swallows (*Hirundo rustica*) showed that young, late-breeding females engaged in EPCs with old, early-breeding males (Møller, 1985). Such a combined effect of male and female age on the occurrence of EPP has been reported in several studies (e.g. Rätti et al., 2001; Roth et al., 2019), but has not been considered in any of the studies inspecting within-individual trajectories (Cooper et al., 2021; Hsu et al., 2017; Raj Pant et al., 2020). Hence, we also consider effects of the partner's age on EPP patterns.

2 | MATERIALS AND METHODS

2.1 | Study system

We studied a population of blue tits in a 40-ha oak-rich plot within a mixed-deciduous forest close to Landsberg am Lech, Germany ('Westerholz', 48°08'26"N 10°53'29"E), from 2007 to 2020. The study area contains 277 nest-boxes permanently equipped with an RFID antenna around the entrance hole and with two light barriers (one on the outside and one on the inside; see Loës et al., 2019). Each blue tit carrying a transponder is automatically recorded when it passes through the nest hole, with data on bird identity, date, time and—based on information from the light barriers—box entry or exit.

Blue tits are small (ca. 10–12 g) cavity-nesting passerines that are usually short-lived in the wild (in our population median longevity: 1 year, mean \pm SD: 1.9 \pm 1.2 years, Figure S1a) although ages >10 years have been documented (Cramp & Perrins, 1993). In our population, on average, 46% of all individuals in the population are yearlings (range: 28%–61%, Figure S2). Blue tits are socially monogamous with occasional social polygyny (Schlicht & Kempenaers, 2021) and frequent EPP (Arct et al., 2022; Badás et al., 2020; Delhey et al., 2003; Kempenaers et al., 1997; Mennerrat et al., 2018; Vedder et al., 2011). In our population, each year on average 43% of nests contain EPY (range 35%–53%) and 10% of young are not sired by their social father (range 8%–15%; see Table S1 for basic metadata and contextual information regarding parentage). Mean clutch size is 10 (range 4–16) with little annual variation (range of annual averages: 9.1–11.2). In our study area, blue tits breed between March and June (nest building to fledging). Individuals may produce a replacement brood if the first breeding attempt fails, but there are no second broods (i.e. additional breeding attempts after fledging of a first brood). Between-year local survival is relatively low: around 45% of individuals breeding

in a given year are observed again in the next spring (Figure S1b). After fledging in May–June, fledglings perform a partial post-juvenile moult between July and October and these yearlings can first reproduce the following spring (Cramp & Perrins, 1993; Jenni & Winkler, 2020). Due to the seasonal occurrence of a single breeding event, the population is composed of individuals from discreet age cohorts, separated in age by full years.

2.2 | Field and laboratory procedures

Each year, we monitored breeding activity in all nest-boxes from early March until the end of June. We visited every nest-box at least weekly (daily around egg laying, hatching and fledging) to record the stage of nest building, the start of laying (laying date), clutch size and the date of hatching and fledging. We banded nestlings and took a blood sample when they were 13–14 days old. We also collected all unhatched eggs and nestlings that died before blood sampling. Overall, we successfully genotyped 91% of all eggs. For a more detailed description of field procedures and ethical implications see Schlicht et al., 2012, 2015. Permits were obtained from the Bavarian government and the Bavarian regional office for forestry (LWF).

We captured blue tits throughout the year, either at the nest-box when they fed nestlings (majority of captures until winter 2014) or with a mist net between September and March (majority of captures since winter 2014). A few birds were caught when they roosted in a nest-box or with a snap trap. Each individual was banded, measured and aged based on plumage characteristics (partial post-juvenile moult, Jenni & Winkler, 2020) as yearling (age = 1 year) or older (age > 1 year). We also took a 5–10- μ L blood sample and implanted a transponder under the skin on the back. For molecular sex determination and parentage analysis we extracted DNA from all blood samples and—when possible—from embryo or nestling tissue. We genotyped each individual using 14 microsatellite markers (Table S2). We compared the genotypes of parents and their offspring using the software CERVUS (Kalinowski et al., 2007). In some cases, offspring could not be assigned to any of the captured individuals, either because an extra-pair father was not sampled (86 young of 58 broods, 7% of EPY), or because of failure to capture the social parents of a nest (31 young of 10 broods).

We used a combination of information to identify the social parents of a nest: (1) observations of individuals defending the box or feeding nestlings, (2) box visits based on the transponder data, (3) individuals caught at the box during nestling feeding, and (4) parentage information. Following Schlicht & Kempnaers, 2021, a male was defined as socially polygynous when he was assigned as the social father at more than one nest and egg laying of the later brood started before the earlier brood had fledged or failed. In all analyses, we excluded males ($N=68$ male-year-combinations) and females ($N=65$ female-year combinations) in a year they were involved in a case of social polygyny.

2.3 | Age variables

Exact age is known for birds ringed as nestling or captured as yearling. Analyses of age-related changes in performance traits only include birds with known exact age. Although we are mainly interested in age as a continuous variable, for some analyses we used a categorical age variable with the classes ‘yearling’ and ‘older’. Individuals with missing age assignments at first observation were categorized as ‘older’ in breeding seasons following the season of their first observation. Twenty-six individuals were handled for the first time at age > 1, but produced offspring in preceding seasons (identified via parentage analysis). These individuals were not assigned to an age class in the season(s) preceding their first handling. For a subset of individuals ringed as nestlings, the first observed breeding event is not at age = 1 ($N=34$ males or 4.5% of males and $N=36$ females or 4.6% of females). These individuals are excluded from the analyses of age-related changes in performance traits (Supplementary Methods S1).

2.4 | Measurements of survival and longevity

For each bird we determined its last record based on the combined information from direct observation, capture, breeding, parentage and transponder data. If a bird was present after 15 March of a given year, the individual was categorized as having survived to that breeding season. Overall, 92% of males ($N=689$) and 92% of females ($N=710$) were last present in the season they were last observed to breed. Note that none of the results changed when survival was assigned based on the last season present compared to the last season breeding (details not shown). We used the breeding, parentage, transponder and capture data of 2020 to determine which individuals survived after 2019, the end of the study period considered here. Individuals observed in 2020 were not included in the data set. We assumed that all other individuals were dead in 2020. We defined longevity for each individual as the age when last recorded. Thus, we ignored breeding dispersal outside the study area (which is rare, especially in males, see Bauer & von Blotzheim, 1993; Cramp & Perrins, 1993; Valcu & Kempnaers, 2008) and failed detection (1.7% of males and 3% of females that bred both in year $X-1$ and in year $X+1$ were not detected in year X).

2.5 | Model structure

To describe effects of age on extra-pair siring success, we inspected the relationship between male age and (a) the probability of siring at least one EPY, (b) the number of extra-pair mates and (c) the total number of EPY sired, as well as the proportion of EPY sired among all genotyped eggs laid by the respective extra-pair female(s). All models were generalized linear mixed-effect models (GLMMs) fitted using the R-package ‘lme4’ (version 1.1.23, Bates et al., 2015). All models are based on data from 2007 to 2019, and in all models, we included year of the study and individual identity as random

intercepts. For (a), males were compared according to whether or not they sired EPY in the focal year (yes/no, binomial error structure, logit-link function). For (b), among the males that sired EPY, we compared the number of extra-pair mates as a measure of extra-pair mating success (Poisson error structure, log-link function). For (c), to compare fertilization success among males that sired at least one EPY, we analysed the proportion of EPY sired (binomial error structure, logit-link function), that is, the number of EPY sired by a given extra-pair sire in a given year (binomial numerator) divided by the total number of genotyped young in the nests where the male sired young (binomial denominator). We also compared the total number of EPY sired among the males with paternity gains, including the number of extra-pair mates as covariate (Poisson error structure, log-link function; Table S3).

To separate within- and between-individual effects, we included longevity as a covariate in all analyses (Supplementary Methods S2). We also included social mate age in all models to examine potentially confounding effects of the age of the social partner (Supplementary Methods S3). Finally, because terminal effects can potentially obscure age-related patterns (Bouwhuis et al., 2009), survival to the following year (yes/no) was included in exploratory analyses. This variable failed to explain variation in extra-pair reproductive performance and did not improve model performance in terms of AIC (Table S4), and we therefore removed it from the final models.

For completeness, we also performed analyses of the effects of age on paternity loss using the same methods as described above (Supplementary Analysis S1). The results are only presented in the Supporting Information, but briefly summarized in the Section 4.7.

Furthermore, we modelled the relationship between age class (yearling versus older) and the probability of siring EPY to allow comparisons with other studies that only have data on age class (categorical model; Table S5).

2.6 | Modelling approaches

To test the shape of the relationship between age and performance, we used four modelling approaches: linear GLMMs, polynomial GLMMs, piecewise regression with one breakpoint (1BP-PC-GLMM) and piecewise regression with two breakpoints (2BP-PC-GLMM). We originally also applied generalized additive mixed-effect models (GAMMs), but results provided little additional insight (Supplementary Methods S4) and these models are therefore not further considered.

We compared competing models based on their AIC values. Following Harrison et al. (2018), we considered models within a Δ AIC of 6 to have comparable support. If models within the set of best supported models were nested, the more complex models were excluded (Harrison et al., 2018; Leroux, 2019). Residuals, model assumptions and dispersion were checked following Zuur et al. (2010) and Harrison et al. (2018). Collinearity of predictor variables and multicollinearity was checked by creating correlation matrices between explanatory variables (containing for each pair of variables

the correlation coefficient r ; Graham, 2003) and calculating the variance inflation factor (VIF) using the methods provided by Zuur et al., 2010. Because $|r|$ was always <0.7 and VIF always <3 , we concluded that multicollinearity was non-problematic for all models (Harrison et al., 2018; Zuur et al., 2010).

2.6.1 | Polynomial regression

We tested for non-linear effects of age by including the second-order polynomial of age as explanatory variable using the 'poly'-function in R. This function calculates orthogonal polynomials and thus avoids confounding effects of polynomial terms on each other (sensu Schielzeth, 2010). When no second-order term of the polynomial GLMM was supported ($p > 0.05$), the polynomial GLMM was excluded in favour of the linear GLMM during model comparison via AIC (Table 1 and Table S6).

When a second-order term of the polynomial regression was supported, we further tested for a decline in performance later in life (senescence). We determined the age at which the maximum of the fitted polynomial curve occurred. We then included only individuals older than that age and tested whether the slope of a linear regression was significantly negative. Because the polynomial regression is sensitive to small sample sizes at extreme values (here: a low number of older individuals), we repeated the analysis after pooling ages ≥ 6 and ≥ 5 . Since results were similar (not shown), we only present the results from the post-peak regression without pooling data.

2.6.2 | Piecewise regression

The shape of the polynomial GLMMs assume that there are no abrupt changes in performance with age. However, if there is a threshold effect of age (e.g. an abrupt change from yearling to adult), we expect that the relationship with age follows one pattern up to a certain age and another pattern after that age. To investigate this scenario, we used piecewise regression, where separate regression lines are fitted over different age ranges, one for each of the processes involved (Berman et al., 2009; Crawley, 2007; Froy et al., 2017). Segments of regression lines are separated by breakpoints. We considered three processes (i.e. two breakpoints): early-life improvement, peak performance, senescence. For each process we generated a dummy variable of age ($\text{age}_{\text{early}}$, $\text{age}_{\text{middle}}$, age_{late}), which varied only over the relevant age range (early, middle or late). Specifically,

$$\text{age}_{\text{early}} = \begin{cases} \text{age} & \text{for age} < b_1 \\ b_1 & \text{for age} \geq b_1 \end{cases},$$

$$\text{age}_{\text{middle}} = \begin{cases} 0 & \text{for age} < b_1 \\ \text{age} - b_1 & \text{for age} \geq b_1 \text{ and age} < b_2 \\ b_2 - b_1 & \text{for age} \geq b_2 \end{cases},$$

TABLE 1 AIC-based comparison of models describing effects of male age on extra-pair siring success.

Relationship	Model	Δ AIC	Model details
Male age & probability of paternity gain	2BP-PC-GLMM (breakpoints at ages 2 & 4)	0.0^a	Figure 2c; Table 2
	Polynomial GLMM (quadratic)	0.4	Figure 2a; Table 2
	1BP-PC-GLMM (breakpoint at age 2)	1.6	Figure 2b; Table 2
	Linear GLMM	37.7	–
Male age & number of extra-pair mates (only males that sired EPY)	Linear GLMM	0.0	Table 3
	1BP-PC-GLMM	0.5 ^b	–
	Polynomial GLMM (quadratic)	1.4 ^c	–
	2BP-PC-GLMM	2.3 ^b	–
Male age & proportion of EPY sired (only males that sired EPY)	1BP-PC-GLMM (breakpoint at age 4)	0.0 ^d	–
	2BP-PC-GLMM	1.8 ^{b,d}	–
	Polynomial GLMM (quadratic)	2.0 ^{c,d}	–
	Linear GLMM	2.1	Table 3

Note: Models were ranked by AIC-value and differences to the model with the smallest AIC value (Δ AIC) are shown. Models were retained and discussed in the main text if Δ AIC < 6 (shown in bold, with reference to the table or figure where more details can be found). Complex models were excluded in favour of a linear GLMM, if the latter had equal support. For other model fit criteria see Table S6.

^aSupport of second breakpoint only a trend (see Table 2).

^bExistence of single (1BP-PC-GLMM) or second (2BP-PC-GLMM) breakpoint not supported.

^cSecond-order polynomial term not supported.

^dModel excluded, because simpler model (linear GLMM) received comparable support.

$$\text{age}_{\text{late}} = \begin{cases} 0 & \text{for age} < b_2 \\ \text{age} - b_2 & \text{for age} \geq b_2 \end{cases},$$

where b_1 and b_2 are the breakpoints between early and middle, and between middle and late ages respectively. To avoid that final segments of regression lines are biologically irrelevant, because they are constructed across ages for which sample sizes are too low, we set $b_2 \leq 6$. We included these three dummy variables as explanatory variables and constructed models for all ten possible combinations of breakpoints where $b_1 < b_2$. Of these ten models, we selected the one with the lowest AIC and those within a Δ AIC of 6. We entered these selected models in the AIC-based model comparison together with other modelling approaches. For each of these selected models, we also tested whether the slopes of consecutive segments were significantly different by selectively replacing one of the dummy variables with age such that the model output would reflect the difference in slope to the slope estimated for the selected age range. The existence of a second breakpoint was considered unsupported when the slope for middle ages was not significantly different from the slopes for either early or late ages. Whenever the two-breakpoint GLMM was excluded in the AIC-based model comparison, the existence of a second breakpoint was unsupported. In the next step, we removed the second breakpoint (setting $b_1 = b_2$ and removing $\text{age}_{\text{middle}}$) and repeated the procedure by constructing models for the five possible positions of a single breakpoint and by selecting the best models among these (based on AIC). Again, we entered these selected models in the AIC-based model comparison together with other modelling approaches. We considered the existence of a single breakpoint unsupported when the slopes for

early and late ages were not significantly different. Whenever the one-breakpoint GLMM was excluded in the AIC-based model comparison, the existence of a single breakpoint was unsupported. When the one- or two-breakpoint GLMM remained among the best fitting models in the AIC-based model comparison (i.e. the existence of at least one breakpoint could not be rejected, as was the case for male probability of paternity gain), we further tested for a senescent decline in performance by evaluating whether the slope of the final segment of the piecewise regression was significantly negative.

2.7 | Effect of extra-pair mate age

We used a randomization procedure to examine effects of the age of the extra-pair mate(s) of the males on the occurrence of EPP (see Supplementary Methods S5 for details). Briefly, we randomly re-assigned extra-pair mates among individuals producing EPY in the same year, repeated this procedure 10000 times, and calculated the correlation of age class and age for the original extra-pair pairs and for each of the 10000 sets of simulated extra-pair pairs.

3 | RESULTS

A male's probability of siring EPY was strongly influenced by his age, and unrelated to the age of his social mate (Tables 1, 2 and Tables S7, S8). The effect was clearly non-linear (Figure 1): the polynomial GLMM, and the one- and two-breakpoint piecewise regressions received similar support (Δ AIC < 1, Table 1). However, we found no evidence for an effect of between-individual variation in longevity on

TABLE 2 Model details for effects of male age on the probability of siring at least one EPY.

Model	Effect	Term (fixed) or group (random)	Estimate (fixed) or SD (random)	Lower 95% CI	Upper 95% CI	z	p
Polynomial GLMM AIC=999	Fixed	(intercept)	-1.37	-1.8	-0.994		
		Longevity	0.0975	-0.0591	0.255	1.2	0.22
		Age (linear coefficient)	16.3	10.3	23.4	4.9	<0.0001
		Age (quadratic coefficient)	-15.8	-20.6	-9.99	-5.5	<0.0001
	Random	ID	0.628	0.00	1.03		
		Year	0.375	0.151	0.703		
Post-peak GLMM	Fixed	(Intercept)	3.36	-0.151	22		
		Longevity	-0.656	-2.04	0.211	-1.5	0.13
		Age (age > 3)	-0.28	-2.24	0.841	-0.5	0.61
	Random	ID	0.909	0.00	3.87		
		Year	<0.0001	0.00	6.21		
1BP-PC-GLMM AIC=1000	Fixed	(Intercept)	-2.02	-2.48	-1.62		
		Longevity	0.108	-0.0519	0.267	1.3	0.18
		Age, first segment (ages 1-2)	1.57 ^a	1.15	2.02	7.1	<0.0001
		Age, final segment (ages 2-7)	-0.0862 ^a	-0.354	0.19	-0.6	0.53
	Random	ID	0.671	0.118	1.08		
	Year	0.374	0.147	0.701			
2BP-PC-GLMM AIC=998	Fixed	(Intercept)	-2.01	-2.48	-1.62		
		Longevity	0.102	-0.0572	0.262	1.3	0.21
		Age, first segment (ages 1-2)	1.54 ^b	1.08	1.96	6.8	<0.0001
		Age, middle segment (ages 2-4)	0.125 ^b	-0.224	0.474	0.7	0.48
		Age, final segment (ages 4-7)	-0.826 ^b	-1.79	0.00681	-1.9	0.06
	Random	ID	0.668	0.123	1.08		
	Year	0.375	0.149	0.704			

Note: Only the three models with the best support (Table 1) are included. Shown are (a) the polynomial regression (polynomial GLMM), (b) the regression among the ages beyond the age at peak performance (defined based on the peak at 3.3 of the polynomial regression, 'post-peak' GLMM) and (c) the one- and two-breakpoint piecewise regressions (1BP-PC-GLMM, 2BP-PC-GLMM). All models have a binomial error structure (estimates on logit scale) and include male identity and year as random intercepts. $N = 924$ observations from 553 males across 13 years (2007–2019) for the polynomial and piecewise GLMMs and $N = 69$ observations from 47 males across 10 years (2010–2019) for the post-peak GLMM.

^aThe slopes of the first and the final segment differ significantly from each other ($p < 0.0001$).

^bThe slope of the first segment differs significantly from the slope of both the middle and the final segment. The slopes of the middle and the final segments are not significantly different ($p = 0.07$).

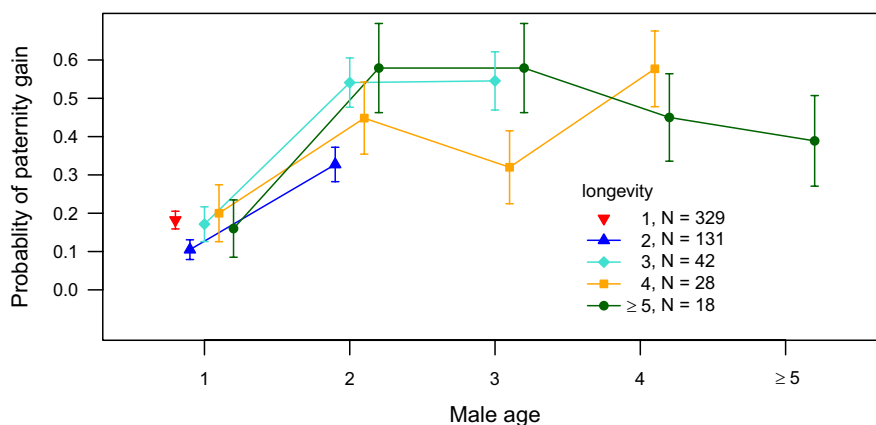


FIGURE 1 Relationship between male age and the probability of paternity gain: raw data for males of different longevity. Shown are means (symbols) and standard errors (error bars). Age is presented with scatter added to separate points. Ages ≥ 5 are pooled because of small sample size.

TABLE 3 Model details for effects of male age on the number of extra-pair mates and the proportion of EPY sired among males that sired at least one EPY.

Response	Effect	Term (fixed) or group (random)	Estimate (fixed) or SD (random)	Lower 95% CI	Upper 95% CI	z	p
Number of extra-pair mates AIC=630	Fixed	(Intercept)	0.219	0.0345	0.396		
		Longevity	-0.0277	-0.125	0.0643	-0.6	0.57
		Age	0.099	-0.0263	0.225	1.5	0.12
	Random	Id	<0.0001	<0.0001	0.131		
		Year	<0.0001	<0.0001	0.134		
Proportion of EPY sired AIC=770	Fixed	(Intercept)	-1.73	-1.88	-1.58		
		Longevity	-0.000802	-0.0749	0.0712	-0.02	0.98
		Age	0.0630	-0.0340	0.160	1.3	0.20
	Random	Id	<0.0001	<0.0001	0.147		
		Year	<0.0001	<0.0001	0.141		

Note: For both relationships the simple linear GLMM is presented, because more complex models did not improve the model fit (Table 1). The model for the number of extra-pair mates has a Poisson error structure (estimates on log scale) and the model for the proportion of EPY sired has a binomial error structure (estimates on logit scale). Both models include male identity and year as random intercepts. $N=256$ observations from 187 males that sired EPY. Data span 13 years (2007–2019).

male extra-pair siring success (Tables 2, 3 and Table S9), suggesting that the observed age effect is not due to selective disappearance of low-success males.

The polynomial GLMM indicated a strong increase in the probability of paternity gain early in life, followed by a decline, with a peak around age 3 (Figure 2a). However, the post-peak slope was not significantly different from zero (Figure 2a; Table 2). Both the one- and the two-breakpoint piecewise regressions identified age 2 as a breakpoint, indicating a genuine structural change in the data between yearlings and 2-year-old birds (Figure 2b,c; Table 2).

In the two-breakpoint regression, the slope of the middle segment was not significantly different from zero, in line with a plateau (Table 2). However, the slope of the final segment—although negative—was also not significantly different from zero ($p=0.06$; Table 2) and did not differ significantly from the slope of the middle segment ($p=0.07$; Figure 2c; Table 2). Taken together, the model results indicate that the transition to a phase of declining performance is less clear. Even with one breakpoint between ages 1 and 2, the slope of the regression line fitted to the final segment was not significantly different from zero, suggesting a plateau instead of a decline in performance after an individual becomes older than one year (Figure 2c; Table 2). Thus, our analyses do not provide evidence for senescence in male probability to sire EPY. Age-related changes are mainly the result of an increase between yearling and older individuals.

Variation in extra-pair success among those males that sired at least one EPY was not related to male age (Tables 1, 3). Males of all age groups had a similar number of extra-pair mates, and both the proportion and the number of EPY sired was independent of male age (Table 3 and Table S3).

The proportion of females that had EPY with a yearling male was higher among yearling females than among older females (Figure 3a and Figure S3). Yearling males had a reduced probability of siring

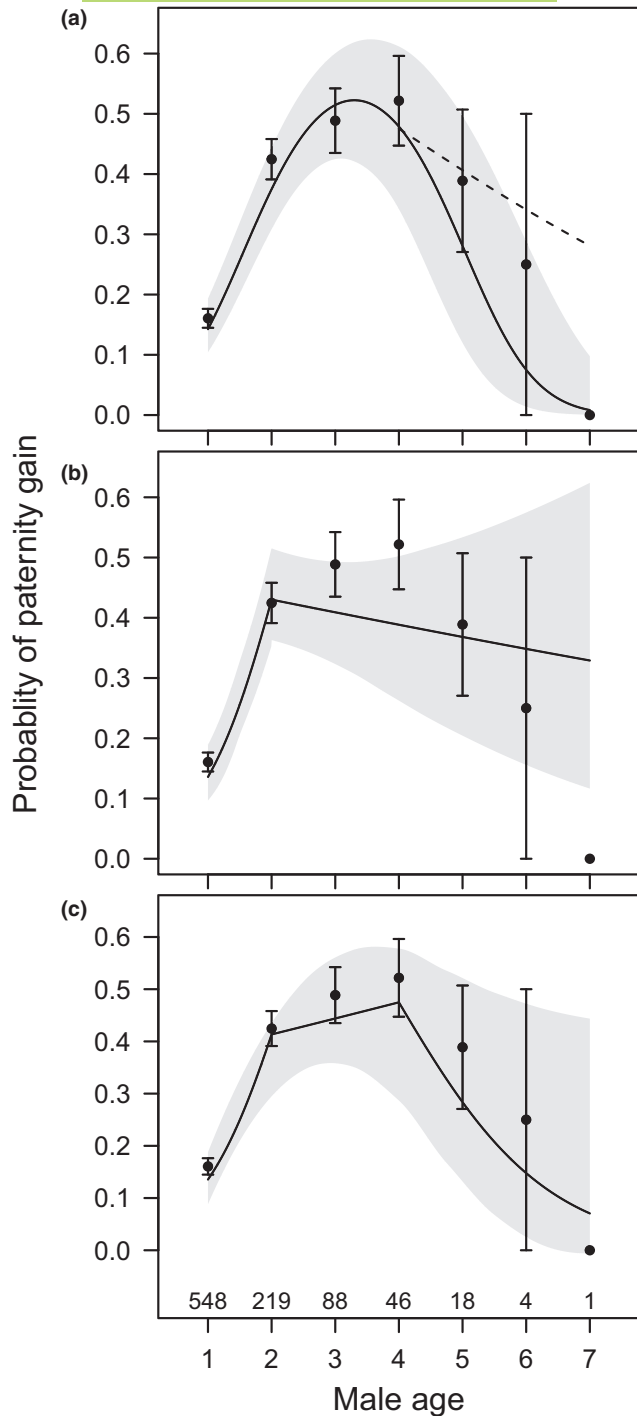
EPY in general (see above), and the probability that a yearling male sired EPY with a female older than himself was even lower (Figure 3b and Figure S3, $p=0.03$).

4 | DISCUSSION

We investigated age-dependent trajectories of extra-pair siring success in blue tits. By using multiple modelling approaches, we show that the key pattern is an increase in performance from yearling to older individuals with little change thereafter.

4.1 | Effects of selective disappearance

Because between-individual variation in longevity was unimportant (Figure 1; Tables 2, 3 and Table S9), neither survival-reproduction trade-offs nor selective disappearance appear to be influential in our population. However, the role of selective disappearance as the cause of the general relationship between male age and extra-pair siring success observed in birds remains difficult to judge, given the small number of studies that examined this. The three previous studies that analysed within-individual changes in paternity with age also found that between-individual effects were absent or much smaller than within-individual effects (Cooper et al., 2021; Hsu et al., 2017; Raj Pant et al., 2020). In addition, we located ten cross-sectional studies that provided some longitudinal information (Table S10). In all of these, the longitudinal results were in line with the results of the cross-sectional analysis. Overall, this suggests that cross-sectional data can provide a good proxy for within-individual patterns of EPP, perhaps because selective disappearance is rare for traits linked to the occurrence of EPP.



4.2 | Age-related increase in siring success: ongoing improvement or threshold effect?

In line with the general pattern in birds (Akçay & Roughgarden, 2007; Cleasby & Nakagawa, 2012; Hsu et al., 2015), extra-pair siring success increases with male age in blue tits, whereby older males have a higher probability to sire EPY than yearling males. We here show that this does not result from a continuous improvement as individuals age, but instead from a sudden increase in performance from first-year to older. Such a result may appear unsurprising in a short-lived species, because the data set is dominated by measurements

FIGURE 2 Relationship between male age and the probability of paternity gain: model fits from the three best-supported models (Table 1). All three panels show the same cross-sectional raw data as means (points) with standard errors (error bars). Each panel also shows one of the three model predictions (lines) with their 95% CI (shading). Sample sizes are indicated in the bottom panel. (a) Polynomial GLMM (quadratic). The dashed line in (a) is the regression line for the ages beyond the fitted peak (at age 3.3). Note that its slope is not significantly different from zero ($p=0.61$). (b) One-breakpoint piecewise regression (breakpoint at age 2). Note that the slopes of the first and the final segment are significantly different from each other ($p<0.0001$) and that the slope of the final segment does not significantly differ from zero ($p=0.53$). (c) Two-breakpoint piecewise regression (breakpoints at ages 2 and 4). Note that the slopes of the middle and the final segment are not significantly different from each other ($p=0.07$) and that the slope of the final segment does not significantly differ from zero ($p=0.06$). Models are binomial GLMMs and correct for between-individual effects of longevity, which were unimportant (all $p>0.10$). Shown are model fits back-transformed to the original scale. See Table 2 for model details.

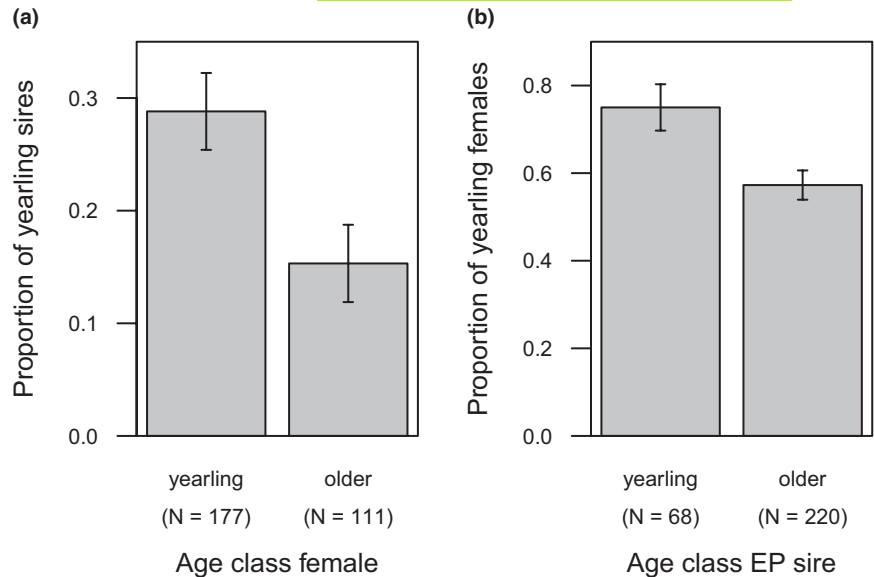
from individuals that are one or two years old. However, age trajectories among individuals with higher longevity mirror the overall age trajectory fitted by our models (Figure 1). This suggests that the breakpoint at age two is due to a genuine structural change in performance and not primarily caused by the data structure.

Could such a threshold pattern also underlie the general effect of male age on extra-pair siring success in birds? This is difficult to judge, because the majority of studies investigating this relationship only consider the difference in performance between yearling and older individuals (Table S11). Of 20 studies that provided some information on the patterns of paternity beyond the two age classes (Table S12), 11 suggest that the main change in performance is indeed between yearling and older males. Most of the studies that supported the idea of a continued increase in siring success were on longer lived species (compared to the blue tit; Table S12). Thus, an effect of male age on paternity gain may be limited to the switch from yearling to older in many species, especially in those that are short-lived.

4.3 | Female preference for older males

One common explanation for higher extra-pair siring success of older males is a preference of females for older males (Akçay & Roughgarden, 2007; Cleasby & Nakagawa, 2012; Hsu et al., 2015; Nakagawa et al., 2015). Selection could favour such a female preference via a good genes mechanism. Age may signal genetic quality, because—all else being equal—older males have demonstrated viability and will transmit the genetic components of this to their offspring (Brooks & Kemp, 2001; Kokko, 1998; Kokko & Lindström, 1996; Trivers, 1972). However, models describing the relationship between male age and male allelic quality predict some form of ongoing improvement (Beck et al., 2002; Beck & Powe, 2000; Kokko, 1998), not the threshold effect observed here.

FIGURE 3 Female age class and the age class of her extra-pair mate(s) are related to each other ($p=0.03$). (a) The proportion of yearling extra-pair sires is higher for yearling than for older females (data shown from female perspective). (b) The proportion of yearling females as extra-pair mates is higher for yearling than for older males (same data shown from male perspective). Sample sizes are given below the bars. Note that overall, 77% of clutches with EPP have males older than yearlings as extra-pair sires, while 61% of clutches with EPP are from yearling females. See Supplementary Methods S5 and Figure S3 for details.



Alternatively, females may exhibit 'non-adaptive' preferences for males with particular traits and abilities (e.g. a high display rate; Hsu et al., 2015; Nakagawa et al., 2015). If these abilities improve as males grow older and become more experienced, this preference would explain higher extra-pair siring success of older males, with an ongoing improvement with increasing age. However, our results suggest that while females may prefer experienced over naïve (yearling) males, further experience with age did not translate into a further increase in extra-pair siring success. Female avoidance of first-time breeding males could be selected in the within-pair context, because whether a male has experience in territory defence and paternal duties may be highly relevant for female reproductive success (Woodard & Murphy, 1999). A female preference for experienced (older) males over naïve (yearling) males may then 'spill over' from the within-pair to the extra-pair context.

4.4 | Disadvantages for inexperienced males in pursuing extra-pair copulations

A performance difference between yearling and older birds may be influenced by the lack of experience of yearlings during autumn and winter or during the mating season (Komdeur, 1996). Previous studies in our population showed that both within- and extra-pair reproductive success is affected by occurrences in the preceding autumn and winter (Beck et al., 2020, 2021; Gilsenan et al., 2020). Moreover, familiarity with the local (social) environment can decrease aggression and increase the probability of territory acquisition, breeding success and the probability of survival during breeding (Brown et al., 2008; Bruinzeel & van de Pol, 2004; Grabowska-Zhang et al., 2012; Piper, 2011; Senar et al., 1990). Older male blue tits usually breed in the same territory they used for breeding in the previous year (Valcu & Kempenaers, 2008). Hence, yearling males that breed for the first time are faced with both new tasks (e.g. performing a dawn chorus, defending a territory, securing and guarding a mate) and with tasks that older birds do not have to perform to the same extent

(e.g. territory acquisition). The combination of lack of familiarity and skills as well as the need for additional investment compared to older birds could then reduce or prevent investment in extra-pair mating by yearlings. Conversely, the experience and prior residency of older birds may allow them to invest more into EPP, for instance by more intense pursuit of EPCs (Curio, 1983) or by higher post-copulatory investment (e.g. production of larger testes; Graves, 2004; Hill, 1994; Kempenaers et al., 2002; Laskemoen et al., 2008; Lifjeld et al., 2022; Merilä & Sheldon, 1999). It may also lead to social dominance (Senar et al., 1990; Yasukawa, 2013), which might suppress the extra-pair mating success of yearling males (Morton et al., 1990).

4.5 | Incomplete maturation

Yearling and older birds not only differ in experience but also in their physical state. While skeletal growth is completed when fledglings become independent, skeletal maturation is ongoing in concert with continuing neurological and muscular maturation (Atterholt & Woodward, 2021; Marchetti & Price, 1989). Moreover, even after completion of feather growth, yearling and older individuals of many species differ in plumage quality because of partial post-juvenile moult and the associated differences in feather length and quality (Jenni & Winkler, 2020). Thus, older males may be physically dominant or more competitive due to improved wing load and flight efficiency, which may continue until the next (post-breeding) moult. The structural change in performance from yearling to older can thus also be explained by effects of not yet fully completed maturation.

4.6 | Age effects on post-copulatory fertilization success

A previous study on captive house sparrows showed an age effect on extra-pair siring success but not on the success of obtaining EPCs

(Girndt et al., 2018), and suggested that older males had higher post-copulatory success (e.g. via higher sperm numbers; Girndt et al., 2019). Our results do not support this hypothesis for blue tits. We found no effect of male age on the proportion of EPY sired or on the number of EPY sired after controlling for variation in the number of extra-pair mates. This suggests that age effects on male extra-pair siring success are due to variation in mating success and not to post-copulatory processes.

4.7 | Effects of partner age

A combined effect of male and female age on the occurrence of EPP has not been considered in the previous studies inspecting within-individual trajectories (Cooper et al., 2021; Hsu et al., 2017; Raj Pant et al., 2020). We found that male extra-pair success was also related to the age of the extra-pair female: the reduced chances of paternity gain for yearling males were further lowered when the extra-pair female was older than one year (i.e. age class was correlated among extra-pair mates; Figure 3 and Figure S3). This effect did not depend on the age-structure of the female's or male's neighbourhood (first-order neighbours; results not shown). Different from a study on great tits (*Parus major*; Roth et al., 2019), male extra-pair success was independent of the age of the social female (Tables S7, S8).

Combined effects of male and female age have been mostly reported for the occurrence of paternity loss (Table S13). However, in our population paternity loss is unrelated to the age of the male and the female (Tables S14, S15), and does not decrease with male age even when controlling for the age of the social mate (Tables S16, S17) and taking into account assortative mating by age class (Figure S4). This is in line with the majority of studies investigating effects of the age of either pair member on the occurrence of EPP in a brood (Tables S11, S13; Cleasby & Nakagawa, 2012).

4.8 | Effects of senescence

Our analyses provide no evidence for senescence in extra-pair siring success. This result appears in contrast to the three previous studies that inspected effects of male age on paternity gain across the lifespan of individuals (Cooper et al., 2021; Hsu et al., 2017; Raj Pant et al., 2020). All three reported senescence in male extra-pair siring success. Two of these studies are on longer-lived, cooperatively breeding species (*Malurus cyaneus*, life expectancy \approx 3 years, Cooper et al., 2021; *Acrocephalus sechellensis*, life expectancy \approx 5 years, Raj Pant et al., 2020), which may explain why senescence in paternity gain is found there, but not in our population. In the third study on house sparrows, the age structure of the population is probably more similar to that in our population (Hsu et al., 2017). Whether a discrepancy exists between the results of Hsu et al. (2017) and our study remains to be shown. Hsu et al. (2017) used a modelling approach that did not explicitly test

for a post-peak decline in performance. Hence, the evidence for senescence in extra-pair siring success remains inconclusive. In our population, the evolutionary relevance of senescence may be limited because individuals rarely survive to ages where performance declines might occur. Because of the low number of long-lived individuals, senescence may occur in our population, but remain undetected due to low statistical power.

5 | CONCLUSIONS

Our results provide evidence for a substantial difference in extra-pair siring success between yearling and older individuals. This may be linked to effects of not fully completed maturation or lack of experience. Alternatively, age class may affect trajectories of reproductive success only indirectly, through an underlying trait that influences extra-pair reproduction (e.g. arrival date, Gilsenan et al., 2020).

We argue that a structural change between yearling and older individuals may be common also in other species and needs to be tested explicitly. We propose that the generality of the age effect on extra-pair siring success is not indicative of a continuous improvement with age. Instead, our study suggests that it hinges on maturation and on whether an individual has breeding experience. Although we here focus on effects on EPP, this type of threshold effect may be important for many life-history traits, for example, those related to seasonal timing and fecundity (Bouwhuis et al., 2009; Cooper et al., 2021; Curio, 1983; Forslund & Pärt, 1995; Hawkins et al., 2012; Martin, 1995). We suggest that a structural change between age classes should be considered in any study on aging (Berman et al., 2009; Cooper et al., 2021; Froy et al., 2017).

AUTHOR CONTRIBUTIONS

Emmi Schlicht: Conceptualization (equal); data curation (lead); formal analysis (lead); methodology (lead); software (lead); visualization (lead); writing – original draft (lead); writing – review and editing (equal). **Bart Kempenaers:** Conceptualization (equal); formal analysis (supporting); funding acquisition (lead); methodology (supporting); supervision (lead); visualization (supporting); writing – original draft (supporting); writing – review and editing (equal).

ACKNOWLEDGEMENTS

We thank Agnes Türk, Andrea Wittenzellner, Corinna Steinmeyer, Lotte Schlicht, Carol Gilsenan, Kristina Beck, Peter Santema and many assistants for field work, Sylvia Kuhn, Alexander Girg, Kim Teltcher and Christine Baumgartner for genotyping, and Kristina Beck, Peter Santema, Lotte Schlicht, Mihai Valcu and other members of the Kempenaers department for discussion. This research was funded by the Max Planck Society. Open access funding enabled and organized by Projekt DEAL.

CONFLICT OF INTEREST STATEMENT

The authors have no conflicts of interest to declare.

PEER REVIEW

The peer review history for this article is available at <https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/jeb.14201>.

DATA AVAILABILITY STATEMENT

All data and code used in this study are available from the Open Science Foundation digital repository (<https://osf.io/yvaqz>; Schlicht & Kempnaers, 2023).

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How to cite this article: Schlicht, E., & Kempnaers, B. (2023). Age trajectories in extra-pair siring success suggest an effect of maturation or early-life experience. *Journal of Evolutionary Biology*, *36*, 1213–1225. <https://doi.org/10.1111/jeb.14201>

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Supporting Information

for

Age trajectories in extra-pair siring success suggest an effect of maturation or early-life experience

by

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This supporting information includes:

- Supplementary Methods S1 to S5
- Supplementary Analysis S1
- Supplementary Tables S1 to S20
- Supplementary Figures S1 to S5
- Supplementary References

SUPPLEMENTARY METHODS

SUPPLEMENTARY METHODS S1: Age at first reproduction

In the analyses of age-related performance, we excluded individuals whose age of first observed breeding was >1 (approximately 6% of individuals, see Methods), because they represent a mixture of (1) individuals for which we missed their first breeding attempt as yearling (e.g. because they bred in a natural cavity), (2) individuals that dispersed to the study site after performing their first breeding as yearling elsewhere (i.e. immigrants) and (3) individuals that did not breed as yearling (i.e. individuals without previous breeding experience). Thus, our data set consists of individuals without variation in their age at first reproduction. This implies that we cannot separate age effects from experience effects (e.g., reduced performance due to lack of experience) and we do not consider effects of selective appearance or of survival-

reproduction trade-offs that lead to a delay in initiation of performance.

SUPPLEMENTARY METHODS S2: Effects of longevity

In analyses of age effects data for higher ages by definition include individuals that survive longer, while data for lower ages often represent a mixture of shorter- and longer-lived individuals. Individuals that die early may perform differently than long-lived individuals due to selective disappearance and survival costs of performance. Thus, a pattern of changing performance with age may not reflect the within-individual trajectory of performance, but between-individual differences that are linked to variation in longevity. To separate within-individual changes with age from effects of selective disappearance and survival costs of performance we therefore included longevity in all models (van de Pol and Verhulst 2006; van de Pol & Wright 2009). Any effects of the age term are then due to variation that is not explained by the longevity term. Effects of longevity may be non-linear, if survival is both a correlate (selective disappearance) and a consequence (e.g., survival-reproduction trade-offs) of performance. For example, an overall curved relationship may arise from an increase of performance with longevity at the lower end, because individuals that die very early also perform badly, combined with a decrease of performance with longevity at the upper end, because very high-performing individuals die earlier due to survival costs of reproduction (Reid et al. 2003; Bouwhuis et al. 2009). Therefore, we initially included both the linear and the quadratic terms of longevity in all analyses. However, because models including quadratic effects did not outperform models including only linear effects in terms of AIC (Table S9), we removed the quadratic term in the final models. There was no evidence for significant effects of either term (Table 2, 3, S9), but we maintained the linear term in all models to remove between-individual effects when examining effects of age.

SUPPLEMENTARY METHODS S3: Effects of social mate age

Performance may be influenced by both an individual's age and the age of its social or its extra-pair mate (see Introduction). To consider effects of the age of the social mate, we included the age of the mate of a focal individual in the initial models. We first tested for an interaction effect of the age of the focal individual and the age of its social mate on performance by including for each term of the focal individual's age the interaction with either the age or the age class of its social mate. We found no evidence for any interaction between individual age and social mate age (no decrease in AIC, $p > 0.05$; see Schlicht & Kempenaers 2023 for details) and therefore removed any interaction terms. Next, we included social mate age as additive term (either linear or quadratic). These analyses revealed (Table S7, S8) no effects of social mate age on extra-pair reproductive performance and we therefore removed social mate age from the final models.

SUPPLEMENTARY METHODS S4: GAMMs

A polynomial regression can be helpful in identifying non-linear patterns, but it requires the model fit to have a specific shape (e.g., in a second-order polynomial, pre- and post-peak effects need to be symmetric) and it cannot account for the periods of constant performance ('plateaus'). To circumvent these issues, generalized additive mixed-effect models (GAMMs) can be used, because a non-parametric smoothing function allows a more flexible specification of the relationship with age. We used the smoothing function 's' of the R-package 'gamm4' (version 0.2-6, Wood & Scheipl 2020) to enter a smoothed age-term in a GLMM (fitted with 'lme4'). Specifically, we chose a thin-plate regression spline (Wood 2003) with the parameter k set to the maximum (here: the number of unique ages present in the data), which ensured that the effective degrees of freedom were substantially smaller than k in all cases. The predictions from the model fit obtained with the GAMM were similar to those obtained with the polynomial GLMM (Figure S5). This suggests that in our study there is no evidence for a decline in performance with age following a performance plateau. Because interpretation of estimates from GAMMs is less straightforward than those from polynomial GLMMs, we only report the latter in the main

text. We also note that the GAMM never provided a better fit than the polynomial GLMM in model comparisons based on AIC values (Table S6).

SUPPLEMENTARY METHODS S5: Age correlations among social and extra-pair partners

We simulated the age of extra-pair partners under random mating. Because polygyny may affect EPP (Schlicht & Kempenaers 2021), we excluded females involved in social polygyny. To avoid pseudo-replication, we included only one breeding event for each unique male-female combination (the last, to increase the sample size of older individuals, leading to the exclusion of 3% of annual pairings). Then, we randomly reassigned extra-pair partners among individuals breeding in the same year, repeated this procedure 10000 times, and calculated four parameters for the original extra-pair partners and for each of the 10000 sets of simulated partners. (i) The proportion of pairings where both extra-pair partners belonged to the same age class (yearling or older), (ii) the proportion of pairings where both extra-pair partners were of the same exact age (in years), (iii) the mean absolute difference (in years) in age between extra-pair partners and (iv) the Pearson correlation coefficient of age between extra-pair partners. For (i) we included all pairings where the age class of both extra-pair partners was known, including pairings involving birds with unknown exact ages. For (ii-iv) we excluded all pairings (original or assigned in simulation) where the exact age of one of the extra-pair partners was unknown. Because in the initial years of the study exact age was unknown for many individuals, we restricted the analysis of (ii – iv) to the years after 2011, when exact age was known for at least 80% of breeding males and females (Figure S2). Results were similar when all years were included (not shown). We compared the value of (i-iv) obtained from the original extra-pair pairings with the distribution of the 10000 values obtained from the simulated extra-pair pairings. To inspect to what extent the similarity in age between extra-pair partners was driven by yearling individuals mating among each other, we repeated the calculation of (ii-iv) including only pairings (original or assigned in simulation) where both extra-pair partners were older than one year.

We used the same simulation procedure to inspect the correlation of age among social pair members. We again excluded pairs where an individual bred with more than one individual in a given breeding season (due to social polygyny or to a replacement brood that involved a mate change) and included only the last breeding event for each pair (excluding 7% of annual pairings). We then randomly reassigned social pair members to each other within years as described before and calculated the parameters (i-iv) using either all pairings (i) or only those where the exact age of both extra-pair partners was known (ii-iv).

SUPPLEMENTARY ANALYSIS

SUPPLEMENTARY ANALYSIS S1: Analysis of age effects of pair members on occurrence of EPP in their nest

Methods Supplementary Analysis S1

To describe effects of age of pair members on the occurrence of EPP in their nest, we inspected the relationship between (a) male age and the probability of paternity loss, and (b) female age and the probability of EPP in her clutch ('female EPP') using the methods described in the main text. That is, we implemented multiple modelling approaches, compared models based on AIC-values and maintained models within $\Delta AIC \leq 6$ of the best performing model. Similarly, we performed all tests for confounding factors, such as non-linear effects of longevity, survival to the next season (to account for terminal effects) or an interaction with mate age. We considered effects of male age on paternity loss in a model with the probability of paternity loss as response variable (yes/no, binomial error structure, logit-link function) and we tested effects of female age on the occurrence of EPP in her clutch (yes/no, binomial error structure, logit-link function). For comparison, we also combined the two models in a cross-sectional analysis to test simultaneously for the effect of the age of the social male and the age of the social female on the occurrence of EPP in their clutch. This model does not correct for longevity and thus cannot separate between- from within-individual effects.

Results Supplementary Analysis S1

A male's probability of losing paternity in his own brood was independent of his age (Table S14, S15). Female age also had no effect on the probability of EPY in her nest (her mate's paternity loss, Table S14, S15). This conclusion did not change when mate age was entered in the same models as an interaction term (not shown, see Schlicht & Kempenaers 2023 for details) or when the ages of both partners were combined in a single cross-sectional model (Table S16). Mate age did not explain variation in the probability of paternity loss for males or in the occurrence of EPY for females (Table S16, S17). A male's probability of paternity loss increased with male age when accounting for the age of the mate (Table S16). However, this effect was driven by a high rate of paternity loss

in 3 out of 4 males that were age 6 or older, and is no longer significant when these four instances were excluded (details not shown). Female age remained unrelated to the probability of EPY in her nest when mate age was included (Table S16, S17). In all of these analyses there was no evidence for between-individual (Table S15, S18) or terminal (Table S19) effects.

SUPPLEMENTARY TABLES

Table S1. Basic parentage metadata and contextual information for the present study (following Brouwer & Griffith 2019).

Location of study population	latitude: 48°08'26"N, longitude: 10°53'29"E	
Time of study	2007 – 2020 (only data up to 2019 included for age trajectories)	
Social context of families	social monogamy (cases of facultative polygyny excluded)	
Basic metadata	number of families sampled	1456
	number of broods sampled	1583
	number of offspring sampled	13872
	number of offspring found to be within-pair	12239
	number of offspring found to be extra-pair	1633
	number of broods that contained EPY	706

Table S2. Information about microsatellite markers used for parentage analysis of blue tits.

Locus	Accession no.	Reference	Primer sequences (5' - 3')	C (µM)	Multiplex Mix	Size range (bp)	Number of alleles
ADCYAP1_bm	FJ464427	Steinmeyer et al. 2009, supplement	VIC-GATGTGAGTAACCAGCCACT ATAACACAGGAGCGGTGA	0.2	2 ^a	160 – 172	10
ClkpolyQ	AY338423-28	Johnsen et al. 2007	6FAM-TTTTCTCAAGGTCAGCAGCTTGT CTGTAGGAAGTGTGCGGTGCTG	0.36	4 ^b	266 – 283	7
Mcµ4	U82388	Double et al. 1997	PET-ATAAGATGACTAAGGTCTCTGGTG TAGCAATTGTCTATCATGGTTTG	1.1	2 ^a	156 – 194	19
PAT MP 2-43	AM056063	Otter et al. 1998	6FAM- ACAGGTAGTCAGAAATGGAAAG GTATCCAGAGTCTTTGCTGATG	0.24	4 ^b	125 – 155	8
Pca3	AJ279805	Dawson et al. 2000	PET-GGTGTTTGTGAGCCGGGG TGTTACAACCAAAGCGGTCATTTG	0.8	1 ^c	154 – 234	43
Pca4	AJ279806	Dawson et al. 2000	NED-AATGTCTTACAGGCAAAGTCCCCA AACTTGAAGCTTCTGGCCTGAATG	0.42	4 ^b	149 – 201	18
Pca7	AJ279809	Dawson et al. 2000	6FAM-TGAGCATCGTAGCCCAGCAG GGTTCAGGACACCTGCACAATG	0.25	1 ^c	105 – 141	18
Pca8	AJ279810	Dawson et al. 2000	NED-ACTTCTGAAACAAAGATGAAATCA TGCCATCAGTGCAAACCTG	0.48	1 ^c	255 – 401	73
Pca9	AJ279811	Dawson et al. 2000	VIC-ACCCACTGTCCAGAGCAGGG AGGACTGCAGCAGTTTGTGGG	0.3	3 ^d	111 – 135	13
Phtr3 ^e	AM056070	Fridolfsson et al. 1997	NED-ATTTGCATCCAGTCTTCAGTAATT CTCAAAGAAGTGCATAGAGATTTTCAT	1.4	2 ^{a,e}	118 - 148 ^e	16 ^e
PK11	AF041465	Tanner et al. 1995	PET-CTTTAAGAATTCAAATACAGAGTAGG GTTTTCTCCTTTCTACTGAGG	0.54	4 ^b	63 – 97	14
PK12	AF041466	Tanner et al. 1995	VIC-CCTCCTGCAGTTGCCTCCCG CGTGGCCATGTTTATAGCCTGGCACTAAGAAC	1.14	4 ^b	168 – 226	27
PmaTAGAn71 ^e	AY260537	Saladin et al. 2003	NED-TCAGCCTCCAAGGAAAACAG GCATAAGCAACACCATGCAG	0.3	2 ^{a,e}	190 - 310 ^e	29 ^e
POCC1	U59113	Bensch et al. 1997	6FAM- TTCTGTGCTGCAATCACACA GCTTCCAGCACCCTTCAAT	0.8	3 ^d	219 – 255	25
POCC6	U59117	Bensch et al. 1997	VIC-TCACCCTCAAAAACACACACA ACTTCTCTGAAAAGGGGAGC	0.25	1 ^c	195 – 253	28

Note: Microsatellite amplifications were performed in multiplexed PCRs using the Qiagen Type-it Microsatellite PCR Kit with primer mixes containing two to five primer pairs. Each 10 µl multiplex PCR contained 20–80 ng DNA (see footnotes below for PCR cycling conditions). The PCR products were analysed on an ABI 3130xl Genetic Analyzer. Primer sequences include information on fluorescence labels used. C refers to the primer concentration in the multiplex primer mix. Size range and number of alleles refer to the 2018 data (N =1696; Phtr3 from 2017, N =1905).

^a Cycling conditions for mix 2: 5 min initial denaturation at 95°C; 27 cycles of 30 s denaturation at 94°C, 90 s annealing at 56°C, and 1 min extension at 72°C; followed by a 30 min completing final extension at 60°C.

^b Cycling conditions for mix 4: 5 min initial denaturation at 95°C; 23 cycles of 30 s denaturation at 94°C, 90 s annealing at 58°C, and 1 min extension at 72°C; followed by a 30 min completing final extension at 60°C.

^c Cycling conditions for mix 1: 5 min initial denaturation at 95°C; 15 cycles of 30 s denaturation at 94°C, 90 s touch down annealing at 60°C decreasing by 0.3°C per cycle, and 1 min extension at 72°C; 11 cycles of 30 s denaturation at 94°C, 90 s annealing at 53°C, and 1 min extension at 72°C; followed by a 30 min completing final extension at 60°C.

^d Cycling conditions for mix 3: 5 min initial denaturation at 95°C; 14 cycles of 30 s denaturation at 94°C, 90 s annealing at 56°C, and 1 min extension at 72°C; 11 cycles of 30 s denaturation at 94°C, 90 s annealing at 57°C, and 1 min extension at 72°C; followed by a 30 min completing final extension at 60°C.

^e Phtr3 was replaced by PmaTAGAn71 from 2018 onwards.

Table S3. Details of models testing effects of male age on the number of EPY sired among males that sired at least one EPY.

Model	Effect	Term (fixed) or group (random)	Estimate (fixed) or SD (random)	Lower 95% CI	Upper 95% CI	z	p
categorical GLMM AIC = 845	fixed	(intercept)	0.0670	-0.122	0.252		
		Longevity	0.0255	-0.0442	0.0927	0.7	0.47
		extra-pair mate number	0.504	0.425	0.581	13	< 0.0001
		age	0.0541	-0.0364	0.145	1.2	0.24
	random	ID	< 0.0001	< 0.0001	0.182		
		year	< 0.0001	< 0.0001	0.164		

Note: The simple linear GLMM is presented, because more complex models did not improve the model fit (Table S6). The model has a Poisson error structure (estimates on log scale), includes male identity and year as random intercepts, and accounts for the number of extra-pair mates. N = 256 observations from 187 males that sired EPY. Data span 13 years (2007 – 2019).

Table S4. Details of models testing the relationship between extra-pair siring success and male age, accounting for terminal effects.

Relationship - Reference model -	Effect	Term (fixed) or group (random)	Estimate (fixed) or SD (random)	Lower 95% CI	Upper 95% CI	Statistic (z or t)	<i>p</i>
Male age & probability of paternity gain AIC = 1000 - Table 2, polynomial -	fixed	(intercept)	-1.61	-2.31	-0.951		
		<i>terminal</i>	<i>0.241</i>	<i>-0.293</i>	<i>0.781</i>	<i>0.9</i>	<i>0.38</i>
		longevity	0.175	-0.0583	0.409	1.5	0.14
		age (linear coefficient)	13.9	5.86	22.4	3.3	0.0009
	random	age (quadratic coefficient)	-15.8	-21.7	-10.4	-5.5	< 0.0001
		ID	0.636	< 0.0001	1.04		
Male age & number of extra-pair mates (only males that sired EPY) AIC = 632 - Table 3 -	fixed	year	0.361	0.128	0.688		
		(intercept)	0.218	-0.122	0.552		
		<i>terminal</i>	<i>0.00156</i>	<i>-0.342</i>	<i>0.348</i>	<i>0.01</i>	<i>0.99</i>
		longevity	-0.0272	-0.185	0.119	-0.4	0.73
	random	age	0.0985	-0.0702	0.276	1.1	0.26
		ID	< 0.0001	< 0.0001	0.131		
Male age & proportion of EPY sired (only males that sired EPY) AIC = 772 - Table 3 -	fixed	year	< 0.0001	< 0.0001	0.134		
		(intercept)	-1.74	-2.00	-1.48		
		<i>terminal</i>	<i>0.00948</i>	<i>-0.258</i>	<i>0.278</i>	<i>0.07</i>	<i>0.97</i>
		longevity	0.00234	-0.115	0.115	0.04	0.38
	random	age	0.0598	-0.0711	0.194	0.9	0.94
		ID	< 0.0001	< 0.0001	0.146		
		year	< 0.0001	< 0.0001	0.141		

Note: Model structure, type of statistic and sample size as provided in table of reference model. Terminal effects are never important (shown in italics).

Table S5. Details of models testing effects of male age class (yearling or older) on the probability of siring at least one EPY.

Model	Effect	Term (fixed) or group (random)	Estimate (fixed) or SD (random)	Lower 95% CI	Upper 95% CI	z	p
categorical GLMM AIC = 999	fixed	(intercept)	-1.79	-2.28	-1.38		
		longevity (> 1 year vs. 1 year)	-0.226	-0.738	0.283	-0.8	0.38
		age class (older vs. yearling)	1.76	1.33	2.34	7.6	< 0.0001
	random	ID	0.661	0.0736	1.066		
		year	0.331	0.880	0.646		

Note: Because the changing effect of age on paternity gains across an individual's lifetime is the focus of this study, this model is provided only for comparison with studies that only have age class data and is not included in formal model comparisons. The model has a binomial error structure (estimates on logit scale) and includes male identity and year as random intercepts. The between-individual effect is taken into account by measuring longevity as a two-level factor (longevity one year or more than one year). N = 924 observations from 553 males across 13 years (2007 – 2019).

Table S6. Model fit information for the relationship between extra-pair siring success and male age for five types of modelling approaches.

Relationship	Model	Log-likelihood ^a	Relative deviance	AIC	BIC ^b	Model details
Male age & probability of paternity gain	linear GLMM	-513	905	1036	1060	-
	polynomial GLMM (quadratic)	-493	858	999	1028	Figure 2a; Table 2
	GAMM	-498	867	1008	1037	Figure S5
	1BP-PC-GLMM (breakpoint at age 2)	-494	847	1000	1029	Figure 2b; Table 2
	2BP-PC-GLMM (breakpoints at ages 2 & 4)	-492	845	998	1032	Figure 2c; Table 2
Male age & number of extra-pair mates (only males that sired EPY)	linear GLMM	-310	63	630	648	Table 3
	polynomial GLMM (quadratic) ^c	-310	62	631	652	-
	GAMM	-310	63	632	653	-
	1BP-PC-GLMM ^d	-309	62	630	652	-
	2BP-PC-GLMM ^d	--309	61	632	657	-
Male age & proportion of EPY sired (only males that sired EPY)	linear GLMM	-380	127	770	788	Table 3
	polynomial GLMM (quadratic) ^c	-379	125	770	792	-
	GAMM	-380	127	772	794	-
	1BP-PC-GLMM (breakpoint at age 4)	-378	123	768	790	-
	2BP-PC-GLMM ^d	-378	123	770	795	-
Male age & number of EPY sired (only males that sired EPY, accounting for the number of extra-pair mates)	linear GLMM	-416	156	845	866	Table S3
	polynomial GLMM (quadratic) ^c	-415	153	844	868	-
	GAMM	-416	156	847	872	-
	1BP-PC-GLMM (breakpoint at age 4)	-414	152	842	867	-
	2BP-PC-GLMM ^d	-414	152	844	872	-

Note: The five modelling approaches are linear GLMM, polynomial GLMM, GAMM, 1BP-PC-GLMM and 2BP-PC-GLMM (see Methods and Supplementary Methods S4 for details). For each model the log-likelihood, the relative deviance (relative to the saturated model, see documentation of R-package lme4, Bates et al. 2011), the AIC and the BIC is presented. Models that are part of the set of best models (Table 1) are indicated in bold.

^a Relative deviance differs from $-2 \times \text{log-likelihood}$ for these models with non-Gaussian error structure, because the log-likelihood of the saturated model is not (necessarily) 0.

^b The applicability of BIC in an exploratory analysis is debatable (Aho et al. 2014).

^c Second-order polynomial term not supported.

^d Existence of single (1BP-PC-GLMM) or second (2BP-PC-GLMM) breakpoint not supported.

Table S7. Details of models testing the relationship between extra-pair siring success and male age, accounting for effects of mate age.

Relationship - Reference model -	Effect	Term (fixed) or group (random)	Estimate (fixed) or SD (random)	Lower 95% CI	Upper 95% CI	Statistic (z or t)	p
Male age & probability of paternity gain ^a AIC = 999 - Table 2, polynomial -	fixed	(intercept)	-1.23	-1.61	-0.799		
		longevity	0.127	-0.0505	0.268	1.6	0.12
		<i>mate age</i>	<i>-0.0624</i>	<i>-0.254</i>	<i>0.100</i>	<i>-0.7</i>	<i>0.47</i>
		age (linear coefficient)	13.7	7.39	20.3	4.1	< 0.0001
		age (quadratic coefficient)	-14.1	-19.8	-9.44	-5.2	< 0.0001
	random	ID	0.430	< 0.0001	0.830		
		year	0.326	< 0.0001	0.533		
Male age & number of extra-pair mates (only males that sired EPY) ^b AIC = 669 - Table 3 -	fixed	(intercept)	0.211	0.0117	0.403		
		longevity	-0.0342	-0.137	0.063	-0.7	0.50
		<i>mate age</i>	<i>0.0285</i>	<i>-0.0765</i>	<i>0.127</i>	<i>0.5</i>	<i>0.58</i>
		age	0.0933	-0.0412	0.229	1.4	0.17
	random	ID	< 0.0001	< 0.0001	0.137		
		year	< 0.0001	< 0.0001	0.143		
Male age & proportion of EPY sired (only males that sired EPY) ^b AIC = 805 - Table 3 -	fixed	(intercept)	-1.73	-1.89	-1.57		
		longevity	0.00111	-0.0760	0.0759	0.03	0.98
		<i>mate age</i>	<i>0.0368</i>	<i>-0.0455</i>	<i>0.117</i>	<i>0.9</i>	<i>0.37</i>
		age	0.0434	-0.0606	0.148	0.8	0.41
	random	ID	< 0.0001	< 0.0001	0.156		
		year	< 0.0001	< 0.0001	0.127		

Note: There was no interaction effect between the age of the focal individual and the age of the extra-pair mate (see Supplementary Methods S3 and Schlicht & Kempenaers 2023). Model structure and type of statistic as in reference model. Sample size deviates, because only observations where mate age is known are included. Sample size provided in footnotes. The effect of mate age (shown in italics) is irrelevant for EPP. Note that despite age class of social mates being correlated (supplementary Analysis S1, Figure S4), (multi-)collinearity issues for these models are limited (all $r < 0.7$, all VIF < 3, see Methods).

^a N = 797 observations of 499 males across 13 years.

^b N = 232 observations of 176 males across 13 years.

Table S8. Details of models testing the relationship between extra-pair siring success and male age, accounting for non-linear effects of mate age.

Relationship - Reference model -	Effect	Term (fixed) or group (random)	Estimate (fixed) or SD (random)	Lower 95% CI	Upper 95% CI	Statistic (z or t)	p
Male age & probability of paternity gain ^a AIC = 1000 - Table 2, polynomial -	fixed	(intercept)	-1.28	-1.62	-0.929		
		longevity	0.127	-0.0418	0.270	1.6	0.12
		mate age (linear coefficient)	-2.05	-8.35	2.64	-0.8	0.42
		<i>mate age (quadratic coefficient)</i>	<i>2.81</i>	<i>-2.01</i>	<i>7.72</i>	<i>1.2</i>	<i>0.24</i>
		age (linear coefficient)	14.3	7.90	21.2	4.2	< 0.0001
	age (quadratic coefficient)	-14.2	-20.0	-9.69	-5.2	< 0.0001	
	random	ID	0.456	< 0.0001	0.784		
		year	0.326	< 0.0001	0.548		
Male age & number of extra-pair mates (only males that sired EPY) ^b AIC = 671 - Table 3 -	fixed	(intercept)	0.236	0.0389	0.425		
		longevity	-0.0332	-0.137	0.0643	-0.6	0.52
		mate age (linear coefficient)	0.511	-1.32	2.24	0.6	0.57
		<i>mate age (quadratic coefficient)</i>	<i>-0.684</i>	<i>-2.57</i>	<i>0.958</i>	<i>-0.8</i>	<i>0.45</i>
	age	0.0877	-0.0478	0.224	1.3	0.21	
	random	ID	< 0.0001	< 0.0001	0.137		
		year	< 0.0001	< 0.0001	0.143		
Male age & proportion of EPY sired (only males that sired EPY) ^b AIC = 807 - Table 3 -	fixed	(intercept)	-1.70	-0.206	0.211		
		longevity	0.000612	-0.0357	0.107	0.02	0.99
		mate age (linear coefficient)	0.626	-1.02	1.51	0.9	0.37
		<i>mate age (quadratic coefficient)</i>	<i>0.145</i>	<i>-1.61</i>	<i>1.03</i>	<i>0.2</i>	<i>0.84</i>
	age	0.0448	-0.0724	0.123	0.8	0.40	
	random	ID	< 0.0001	< 0.0001	0.171		
		year	< 0.0001	< 0.0001	0.126		

Note: Model structure and type of statistic as in reference model. Sample size deviates, because only observations where mate age is known are included. Sample size provided in footnotes. Non-linear effects of mate age (shown in italics) are irrelevant for EPP. Note that despite age class of social mates being correlated (supplementary Analysis S1, Figure S4), (multi-)collinearity issues for these models are limited (all $r < 0.7$, all VIF < 3 , see Methods).

^a N = 797 observations of 499 males across 13 years.

^b N = 232 observations of 176 males across 13 years.

Table S9. Details of models testing the relationship between extra-pair siring success and male age, accounting for non-linear effects of longevity.

Relationship - Reference model -	Effect	Term (fixed) or group (random)	Estimate (fixed) or SD (random)	Lower 95% CI	Upper 95% CI	Statistic (z or t)	p
Male age & probability of paternity gain AIC = 1001 - Table 2, polynomial -	fixed	(intercept)	-1.22	-1.5	-0.911		
		longevity (linear coefficient)	4.45	-2.4	11.1	1.2	0.22
		<i>longevity (quadratic coefficient)</i>	<i>-0.277</i>	<i>-5.89</i>	<i>5.93</i>	<i>-0.1</i>	<i>0.93</i>
		age (linear coefficient)	16.2	8.9	22.2	4.8	< 0.0001
	random	age (quadratic coefficient)	-15.7	-22.4	-9.43	-5.1	< 0.0001
		ID	0.627	< 0.0001	0.884		
Male age & number of extra-pair mates (only males that sired EPY) AIC = 631 - Table 3 -	fixed	year	0.376	< 0.0001	0.555		
		(intercept)	0.176	-0.0136	0.357		
		longevity (linear coefficient)	-0.531	-2.93	1.78	-0.4	0.66
		<i>longevity (quadratic coefficient)</i>	<i>-0.676</i>	<i>-2.54</i>	<i>1.12</i>	<i>-0.7</i>	<i>0.47</i>
	random	age	0.087	-0.0426	0.217	1.3	0.19
		ID	< 0.0001	< 0.0001	0.131		
Male age & proportion of EPY sired (only males that sired EPY) AIC = 772 - Table 3 -	fixed	year	< 0.0001	< 0.0001	0.135		
		(intercept)	-1.73	-1.88	-1.58		
		longevity (linear coefficient)	0.0753	-1.77	1.89	0.08	0.94
		<i>longevity (quadratic coefficient)</i>	<i>-0.317</i>	<i>-1.81</i>	<i>1.15</i>	<i>-0.4</i>	<i>0.67</i>
	random	age	0.0568	-0.0447	0.158	1.1	0.27
		ID	< 0.0001	< 0.0001	0.146		
		year	< 0.0001	< 0.0001	0.140		

Note: See Supplementary Methods S2 for details. Model structure, type of statistic and sample size as provided in table of reference model. The effect of the second-order polynomial of longevity is always irrelevant (shown in italics).

Table S10. Summary of thirteen studies that provide some information on within-individual changes (see Table S20).

Longitudinal information for ^a			Species	Reference
male paternity gain	male paternity loss	female EPP		
●	●	●	<i>Acrocephalus sechellensis</i>	Raj Pant et al. 2020
○	●	○	<i>Dendroica petechia</i>	Yezerinac et al. 1996
○	●	○	<i>Emberiza schoeniclus</i>	Bouwman et al. 2007
○	●	●	<i>Emberiza schoeniclus</i>	Bouwman & Komdeur 2005
●	○	○	<i>Hirundo rustica</i>	Lifjeld et al. 2011
●	○	○	<i>Malurus cyaneus</i>	Cooper et al. 2021
○	●	○	<i>Parus major</i>	Lubjuhn et al. 2007
●	●	○	<i>Passer domesticus</i>	Hsu et al. 2017
○	●	○	<i>Passer domesticus</i>	Schroeder et al. 2016
●	○	○	<i>Periparus ater</i>	Schmoll et al. 2007
○	●	○	<i>Progne subis</i>	Tarof et al. 2012
○	●	○	<i>Setophaga ruticilla</i>	Perreault et al. 1997
●	○	○	<i>Sialia mexicana</i>	Ferree & Dickinson 2011

^a Effect examined: ● = yes, ○ = no.

Table S11. Summary of studies that consider male age effects on EPP with age measurement and the results (see Table S20).

Age effect on paternity			Age measure	
			age class	continuous
A1: Akçay & Roughgarden 2007		total number of studies	8	6
	gain	increase with age	4	1
		decrease with age	0	0
		no age effect	1	2
		age effect not tested	3	3
	loss	increase with age	0	0
		decrease with age	0	1
		no age effect	5	3
		age effect not tested	3	2
	pair-wise (EP – WP)	EP older than WP	4	4
		EP younger than WP	0	0
		no age difference between EP and WP	3	2
		no pair-wise test conducted	1	0
A2: Cleasby & Nakagawa 2012		total number of studies	43	18
	gain	increase with age	12	3
		decrease with age	0	0
		no age effect	6	2
		age effect not tested	25	13
	loss	increase with age	2	1
		decrease with age	8	3
		no age effect	28	11
		age effect not tested	5	3
	pair-wise (EP – WP)	EP older than WP	4	7
		EP younger than WP	1	0
		no age difference between EP and WP	8	5
		no pair-wise test conducted	30	6
A3: Hsu et al. 2015		total number of studies	13	14
	gain	increase with age	5	5
		decrease with age	0	0
		no age effect	2	2
		age effect not tested	6	7
	loss	increase with age	0	1
		decrease with age	1	2
		no age effect	8	6
age effect not tested		4	5	

	pair-wise (EP – WP)	EP older than WP	3	8
		EP younger than WP	1	0
		no age difference between EP and WP	8	6
		no pair-wise test conducted	1	0
B: New studies		total number of studies	27	21
	gain	increase with age	11	10
		decrease with age	0	1
		no age effect	5	1
		age effect not tested	11	9
	loss	increase with age	0	3
		decrease with age	5	5
		no age effect	13	5
		age effect not tested	9	8
	pair-wise (EP – WP)	EP older than WP	1	3
		EP younger than WP	0	1
		no age difference between EP and WP	1	3
		no pair-wise test conducted	25	14

Note: Effects are effects of male age on gains, effects of male age on losses or the pair-wise comparison of the age of males gaining paternity (EP) and the males they cuckold (WP); for the latter the age difference is expressed as the age (class) of the extra-pair sire minus the age (class) of the cuckolded male (EP – WP). Studies are split up by the meta-analysis using them (A1-3) or represent new studies not included in previous meta-analyses (B).

Table S12. Summary of twenty studies that provide some information on the relationship between male age and extra-pair siring success beyond the transition from yearling to older (see Table S20).

Information on age trajectory	No. of studies	Species	Approximate life expectancy in years	Reference
main change between yearling and older	11	<i>Acrocephalus arundinaceus</i>	3	Hasselquist et al. 1996
		<i>Agelaius phoeniceus</i>	3	Westneat 1995
		<i>Cyanistes caeruleus</i>	1	Kempenaers et al. 1997
		<i>Hirundo rustica</i>	1	Lifjeld et al. 2022
		<i>Notiomystis cincta</i>	4	Brekke et al. 2013
		<i>Passer domesticus</i>	1	Hsu et al. 2017
		<i>Passer domesticus</i>	1	Girndt et al. 2018
		<i>Periparus ater</i>	1	Schmoll et al. 2007
		<i>Progne subis</i>	1	Tarof et al. 2012
		<i>Sialia mexicana</i>	1	Ferree & Dickinson 2011
		<i>Troglodytes aedon</i>	1	Bowers et al. 2015
ambiguous age effect beyond transition from yearling to older	4	<i>Agelaius phoeniceus</i>	3	Weatherhead & Boag 1995
		<i>Geospiza fortis</i>	5	Grant & Grant 2011
		<i>Passer domesticus</i>	1	Wetton et al. 1995
		<i>Zonotrichia leucophrys</i>	1	Sherman & Morton 1988
continued increase in siring success with age beyond the transition from yearling to older	5	<i>Acrocephalus sechellensis</i>	3	Raj Pant et al. 2020
		<i>Hirundo rustica</i>	1	Micháľková et al. 2019
		<i>Malurus cyaneus</i>	3	Cooper et al. 2021
		<i>Setophaga ruticilla</i>	1	Perreault et al. 1997
		<i>Sula nebouxii</i>	15	Ramos et al. 2014

Note: Life expectancy marked in bold for species with a life expectancy similar to the blue tit.

Table S13. Summary of 50 studies that consider an effect of female age on the occurrence of EPP in her clutch (see Table S20).

Female age effect on EPP	No. of studies	Species	References
Increase with age ^a	4	<i>Acrocephalus sechellensis</i> <i>Acrocephalus sechellensis</i> <i>Geospiza fortis</i> <i>Hirundo rustica</i>	Edwards et al. 2018 Raj Pant et al. 2020 Grant & Grant 2011 Micháلكová et al. 2019
Decrease with age ^b	3	<i>Ficedula hypoleuca</i> <i>Notiomystis cincta</i> <i>Wilsonia citrina</i>	Moreno et al. 2015 Brekke et al. 2013 Stutchbury et al. 1997
Interaction with age of social mate ^c	5	<i>Cyanistes caeruleus</i> <i>Dolichonyx oryzivorus</i> <i>Emberiza schoeniclus</i> <i>Periparus ater</i> <i>Sula neboxii</i>	Arct et al. 2022 Bollinger & Gavin 1991 Bouwman & Komdeur 2005 Dietrich et al. 2004 Ramos et al. 2014
No age effect	38	see Table S20	see Table S20

^a Explained by (i) an age-related increase in female attractiveness (e.g. because of higher fecundity) making them more frequent targets of male EPC attempts (Bouwman & Komdeur 2005; Raj Pant et al. 2020), (ii) an increase in female competence in obtaining EPY (e.g. improved evasion of male mate guarding or better timing of extra-pair activities ; Dietrich et al. 2004; Bouwman & Komdeur 2005; Edwards et al. 2018; Micháلكová et al. 2019; Raj Pant et al. 2020), or (iii) early-life improvement causing an increase in time available for non-essential mating activities (such as EPCs) and reduced constraints imposed by the costs of a male response to perceived EPC attempts (Hoi-Leitner et al. 1999), for example if physical strength plays a role (Wagner et al. 1996; Ramos et al. 2014).

^b Explained by increasing female competence in either (i) securing a high-quality social mate (Stutchbury et al. 1997), reducing their incentive to improve on their partner's quality, or in (ii) avoiding EPC attempts by males (Brekke et al. 2013; Moreno et al. 2015).

^c See also Møller 1985 and Rätti et al. 2001.

Table S14. Model fit information for models describing effects of male age on paternity loss and female age on the occurrence of EPY.

Relationship	Model	Log-likelihood ^a	Relative deviance	AIC	BIC ^b	Model details
Male age & probability of paternity loss	linear GLMM	-623	1187	1256	1280	Table S15
	polynomial GLMM (quadratic) ^c	-622	1184	1257	1286	-
	GAMM	-623	1187	1258	1287	-
	1BP-PC-GLMM ^d	-622	1181	1255	1284	-
	2BP-PC-GLMM ^d	-622	1180	1257	1291	-
Female age & probability of EPY in nest	linear GLMM	-620	1048	1250	1274	Table S15
	polynomial GLMM (quadratic) ^c	-620	1050	1252	1281	-
	GAMM	-620	1048	1252	1281	-
	1BP-PC-GLMM ^d	-620	1051	1251	1280	-
	2BP-PC-GLMM ^d	-619	1049	1253	1287	-

Note: See Supplementary Analysis S1 for details. Comparison of five types of modelling approaches: linear GLMM, polynomial GLMM, GAMM, 1BP-PC-GLMM and 2BP-PC-GLMM (see Methods and Supplementary Methods S4 for details). For each model the log-likelihood, the relative deviance (relative to the saturated model, see documentation of R-package lme4, Bates et al. 2011), the AIC and the BIC is presented. Models that are part of the set of best models are indicated in bold.

^a Relative deviance differs from $-2 \times \log\text{-likelihood}$ for these models with binomial error structure, because the log-likelihood of the saturated model is not (necessarily) 0.

^b The applicability of BIC in an exploratory analysis is debatable (Aho et al. 2014).

^c Second-order polynomial term not supported.

^d Existence of single (1BP-PC-GLMM) or second (2BP-PC-GLMM) breakpoint not supported.

Table S15. Details of models describing effects of male age on paternity loss and female age on the occurrence of EPY.

Response	Effect	Term (fixed) or group (random)	Estimate (fixed) or SD (random)	Lower 95% CI	Upper 95% CI	z	p
Male probability of paternity loss AIC = 1256	fixed	(intercept)	-0.246	-0.452	-0.0547		
		longevity	-0.0901	-0.211	0.0348	-1.4	0.15
		age	0.151	-0.0226	0.32	1.7	0.08
	random	ID	0.372	< 0.0001	0.698		
		year	< 0.0001	< 0.0001	0.227		
Female probability of having EPP in her clutch AIC = 1250	fixed	(intercept)	-0.398	-0.578	-0.199		
		longevity	-0.00395	-0.143	0.133	-0.05	0.96
		age	-0.00410	-0.184	0.174	-0.04	0.97
	random	ID	0.729	0.166	0.766		
		year	< 0.0001	< 0.0001	0.218		

Note: See Supplementary Analysis S1 for details. For both relationships the simple linear GLMM is presented, because more complex models did not improve the model fit (Table S14). Models have a binomial error structure (estimates on logit scale). A positive estimate indicates an increased probability of paternity loss or of the occurrence of EPY with age. All models include male or female identity and year as random intercepts. N for probability of loss: N = 913 observations from 548 males. N for probability of female EPP: N = 922 observations from 592 females. Data always span 13 years (2007 – 2019).

Table S16. Details of models describing effects of male age on paternity loss and female age on the occurrence of EPY, accounting for effects of mate age.

Relationship - Reference model -	Effect	Term (fixed) or group (random)	Estimate (fixed) or SD (random)	Lower 95% CI	Upper 95% CI	Statistic (z or t)	p
Male age & probability of paternity loss ^a AIC = 1282 - Table S15 -	fixed	(intercept)	-0.256	-0.468	-0.0433		
		longevity	-0.105	-0.247	0.0243	-1.5	0.14
		<i>mate age</i>	<i>-0.0944</i>	<i>-0.270</i>	<i>0.0458</i>	<i>-1.2</i>	<i>0.21</i>
		age	0.216	0.0513	0.412	2.2	0.03 ^a
	random	ID	0.487	< 0.0001	0.638		
		year	< 0.0001	< 0.0001	0.234		
Female age & probability of EPY in nest ^b AIC = 1294 - Table S15 -	fixed	(intercept)	-0.399	-0.644	-0.150		
		longevity	-0.0158	-0.146	0.128	-0.2	0.83
		<i>mate age</i>	<i>0.0591</i>	<i>-0.0958</i>	<i>0.196</i>	<i>0.8</i>	<i>0.45</i>
		age	-0.0489	-0.234	0.151	-0.5	0.63
	random	ID	0.652	< 0.0001	0.710		
		year	< 0.0001	< 0.0001	0.219		
Probability of occurrence of EPP in clutch ^c AIC = 1279	fixed	(intercept)	-0.388	-0.582	-0.181		
		male age	0.134	-0.0220	0.272	1.6	0.10
		female age	-0.0825	-0.255	0.0779	-1.0	0.31
	random	male ID	0.0249	< 0.0001	0.492		
		female ID	0.524	< 0.0001	0.741		
		year	< 0.0001	< 0.0001	0.240		

Note: For comparison we also show a cross-sectional model combining the effects of the ages of both social partners on the occurrence of EPY in their nest (this model cannot separate between- and within-individual effects). See Supplementary Analysis S1 for details. There was no interaction effect between the age of the focal individual and the age of the mate (see Supplementary Analysis S1 and Schlicht & Kempenaers 2023). Model structure and type of statistic as in reference model. Sample size deviates, because only observations where mate age is known are included. Sample size provided in footnotes. The effect of mate age (shown in italics) is irrelevant for the occurrence of EPP. Note that despite age class of social mates being correlated (Figure S4), (multi-)collinearity issues for these models are limited (all $r < 0.7$, all VIF < 3 , see Methods).

^a N = 791 observations of 496 males across 13 years. The increase with male age is driven by four observations of males with age 6 or older, and the effect is no longer significant when these individuals are excluded (N = 787 observations; $p = 0.09$). Moreover, the probability of paternity loss did not differ between yearlings and older males (categorical GLMM with all data, $p = 0.16$, details not shown).

^b N = 804 observations of 539 females across 13 years.

^c N = 791 observations from 496 males and 539 females across 13 years.

Table S17. Details of models describing effects of male age on paternity loss and female age on the occurrence of EPY, accounting for non-linear effects of mate age.

Relationship - Reference model -	Effect	Term (fixed) or group (random)	Estimate (fixed) or SD (random)	Lower 95% CI	Upper 95% CI	Statistic (z or t)	p
Male age & probability of paternity loss ^a AIC = 1284 - Table S15 -	fixed	(intercept)	-0.318	-0.546	-0.0969		
		longevity	-0.106	-0.250	0.0338	-1.5	0.14
		mate age (linear coefficient)	-2.81	-7.40	1.62	-1.2	0.22
		<i>mate age (quadratic coefficient)</i>	-1.00	-5.81	3.31	-0.4	0.66
	random	age	0.212	0.0189	0.409	2.1	0.03
		ID	0.493	< 0.0001	0.840		
		year	< 0.0001	< 0.0001	0.231		
Female age & probability of EPY in nest ^b AIC = 1295 - Table S15 -	fixed	(intercept)	-0.359	-0.567	-0.119		
		longevity	-0.0112	-0.165	0.144	-0.1	0.88
		mate age (linear coefficient)	1.70	-2.88	6.31	0.7	0.47
		<i>mate age (quadratic coefficient)</i>	2.23	-1.94	6.52	1.0	0.32
	random	age	-0.0498	-0.226	0.141	-0.5	0.62
		ID	0.652	< 0.0001	0.713		
		year	< 0.0001	< 0.0001	0.219		

Note: See Supplementary Analysis S1 for details. Model structure and type of statistic as in reference model. Sample size deviates, because only observations where mate age is known are included. Sample size provided in footnotes. Non-linear effects of mate age (shown in italics) are irrelevant for the occurrence of EPP. Note that despite age class of social mates being correlated (Figure S4), (multi-)collinearity issues for these models are limited (all $r < 0.7$, all VIF < 3 , see Methods).

^a N = 791 observations of 496 males across 13 years.

^b N = 804 observations of 539 females across 13 years.

Table S18. Details of models describing the effect of male age on the probability of paternity loss and of female age on the occurrence of EPY, accounting for non-linear effects of longevity.

Relationship - Reference model -	Effect	Term (fixed) or group (random)	Estimate (fixed) or SD (random)	Lower 95% CI	Upper 95% CI	Statistic (z or t)	p
Male age & probability of paternity loss AIC = 1258 - Table S15 -	fixed	(intercept)	-0.386	-0.575	-0.199		
		longevity (linear coefficient)	-4.01	-9.15	1.27	-1.4	0.15
		<i>longevity (quadratic coefficient)</i>	<i>-0.883</i>	<i>-5.96</i>	<i>3.58</i>	<i>-0.4</i>	<i>0.69</i>
	random	age	0.150	-0.0305	0.314	1.7	0.08
		ID	0.370	< 0.0001	0.536		
		year	< 0.0001	< 0.0001	0.206		
Female age & probability of EPY in nest AIC = 1249 - Table S15 -	fixed	(intercept)	-0.407	-0.579	-0.200		
		longevity (linear coefficient)	-0.890	-7.41	5.70	-0.3	0.78
		<i>longevity (quadratic coefficient)</i>	<i>-4.49</i>	<i>-10.4</i>	<i>0.735</i>	<i>-1.7</i>	<i>0.09</i>
	random	age	0.000809	-0.192	0.188	0.01	0.99
		ID	0.722	< 0.0001	0.788		
		year	< 0.0001	< 0.0001	0.206		

Note: See Supplementary Analysis S1 and Supplementary Methods S2 for details. Model structure, type of statistic and sample size as provided in table of reference model. The effect of the second-order polynomial of longevity is always irrelevant (shown in italics).

Table S19. Details of models describing the effect of male age on the probability of paternity loss and of female age on the occurrence of EPY, accounting for terminal effects.

Relationship - Reference model -	Effect	Term (fixed) or group (random)	Estimate (fixed) or SD (random)	Lower 95% CI	Upper 95% CI	Statistic (z or t)	p
Male age & probability of paternity loss AIC = 1258 - Table S15 -	fixed	(intercept)	-0.293	-0.699	0.105		
		<i>terminal</i>	<i>0.0569</i>	<i>-0.372</i>	<i>0.48</i>	<i>0.3</i>	<i>0.79</i>
		longevity	-0.0704	-0.264	0.12	-0.7	0.47
	random	age	0.132	-0.0871	0.357	1.2	0.24
		ID	0.374	< 0.0001	0.700		
		year	< 0.0001	< 0.0001	0.226		
Female age & probability of EPY in nest AIC = 1251 - Table S15 -	fixed	(intercept)	-0.195	-0.674	0.27		
		<i>terminal</i>	<i>-0.233</i>	<i>-0.721</i>	<i>0.27</i>	<i>-1.0</i>	<i>0.34</i>
		longevity	-0.0912	-0.333	0.132	-0.8	0.43
	random	age	0.0755	-0.157	0.326	0.6	0.55
		ID	0.720	0.168	0.759		
		year	< 0.0001	< 0.0001	0.207		

Note: See Supplementary Analysis S1 for details. Model structure, type of statistic and sample size as provided in table of reference model. Terminal effects are never important (shown in italics).

Table S20. Overview of studies analysing the relationship between male or female age and the occurrence of EPP.

Reason	Species	Population	Metanalysis (a)	Age measure	Age effect male gains	Age effect male losses	Age-effect pair-wise comparison of males (WP vs. EP)	Age-effect female EPP (c)	Young-age effects ongoing? (d)	Within-individual changes (e)	Comments	Reference
(b)	<i>Acanthiza pusilla</i>		-	age class ^a	-	yearling > older	-	-	-	-	-	Green et al. 2002
(c)	<i>Accipiter cooperii</i>		-	age class	-	-	-	none	-	-	Age measure: yearling, two-year-old or older; test only run for comparison of yearling vs. older.	Rosenfield et al. 2015
(a), (d)	<i>Acrocephalus arundinaceus</i>		1, 2, 3	continuous ^b	none	-	none	-	probably not	-	-	Hasselquist et al. 1996
(a)	<i>Acrocephalus schoenobaenus</i>		2	continuous	-	none	-	-	-	-	Age measure: not explained, but probably minimum age based on previous observation.	Buchanan & Catchpole 2000
(b), (c), (d), (e)	<i>Acrocephalus sechellensis</i>	Cousin Island, 1997-2014	-	continuous ^b	early-life improvement until middle ages and senescent decline	early-life improvement for dominant males until middle ages, no senescent decline	Δ age EP male -WP male significantly > 0	early-life increase until middle ages and senescent decline	yes: see results for gains, losses and female EPP	results refer to within-individual patterns	Cooperative breeder. Unclear, if early life improvement in gains could be driven by dominance status; effect of female age on extra-group paternity found (early-life increase and senescent decline). Data overlap with Edwards et al. 2018.	Raj Pant et al. 2020
(b), (c)	<i>Acrocephalus sechellensis</i>	Cousin Island, 2010 & 2012-2015	-	continuous ^b	older > younger, possibly non-linear	-	-	older > younger, non-linear, possibly senescent decline	-	-	Cooperative breeder. Effects on gains present only in pair-wise analysis (Table S4), not in individual analyses (Figure S6, S12), and non-linear (quadratic) term only trend. Effects on female EPP only present in one of two tests of individual analyses (Figure S3 vs. Figure S9) and not present in pair-wise analysis (Table S3). Data included in Raj Pant et al. 2020.	Edwards et al. 2018
(a), (c), (d)	<i>Agelaius phoeniceus</i>	New York	2	continuous ^c	-	none	-	none	no evidence based on data presented	-	Polygynous species.	Westneat 1995
(a), (d)	<i>Agelaius phoeniceus</i>	Ontario	1, 2, 3	continuous ^d	older > younger	none	EP older WP, beyond age 1	-	probably ongoing for pair-wise comparison and possibly ongoing for gains (but data shown are based on longevity)	-	Polygynous species.	Weatherhead & Boag 1995
(a), (c)	<i>Anthus spinoletta</i>		2	age class ^e	-	none	-	none	-	-	Method and result extremely brief in description and difficult to assess.	Reyer et al. 1997
(b), (c)	<i>Aphelocoma ultramarina</i>		-	continuous ^d	tendency for younger > older	-	-	none	-	-	Result for gains mentioned as unpublished data. Species with some cooperative breeding,	Li & Brown 2000

Reason	Species	Population	Metanalysis (a)	Age measure	Age effect male gains	Age effect male losses	Age-effect pair-wise comparison of males (WP vs. EP)	Age-effect female EPP (c)	Young-age effects ongoing? (d)	Within-individual changes (e)	Comments	Reference
											delayed breeding (2 years onwards for females, 3 years onwards for males) and delayed plumage maturation (two pre-definitive plumages in males). EPP alternative route to reproductive success for males that are socially not successful. Ongoing low-age effects not inspected for males, for females absent.	
(b)	<i>Cardellina canadensis</i>		-	continuous ^d	-	-	none	-	-	-	Age and extra-pair success possibly interact in their effects on losses.	Reitsma et al. 2018
(a)	<i>Carduelis tristis</i>		2	age class ^a	-	none	-	-	-	-	-	Gissing et al. 1998
(a)	<i>Carpodacus mexicanus</i>		2	continuous ^f	-	none	-	-	-	-	-	Hill et al. 1994
(a), (d)	<i>Cyanistes caeruleus</i>	Calixbergen	2	continuous ^d	-	none	sign Δ age EP-WP significantly larger than 0	-	losses: no ongoing effect present in data shown	-	-	Kempnaers et al. 1997
(a)	<i>Cyanistes caeruleus</i>	Corsica and Rouvière, 2000-2002	1, 2, 3	continuous ^b	-	none	none	-	-	-	Age measurement not explained, but age defined in years.	Charmantier et al. 2004
(a)	<i>Cyanistes caeruleus</i>	De Vosbergen	2	age class ^a	older > yearling	none	-	-	-	-	-	Vedder et al. 2011
(b), (c)	<i>Cyanistes caeruleus</i>	Gotland	-	age class ^a	-	none	-	none	-	-	Data included in Arct et al. 2022.	Podmokla et al. 2015
(b), (c)	<i>Cyanistes caeruleus</i>	Gotland	-	age class ^a	-	trend for yearling > older for males mated to older females, absent for males mated to yearling females	-	yearling > older for females mated to older males, absent for females mated to yearling males	-	-	Ages of mates interact in their effect on EPP. Data overlap with Podmokla et al. 2015.	Arct et al. 2022
(a), (c)	<i>Cyanistes caeruleus</i>	Jomfruland	2	age class ^a	-	none	-	none	-	-	-	Krokene et al. 1998
(a)	<i>Cyanistes caeruleus</i>	Kolbeterberg, 2001	2	age class ^a	older > yearling	none	WP: yearling, EP: older	-	-	-	Data included in Delhey et al. 2007. Data overlap also with Foerster et al. 2003 and Schlicht et al. 2015b.	Delhey et al. 2003
(a)	<i>Cyanistes caeruleus</i>	Kolbeterberg, 2001-2003	1, 3	age class ^a	older > yearling	none	WP: yearling, EP: older	-	-	-	Includes data of Delhey et al. 2003, Foerster et al. 2003 and Schlicht et al. 2015b.	Delhey et al. 2007
(a)	<i>Cyanistes caeruleus</i>	Kolbeterberg, 1998-2001	1, 3	continuous ^d	-	-	direct neighbours: WP: yearling, EP: older; non-neighbours: none	-	-	-	Overlap with data of Delhey et al. 2003, Delhey et al. 2007 and Schlicht et al. 2015b.	Foerster et al. 2003
(b)	<i>Cyanistes caeruleus</i>	Kolbeterberg, 1998-2004	-	age class ^a	older > yearling	-	-	-	-	-	Data overlap with Delhey et al. 2003, Delhey et al. 2007 and Foerster et al. 2003.	Schlicht et al. 2015b
(b), (c)	<i>Cyanistes caeruleus</i>	Montpellier	-	continuous ^d	older > younger among 1st	-	-	none	-	-	-	Mennerat et al. 2018

Reason	Species	Population	Metanalysis (a)	Age measure	Age effect male gains	Age effect male losses	Age-effect pair-wise comparison of males (WP vs. EP)	Age-effect female EPP (c)	Young-age effects ongoing? (d)	Within-individual changes (e)	Comments	Reference
											order neighbours	
(b)	<i>Cyanistes caeruleus</i>	Segovia	-	age class ^a	older > younger	none	-	-	-	-	Gain: age effect present only in one season and in one of two models.	Badás et al. 2020
(b), (c)	<i>Cyanistes caeruleus</i>	Westerholz, 2008-2010	-	age class ^a	none	-	-	none	-	-	Data overlap with Schlicht et al. 2015b and Schlicht et al. 2015a.	Steinmeyer et al. 2013
(b)	<i>Cyanistes caeruleus</i>	Westerholz, 2007-2011	-	age class ^a	older > yearling	-	-	-	-	-	Effect declines with increasing neighbourhood distance. Data overlap with Steinmeyer et al. 2013 and Schlicht et al. 2015a.	Schlicht et al. 2015b
(b)	<i>Cyanistes caeruleus</i>	Westerholz, 2010-2014	-	age class ^a	older > yearling	-	-	-	-	-	Effect analysed on level of neighbourhoods. Data overlap with Steinmeyer et al. 2013 and Schlicht et al. 2015b.	Schlicht et al. 2015a
(b)	<i>Cyanistes caeruleus</i>	Westerholz, 2018	-	age class ^a	older > yearling	-	-	-	-	-	Analysis based on dyads that had or did not have interactions in winter.	Beck et al. 2020
(a)	<i>Dendroica caerulescens</i>		1, 2	age class ^a	none	none	-	-	-	-	-	Webster et al. 2001
(a)	<i>Dendroica petechia</i>	Ontario, 1991-1994	1, 2, 3	continuous ^c	none	none	EP older WP male	-	relationship tested only linearly, i.e., ongoing effects not inspected	-	Data are also used in Yezerinac et al. 1996. Within-individual changes analysed there.	Yezerinac & Weatherhead 1997
(a), (e)	<i>Dendroica petechia</i>	Ontario, 1991-1994	2	age class ^a	-	none	-	-	-	no systematic in- or decrease in losses for 8 males measured at 1 and 2 years of age	Age measurement: Data continuous ^a , but analysis of loss performed using age class ^a . Data are also used in Yezerinac and Weatherhead 1997, but within-individual change not analysed there.	Yezerinac et al. 1996
(b), (c)	<i>Diomedea exulans</i>		-	continuous ^b	-	none	-	none	-	-	Long-lived species with low annual reproductive rate and long-term pair bonds.	Jones et al. 2012
(a), (c)	<i>Dolichonyx oryzivorus</i>		2	age class ^a	none	new breeder > experienced	-	experienced > new breeder, possible interaction with male experience	-	-	-	Bollinger & Gavin 1991
(a), (c)	<i>Emberiza citrinella</i>		2, 3	continuous ^d	-	none	none	none	-	-	In study only one age-related test is performed regarding the absence of yearling EP sires (unlikely assuming random selection of sires from male population). Results given here are based on newly performed tests using the data presented in the study: losses (Y/N or proportion lost) and male or female age (exact, minimum or age class). Pair-wise test of age difference between extra-	Sundberg & Dixon 1996

Reason	Species	Population	Metanalysis (a)	Age measure	Age effect male gains	Age effect male losses	Age-effect pair-wise comparison of males (WP vs. EP)	Age-effect female EPP (c)	Young-age effects ongoing? (d)	Within-individual changes (e)	Comments	Reference
											pair and within-pair male (exact or minimum age, age class comparison not performed, because only one WP male yearling).	
(a)	<i>Emberiza schoeniclus</i>	De Biesbosch, 2001-2003	2	age class ⁹	recaptured > newly captured	newly captured > recaptured	WP: newly, EP: re-captured	-	-	-	Same study as Bouwman et al. 2007 with less and different analyses. Overlap with data of Bouwman & Komdeur 2005.	Bouwman 2005
(a), (e)	<i>Emberiza schoeniclus</i>	De Biesbosch, 2001-2003	1, 2, 3	age class ⁹	recaptured > newly captured	none	WP: newly, EP: re-captured	-	-	decrease in losses for 16 males measured in two successive years (no age class information available)	Same study as Bouwman 2005 with additional and changed analyses. Overlap with data of Bouwman & Komdeur 2005.	Bouwman et al. 2007
(b), (c), (e)	<i>Emberiza schoeniclus</i>	De Biesbosch, 2002-2003	-	age class ⁹	-	newly captured > recaptured for males mated to recaptured females	-	recaptured > newly captured for females mated to newly captured males	-	decrease in losses in males and increase in EPP in females between two successive years (no age class information available)	No assortative mating for age class. Interaction of male and female age class in their effects on paternity in the brood they attend. Overlap with data of Bouwman 2005 and Bouwman et al. 2007.	Bouwman & Komdeur 2005
(a)	<i>Emberiza schoeniclus</i>	Southern Norway	2, 3	age class ⁹	recaptured > newly captured	none	none	-	-	-	Gains measured as Y/N and as no. of EPY sired (results similar). Losses measured as Y/N and as proportion of brood sired (results similar). Pair-wise analysis not performed due to small sample size, but data given and result based on those.	Kleven et al. 2006
(a)	<i>Empidonax minimus</i>		2	age class ⁹	none	-	-	-	-	-	Additional test: extra-pair mating activity not different for yearling and older males. However, extra-pair mating activity is a composite measure of (attempted) EPCs performed by a focal individual and its mate and intruding neighbours.	Tarof et al. 2005
(a)	<i>Ficedula albicollis</i>	Gotland	1, 2, 3	age class ⁹	-	-	none	-	-	-	-	Sheldon & Ellegren 1999
(b)	<i>Ficedula albicollis</i>	Velky Kosir, 2006-2009	-	age class ⁹	-	trend for younger > older, but explained by wing patch size	EP older WP	-	-	-	-	Edme et al. 2016
(b)	<i>Ficedula albicollis</i>	Velky Kosir, 2013-2015	-	age class ⁹	none	none	-	-	-	-	Data part of experiment that manipulated forehead patch size, which did not affect paternity.	Edme et al. 2017

Reason	Species	Population	Metanalysis (a)	Age measure	Age effect male gains	Age effect male losses	Age-effect pair-wise comparison of males (WP vs. EP)	Age-effect female EPP (c)	Young-age effects ongoing? (d)	Within-individual changes (e)	Comments	Reference
(a)	<i>Ficedula hypoleuca</i>	Central Spain, 2003	2	continuous ^d	-	decrease with age	-	-	effect only modelled linearly, i.e., ongoing effects not inspected	-	Difficult to assess from plotted data, if reduction continues throughout the age span.	Moreno et al. 2010
(b), (c)	<i>Ficedula hypoleuca</i>	Central Spain, 2011	-	continuous ^d	-	none	-	reduction with age	-	-	In females possibly ongoing reduction of EPP with age.	Moreno et al. 2015
(a), (c)	<i>Ficedula hypoleuca</i>	Konnevesi	2	age class ^a	-	none	-	none	-	-	-	Rätti et al. 1995
(a), (c)	<i>Ficedula hypoleuca</i>	Ruissalo	2	age class ^a	older > yearling	none	-	none	-	-	Analyses of loss also performed controlling for female age (results similar).	Lehtonen et al. 2009
(b)	<i>Ficedula parva</i>		-	age class ^a	-	yearling > older	-	-	-	-	Anecdotal information: 7 assigned EPY all sired by males older than yearling.	Mitrus et al. 2014
(a), (c), (d)	<i>Geospiza fortis</i>		2, 3	continuous ^b	somewhere around age 5-6 to 9-10 > younger birds	age 1-2 > intermediate ages, which possibly > age 11-12	Δ age EP-WP greater than expected and relatively constant for all ages of WP males (range 1 to 12 years; possibly smaller difference to expected for intermediate age WP males)	age 1-2 < age above 4 < age 3-4	probably, see results for gains	-	Two species (<i>Geospiza fortis</i> and <i>scandens</i>), but decent sample sizes only for <i>G. fortis</i> , which the results in this table refer to. For gains and losses ages were combined in age groups of 1-2, 3-4, 5-6, 7-8, 9-10 and 11-12. Pair-wise test are based on expected age given frequency of age groups.	Grant & Grant 2011
(a), (c)	<i>Geospiza scandens</i>		2, 3	continuous ^b	-	-	none	none (result not shown)	-	-	Age measure not explained, but most likely exact age, given other studies and reference to ages 2 to 10 for female. Experience higher in WP than in EP sires (no test performed). Species with delayed plumage maturation and only males in fully mature plumage (i.e., 2 years or older) involved as EP or WP males, meaning effects detected by pair-wise comparison would be ongoing, but none detected. See Grant & Grant 2011 for further results on this species.	Petren et al. 1999
(a)	<i>Geothlypis trichas</i>		1	age class ^a	trend for experienced > inexperienced in interaction with mask size	none	EP more experienced than WP he cuckolds	-	-	-	-	Thusius et al. 2001
(a)	<i>Hirundo rustica</i>	New York	2	-	-	-	-	-	-	-	No results pertaining to age presented, only references to other studies.	Neuman et al. 2007
(b), (e)	<i>Hirundo rustica</i>	Ontario, bridge colony	-	age class ^a	experienced > novice	-	-	-	-	effect on gain present as trend in longitudinal	Evidence for age assortative mating based on arrival time.	Lifjeld et al. 2011

Reason	Species	Population	Metanalysis (a)	Age measure	Age effect male gains	Age effect male losses	Age-effect pair-wise comparison of males (WP vs. EP)	Age-effect female EPP (c)	Young-age effects ongoing? (d)	Within-individual changes (e)	Comments	Reference
										sample of 34 males		
(b), (c), (d)	<i>Hirundo rustica</i>	Třeboňsko	-	continuous ^f	linear, but no quadratic relationship, suggesting ongoing improvement	no linear or quadratic relationship	none	linear, but no quadratic relationship, suggesting ongoing increase in EPP rate with female age	yes: see results for gains	-	No interaction of male and female age, but potentially assortative mating mediated by arrival. No repeatability of paternity, but within-individual changes not otherwise inspected.	Michálková et al. 2019
(b), (d)	<i>Hirundo rustica</i>	Ontario, four colonies (not bridge colony)	-	continuous ^f	1-year old < older, in one of two study years trend for 2-year old < older	-	EP older than male he cuckolds	-	possibly, but indication very weak (see results for gains) and main increase between yearling and older	-	Patterns highly suggestive of a threshold effect between yearling and older males.	Lifjeld et al. 2022
(a)	<i>Icterus bullockii</i>		2	age class ^a	trend for older > yearling > older	yearling	-	-	-	-	Loss measured as Y/N and as proportion lost (results similar). Species with delayed plumage maturation (yearling males have different plumage).	Richardson & Burke 1999
(a)	<i>Junco hyemalis</i>		2	age class ^a	older > yearling	none	-	-	-	-	Result is based on data including manipulated birds. Effects are similar in both the manipulated and the treatment group. Treatment (testosterone) also has effect on gains and not on losses, but does not interact with age.	Reed et al. 2006
(a)	<i>Luscinia svecica</i>	Øvre Heimdalen, 1992 & 1998-1999	1, 2, 3	age class ^a	older > yearling	none	WP: yearling, EP: older	-	-	-	Gains measured as Y/N and as no. of EPY sired (results similar). Effect similar among older males experienced on the study area and older males new to the study area.	Johnsen et al. 2001
(b)	<i>Luscinia svecica</i>	Øvre Heimdalen, 2013-2015	-	age class ^a	none	none	-	-	-	-	Tests run as part of model inspecting effects of sperm traits on paternity (Table S4).	Sætre et al. 2018
(b), (c)	<i>Malurus cyaneus</i>	Canberra, 1988-2013	-	age class ^a	-	none	-	none	-	-	Cooperative breeder. Data also used in Cooper et al. 2021.	Hajduk et al. 2018
(b), (d), (e)	<i>Malurus cyaneus</i>	Canberra, 1988-2017	-	continuous ^b	early-life improvement until middle ages and senescent decline	-	-	-	yes: see results for gains	results refer to within-individual patterns	Cooperative breeder. Not entirely clear, if improvement in gains is present in both dominant and helper males, but gains are not explained by dominance status. Some data also used in Hajduk et al. 2018.	Cooper et al. 2021
(a)	<i>Malurus splendens</i>		2, 3	age class ^a	none	-	trend for EP males to be younger than WP males ($p = 0.03$)	-	-	-	Cooperative breeder.	Tarvin et al. 2005

Reason	Species	Population	Metanalysis (a)	Age measure	Age effect male gains	Age effect male losses	Age-effect pair-wise comparison of males (WP vs. EP)	Age-effect female EPP (c)	Young-age effects ongoing? (d)	Within-individual changes (e)	Comments	Reference
(a)	<i>Melospiza melodia</i>	Discovery Park	3	continuous ^b	trend for older > younger	trend for older > younger	none	-	-	-	-	Hill et al. 2011
(b)	<i>Melospiza melodia</i>	Mandarte Island	-	age class	2-5 years > older 5 years > 1 year	none	-	-	-	-	Age measure: 1 year / 2-5 years / older 5 years. Not defined based on field-based aging traits, but data driven. Possibly senescence in gains, due to pooling of ages into three age classes an assessment of whether low-age improvement is ongoing is not possible.	Reid et al. 2014
(b), (c), (d)	<i>Notiomystis cincta</i>		-	continuous ^b	-	1 year old > 2-5 year old, 6-9 year old > 2-5 year old, possibly 6-9 year old > 1 year old	-	1 year old > 2-5 year old, 6-9 year old > 2-5 year old, possibly 6-9 year old > 1 year old	low-age improvement probably restricted to switch from yearling to older	-	Species where EPP often is result of forced copulation. Age effects may be partially result of female susceptibility to forced copulation and male ability to protect female from them. Possible effect of senescence, but not formally tested.	Brekke et al. 2013
(a)	<i>Oenanthe oenanthe</i>	Bardsey Island	2	age class ^a	-	none	-	-	-	-	-	Currie et al. 1998
(a)	<i>Oenanthe oenanthe</i>	Rhineland	2	age class ^a	-	none	-	-	-	-	-	Kudernatsch et al. 2010
(a)	<i>Pachycephala pectoralis</i>		2	age class ^a	none	none	-	-	-	-	-	van Dongen & Mulder 2009
(a)	<i>Parus major</i>	Arnhem	2, 3	age class ^a	-	-	none	-	-	-	-	van Oers et al. 2008
(a), (c), (e)	<i>Parus major</i>	Bahrdorf	2	age class ^a	-	yearling > older	-	none	-	decrease of loss with brood sequence in males measured in successive years	Loss measured as Y/N and as proportion lost. Analysis controls for effects of female age. No effects significant, but results could suggest that losses may be especially high in nests of yearling males mated to older females. Within-individual change inspected as brood sequence, but not separating by age.	Lubjuhn et al. 2007
(a), (c)	<i>Parus major</i>	Jomfruland	2	age class ^a	-	none	-	none	-	-	-	Krokene et al. 1998
(b), (c)	<i>Parus major</i>	Starnberg	-	age class ^a	none	-	-	none	-	-	Data are part of an experiment that manipulated perceived predation risk and that had no effect on parentage.	Abbey-Lee et al. 2018
(a), (c)	<i>Parus major</i>	Vlieland	2	age class ^a	-	none	-	none	-	-	-	Verboven & Mateman 1997
(a)	<i>Parus major</i>	Wuppertal	2, 3	age class ^a	-	none	none	-	-	-	-	Strohbach et al. 1998
(a), (c)	<i>Parus major</i>	Wytham Woods 1985-1987	2	age class ^a	-	none	-	none	-	-	-	Blakey 1994
(b), (c)	<i>Parus major</i>	Wytham Woods, 2005-2007	-	continuous ^d	none on neighbourhood level	none on neighbourhood level	-	none on neighbourhood level	-	-	Effect of female age on gains of her social mate detected on neighbourhood level.	Roth et al. 2019

Reason	Species	Population	Metanalysis (a)	Age measure	Age effect male gains	Age effect male losses	Age-effect pair-wise comparison of males (WP vs. EP)	Age-effect female EPP (c)	Young-age effects ongoing? (d)	Within-individual changes (e)	Comments	Reference
(a), (d)	<i>Passer domesticus</i>	Brackenhurst, 1988-1990	2, 3	age class / continuous (see comments)	older > yearling	none	<i>EP male older WP male, no age class effect</i>	-	<i>age difference between EP and WP males is not driven by yearlings</i>	-	Age measurement: Data analysed in study based on age class (yearling / older) or age class correlate (new bird = yearling). Study provides information on exact or minimum ages (assuming age =1 for birds first caught after first autumn) for all males attending or siring offspring in the 29 broods containing EPY. Based on this pair-wise analysis conducted here for both age class and for exact age (results in italics).	Wetton et al. 1995
(b), (c)	<i>Passer domesticus</i>	Brackenhurst, 1994	-	age class ^a	-	none	-	none	-	-	When combining data from both populations (Cab & Brackenhurst, 1994) age effect on loss is just significant ($p = 0.05$), suggesting a trend for more frequent losses among older males than yearlings.	Cordero et al. 1999
(b), (c)	<i>Passer domesticus</i>	Cab	-	age class ^a	-	none	-	none	-	-	When combining data from both populations (Cab & Brackenhurst, 1994) age effect on loss is just significant ($p = 0.05$), suggesting a trend for more frequent losses among older males than yearlings.	Cordero et al. 1999
(b), (c)	<i>Passer domesticus</i>	Collado Villalba	-	age class ^a	-	none	-	none	-	-	-	Veiga & Boto 2000
(a), (c)	<i>Passer domesticus</i>	Kentucky	2, 3	age class	none	none	none	none	-	-	Age measurement: yearling / older with age class correlate used for second of two study years (new bird = yearling).	Stewart et al. 2006
(a)	<i>Passer domesticus</i>	Lundy Island, 2000-2011	3	continuous ^b	-	-	Δ age EP-WP significantly larger than 0 [effect size in years: 0.22 (0.09 to 0.33)]	-	-	-	Improvement after maturation and within-individual change inspected in Hsu et al. 2017. Data overlap also with Schroeder et al. 2016.	Hsu et al. 2015
(b), (d), (e)	<i>Passer domesticus</i>	Lundy Island, 2000-2012	-	continuous ^b	early life improvement	marginal increase of loss early in life	- (presented in Hsu et al. 2015)	-	not entirely clear due to restrictive modelling approach using polynomials, main effect definitely between age 1 and 2	results refer to within-individual patterns	Senescent declines are result of modelling restrictions, no evidence for post-peak decline presented; assortative mating present and results not necessarily unchanged when accounting for female age (Table S4). Pair-wise comparison performed in Hsu et al. 2015. Data overlap also with Schroeder et al. 2016.	Hsu et al. 2017
(b), (e)	<i>Passer domesticus</i>	Lundy Island, 2004-2012	-	continuous ^b	-	decrease in probability of being cuckolded with age	-	-	-	result refers to within-individual pattern	Data overlapping with Hsu et al. 2015 and Hsu et al. 2017. Note difference in effects on losses to Hsu et al. 2017,	Schroeder et al. 2016

Reason	Species	Population	Metanalysis (a)	Age measure	Age effect male gains	Age effect male losses	Age-effect pair-wise comparison of males (WP vs. EP)	Age-effect female EPP (c)	Young-age effects ongoing? (d)	Within-individual changes (e)	Comments	Reference
											which is probably due to deviating response variable (loss Y/N vs. proportion lost) and modelling approach (linear vs. quadratic).	
(b), (d)	<i>Passer domesticus</i>	Seewiesen (captive)	-	continuous ^b	increase of gains with age, possibly in non-linear manner	-	-	-	possibly increase in gains only at low ages (quadratic relationship supported in one of two analyses)	-	Captive population.	Girndt et al. 2018
(a)	<i>Passerina cyanea</i>		2	age class ^a	-	trend for older > yearling	-	-	-	-	Anecdotal information: three assigned EP sires all older than yearling.	Westneat 1990
(a), (c), (d), (e)	<i>Periparus ater</i>		2, 3	continuous ^b	older > younger, non-linear for no. of EPY sired	none	EP older than WP	see comments	probably not	increase in gains for males measured in two successive years, especially for males that start as yearlings. No change in losses.	Pair-wise tests run (a) only for males with known exact age, (b) also including males first caught at age > 1 assuming age = 2 at time of capture, (c) for age class (yearling vs. older). Results consistent. Gain tests run for (b) and (c); results consistent. Loss test run only for (b). Gains measured as Y/N and (standardized) no. of EPY sired. Loss measured as (standardized) no. of WPY sired. Study by Dietrich et al. 2004 inspects within-individual changes and effects of and interaction with female age using one year more of data. Results suggest possible interactive effects of male and female age class on proportion lost (but not of loss Y/N), with highest losses in broods of yearling males mated to older females, and no systematic within-individual change, but some repeatability in proportion lost.	Schmoll et al. 2007
(b)	<i>Petronia petronia</i>	Clarée valley	-	age class ^a	older > yearling	none, trend for older > yearling	-	-	-	-	Age measure: exact or minimum age (based on previous observations and assuming age = 1 for new birds) available, but all statistical comparisons run only for yearling vs. older.	Nemeth et al. 2012
(a)	<i>Petronia petronia</i>	Susa valley	2	age class	-	yearling > older	-	-	-	-	Age measure: yearling / older or correlate (new birds = yearling). Effect of age class possibly adds to effect or male mating	Pilastro et al. 2002

Reason	Species	Population	Metanalysis (a)	Age measure	Age effect male gains	Age effect male losses	Age-effect pair-wise comparison of males (WP vs. EP)	Age-effect female EPP (c)	Young-age effects ongoing? (d)	Within-individual changes (e)	Comments	Reference
											status (more losses in polygynous males).	
(a)	<i>Phylloscopus fuscatus</i>		1, 3	age class ^a	-	-	none	-	-	-	-	Forstmeier 2002
(a)	<i>Phylloscopus trochilus</i>		2, 3	age class ^a	-	yearling > older	none	-	-	-	Age measure: exact or minimum age (based on previous observations and assuming age = 1 for new birds) available, but all statistical comparisons run only for yearling vs. older.	Gil et al. 2007
(b)	<i>Plectrophenax nivalis</i>		-	continuous ^f	-	older > younger	-	-	-	-	-	Hoset et al. 2014
(a)	<i>Poecile atricapillus</i>	Chaffey's Lock	2	age class ^a	-	none	-	-	-	-	-	Mennill et al. 2004
(a)	<i>Poecile atricapillus</i>	Lake Opinicon	2, 3	age class ^a	-	none	none	-	-	-	Pair-wise comparison: test not performed, but some data provided. Age class of males for 8 cases where both males were same age class is not defined, except that both combinations occurred. Therefore, all possible combinations tested. No effect under any scenario.	Otter et al. 1998
(b), (c)	<i>Poecile gambeli</i>		-	age class ^a	-	none	none	none	-	-	Very small sample size in pair-wise comparison (N = 5) and trend for EP male older than WP male (P = 0.08). None of the five WP males older than the EP male.	Bonderud et al. 2018
(a), (c)	<i>Progne subis</i>	Maryland	2	age class ^a	older > yearling	yearling > older	-	none	-	-	Species with delayed plumage maturation (subadult plumage in yearlings).	Wagner et al. 1996
(a), (c), (d), (e)	<i>Progne subis</i>	Pennsylvania	3	continuous ^b	older > younger, non-linear with main effect between yearling and older males	younger > older, non-linear with probably ongoing effect after age 2 (effect of clutch size not entirely clear)	EP older than WP males, main effect probably between yearling and older males	none (based on female age class)	probably for losses (effect of clutch size not entirely clear), but main effect between yearling and older males here and for gains	decline in loss for males measured in two successive years, especially pronounced for males starting as yearlings, but also among older males	Species with delayed plumage maturation (subadult plumage in yearlings). Different results reported in text and tables, apparently from different models, but unclear, what the differences are and why authors take results from models in text as basis for discussion (results presented here follow this choice).	Tarof et al. 2012
(a)	<i>Riparia riparia</i>		2	continuous ^b	-	none	-	-	-	-	-	Augustin et al. 2007
(b)	<i>Setophaga caerulea</i>		-	age class ^a	older > yearling	-	-	-	-	-	Age effect interacts with distance effects, being most pronounced within the direct neighbourhood	Kaiser et al. 2017
(a), (d), (e)	<i>Setophaga ruticilla</i>		1, 2	continuous ^d	-	decrease with age	when male is older than neighbour, it is more likely to sire young in that neighbour's nest	-	yes: ongoing reduction in losses, perhaps even no reduction	anecdotally: decline in loss for four males of varying ages	Pair-wise test is not actually pair-wise between EP and WP males, but pairs male neighbours and compares occurrence of EPP given sign	Perreault et al. 1997

Reason	Species	Population	Metanalysis (a)	Age measure	Age effect male gains	Age effect male losses	Age-effect pair-wise comparison of males (WP vs. EP)	Age-effect female EPP (c)	Young-age effects ongoing? (d)	Within-individual changes (e)	Comments	Reference
(b), (d), (e)	<i>Sialia mexicana</i>	Carmel Valley, 2000-2005	-	continuous ^b	older > younger	-	EP older than WP (Δage 0.5 years and EP male older than WP male twice as often than younger)	-	between age 1 and 2 main effect probably between yearling and older males	measured in two successive years significant within-individual increase in probability of gains	of age difference between neighbouring males. Data also used in Ferree & Dickinson 2014. Analysis of loss and female EPP performed there.	Ferree & Dickinson 2011
(b), (c)	<i>Sialia mexicana</i>	Carmel Valley, 2000-2005	-	continuous ^b	older > younger	none	-	none	-	-	Data also used in Ferree & Dickinson 2011. Pair-wise comparison performed there.	Ferree & Dickinson 2014
(b)	<i>Sialia mexicana</i>	Pajarito Plateau	-	age class ^a	older > yearling	-	-	-	-	-	-	Jacobs et al. 2015
(a), (c)	<i>Sialia sialis</i>	Chaffey's Lock	2	age class ^a	-	none	-	none	-	-	-	Meek et al. 1994
(a), (c)	<i>Sialia sialis</i>	South Carolina	2	age class ^a	-	yearling > older	-	none	-	-	-	Gowaty & Bridges 1991
(b), (c)	<i>Spizella pusilla</i>		-	age class ^a	none	none	-	none	-	-	This thesis chapter is the manuscript for Celis-Murillo et al. 2017, but age information was removed from that paper.	Celis-Murillo 2015
(b), (c)	<i>Stenophaga petechia</i>		-	age class ^a	older > yearling	none	-	none	-	-	Tendency for assortative mating by age class.	Grunst & Grunst 2014
(a), (c)	<i>Sturnus vulgaris</i>		2	age class ^a	-	none	-	none	-	-	Test for males not performed, but data presented.	Pinxten et al. 1993
(b), (c), (d)	<i>Sula nebouxii</i>		-	continuous ^b	-	younger > older for males mated to young females, older > younger for males mated to old females	none	younger > older for females mated to young males, older > younger for females mated to old males	yes; direction of ongoing effect changes in interaction with mate age	-	Long-lived species. Ages of mates interact in their effect on EPP.	Ramos et al. 2014
(a), (c)	<i>Tachycineta bicolor</i>	Chaffey's Lock, 1990	2	age class ^a	-	very badly supported trend for new birds to be more likely to have many EPY in nest than birds banded in previous year	-	none	-	-	Loss measured as many lost vs. few lost, where few lost comprises nests containing no or one EPY.	Lifjeld et al. 1993
(c)	<i>Tachycineta bicolor</i>	Chaffey's Lock, 1995	-	age class ^a	-	-	-	none	-	-	-	Kempnaers et al. 1999
(a)	<i>Tachycineta bicolor</i>	Prince George	2	age class ^a	recaptured > newly captured	-	none	-	-	-	-	Bitton et al. 2007
(b)	<i>Tachycineta bicolor</i>	Tompkins County	-	not explained	-	-	none	-	-	-	-	Hallinger et al. 2020
(b), (d)	<i>Troglodytes aedon</i>	Illinois (not Mackinaw)	-	continuous ^f	-	low-age improvement followed by plateau and probably senescent decline	none	-	no: see results for losses	-	Low-age improvement between ages 1 and 2 only. Senescent decline not explicitly tested and could be consequence of restrictive modelling procedure (parabolic shape). Some age assortative mating in this population	Bowers et al. 2015

Reason	Species	Population	Metanalysis (a)	Age measure	Age effect male gains	Age effect male losses	Age-effect pair-wise comparison of males (WP vs. EP)	Age-effect female EPP (c)	Young-age effects ongoing? (d)	Within-individual changes (e)	Comments	Reference
											(Bowers et al. 2017), which is not considered.	
(a), (c)	<i>Troglodytes aedon</i>	Mackinaw	2	age class ^e	-	none	-	none	-	-	Results confirmed with subset of birds with known age class: nestlings of previous year (yearlings) vs. experienced breeders.	Soukup & Thompson 1997
(a)	<i>Troglodytes aedon</i>	Wisconsin	1	age class ^e	-	-	none	-	-	-	-	Poirier et al. 2004
(a), (c)	<i>Troglodytes aedon</i>	Wyoming	2	age class ^a	-	none	-	none	-	-	-	Johnson et al. 2002
(a), (c)	<i>Wilsonia citrina</i>		2, 3	continuous ^d	-	none	none	younger > older	-	-	Paternity not repeatable. Within-individual changes not otherwise inspected. Ongoing low-age effect not inspected for males, for females ongoing after age 2.	Stutchbury et al. 1997
(b)	<i>Zonotrichia albicollis</i>		-	continuous ^b	-	older > younger for white morph males	-	-	-	-	Age effect on losses only present in white morph males (which gain and lose most paternity) and absent in tan morph males (i.e., Interaction between morph and age in their effect on paternity loss).	Grunst et al. 2017
(a), (c), (d)	<i>Zonotrichia leucophrys</i>		2	continuous ^b	-	older > younger	-	none	effect of higher losses among older males probably driven by the oldest males in the population (age 6 to 8)	-	-	Sherman & Morton 1988

Note: Age was measured either continuously or in age classes. In males, studies could inspect effects of a male's age on his paternity gains (Y/N or number of EPY gained), on his paternity losses (Y/N or proportion of brood lost) or conduct a pair-wise comparison of the age of extra-pair sires and the males they cuckolded. In females, studies inspected effects of female age on the occurrence of EPP in her nest (Y/N or proportion EPY in brood). Studies are listed, (a) if they are part of the meta-analyses by (Akçay & Roughgarden 2007 = 1, Cleasby & Nakagawa 2012 = 2, or Hsu et al. 2015 = 3), (b) if they test for age effects on EPP in males and were not part of the literature available to the authors of the meta-analyses, (c) if they test for an effect of female age on the occurrence of EPP, (d) if they provide information on ongoing age-related changes among young ages and (e) if they provide information on within-individual changes on top of the cross-sectional analysis.

^a Age measure: yearling vs. older.

^b Age measure: exact age.

^c Age measure: minimum age based on previous observation.

^d Age measure: exact or minimum age based on previous observation and assuming age = 2 for birds first caught older than yearlings.

^e Age measure: age class correlate (experienced / new breeder).

^f Age measure: exact or minimum age based on previous observations and assuming age = 1 for new birds.

^g Age measure: age class correlate (recaptured / newly captured).

SUPPLEMENTARY FIGURES

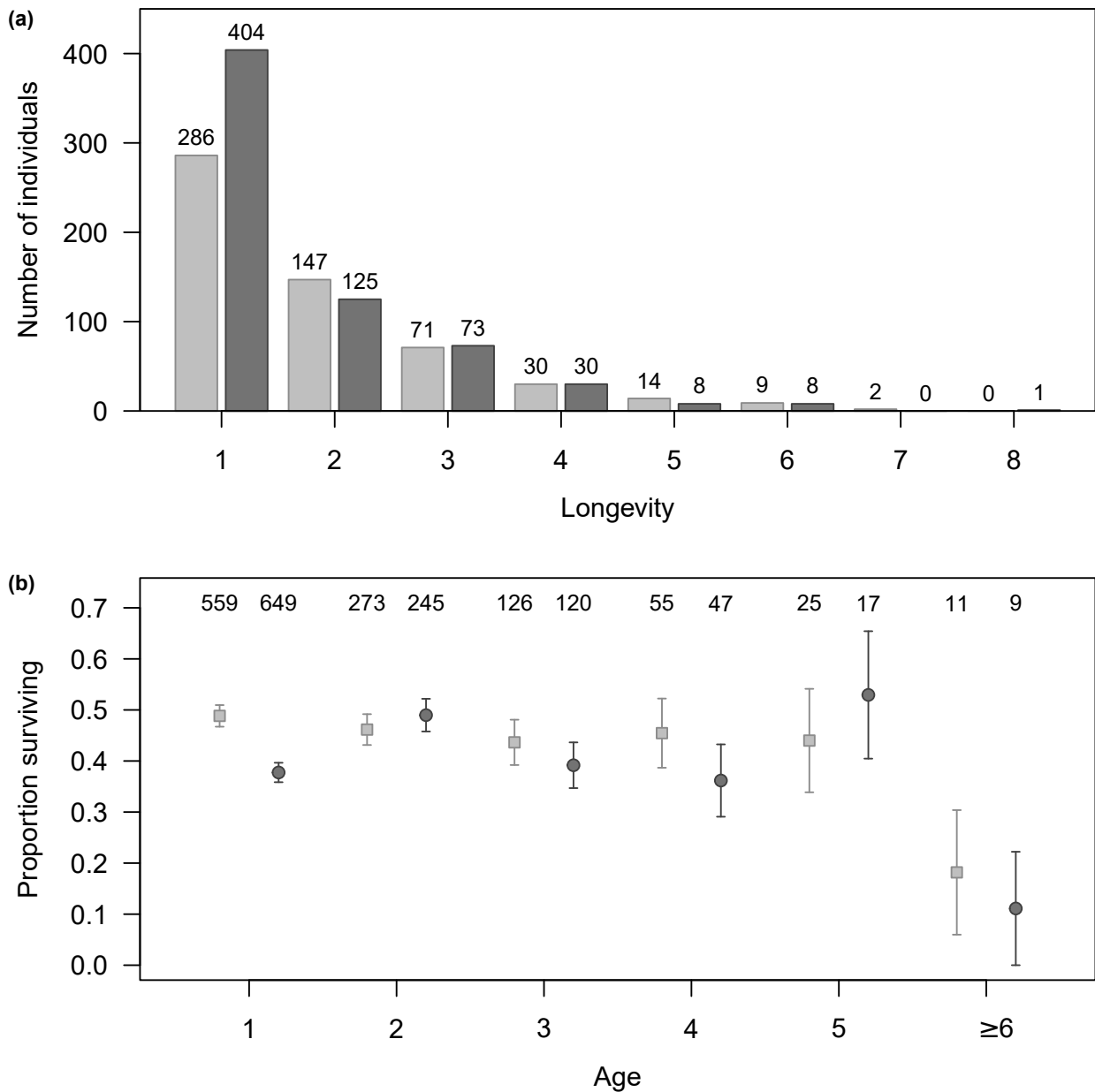


Figure S1. Distribution of longevity (a) and the relationship between age and survival (b) for blue tits from our population (data from 2007-2019). Individuals were considered to have survived, if observed after 15 March of a given breeding season. Longevity is defined as the age at their last observation. Males are shown in light grey (squares), females in dark grey (circles). Sample sizes are indicated above bars or at the top. Data shown in (b) are means (points) and standard errors (bars). There was no relationship between survival and age (binomial GLMM with sex as covariate and year and identity as random effects; the same modelling approaches were compared as for other performance trajectories, see Methods; best model fit was a simple linear GLMM with effect \pm SE of age on probability of survival (logit-scale): -0.11 ± 0.07 , $p = 0.13$).

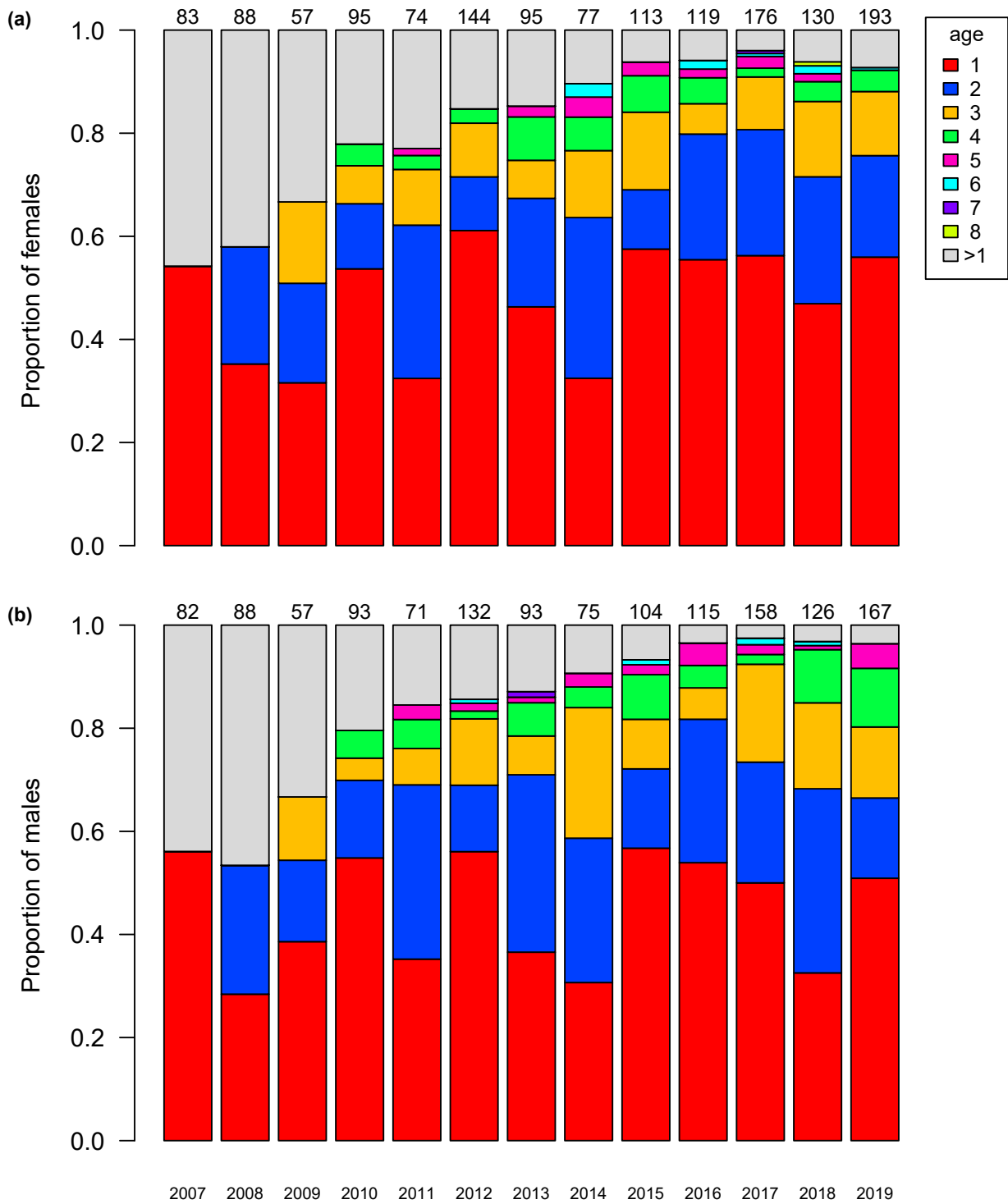


Figure S2. Annual variation in the age structure of the breeding population for males (a) and females (b). Numbers above bars refer to the total number of breeding males or females. Colours indicate age (in years, see legend), where 'grey' refers to individuals older than one with unknown exact age.

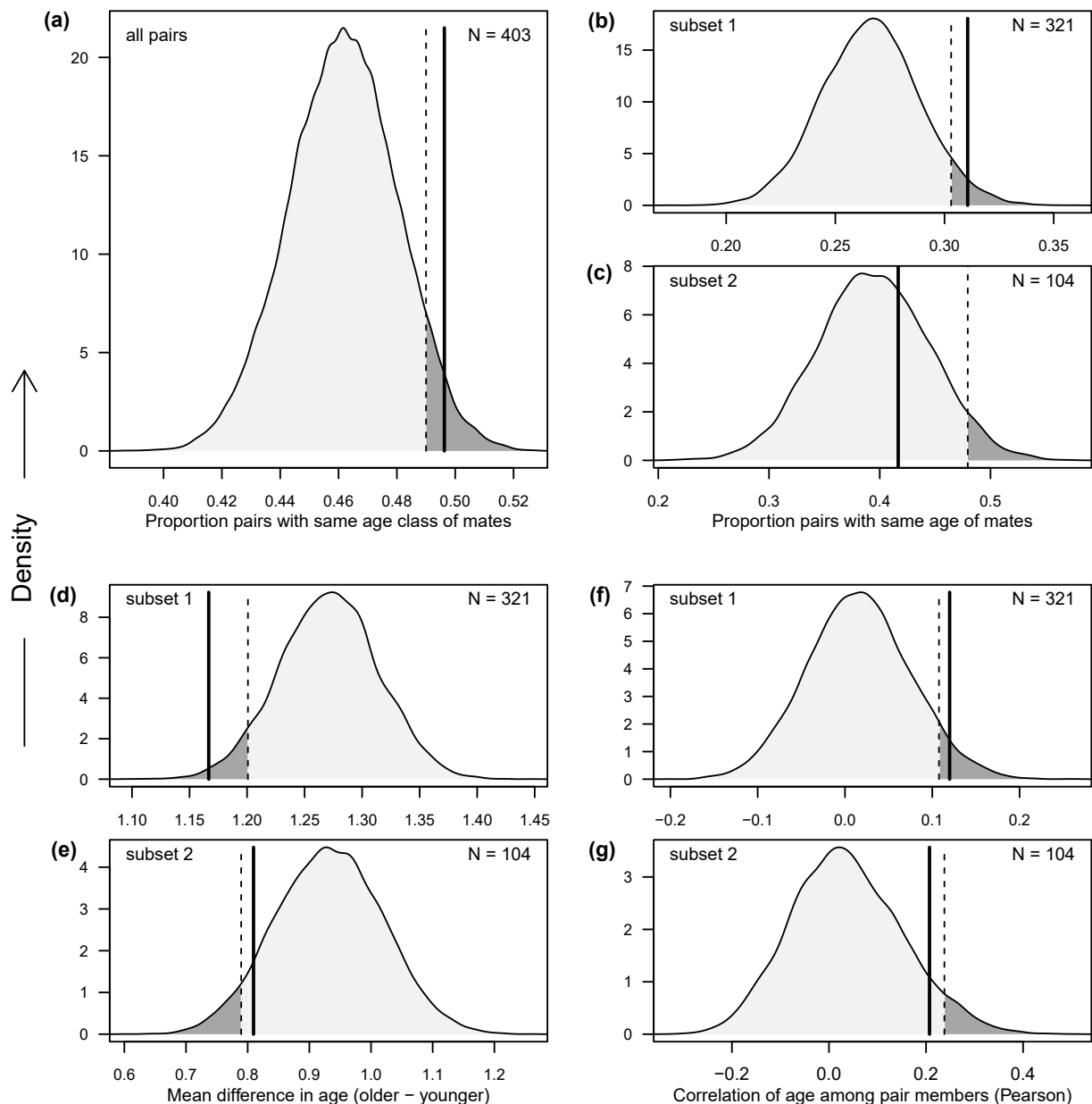


Figure S3. Relationships between female age and the age of their extra-pair mates. We compare the realized value with simulated values under random mating for the proportion of pairings for which the age class (yearling or older) is the same for both individuals (a), the proportion of pairings for which the exact age (in years) is the same for both individuals (b, c), the mean age difference (in years) between individuals (d, e) and the correlation (Pearson's r) of age (in years) among individuals (f, g). Shaded areas show the density distribution obtained from 10000 random pairings of individuals among breeding pairs of the same year (see Supplementary Methods S5). The dashed vertical line in each panel indicates the location of the top or bottom 5% of simulated values; the bold line indicates the realized value. In panels (b-g), only data from 2011 onwards were included (see Supplementary Methods S5). Panels (b), (d) and (f) are based on pairings with exact age known for both individuals (subset 1, $N = 321$). Panels (c), (e) and (g) are based on pairings for which the exact age was known for both individuals and both were older than yearlings (subset 2, $N = 104$). The simulation suggests an association of age between extra-pair partners (a, b, d, f). If only pairings among individuals older than one year are included, this effect disappears (c, e, g), indicating that the effect is mediated by age class.

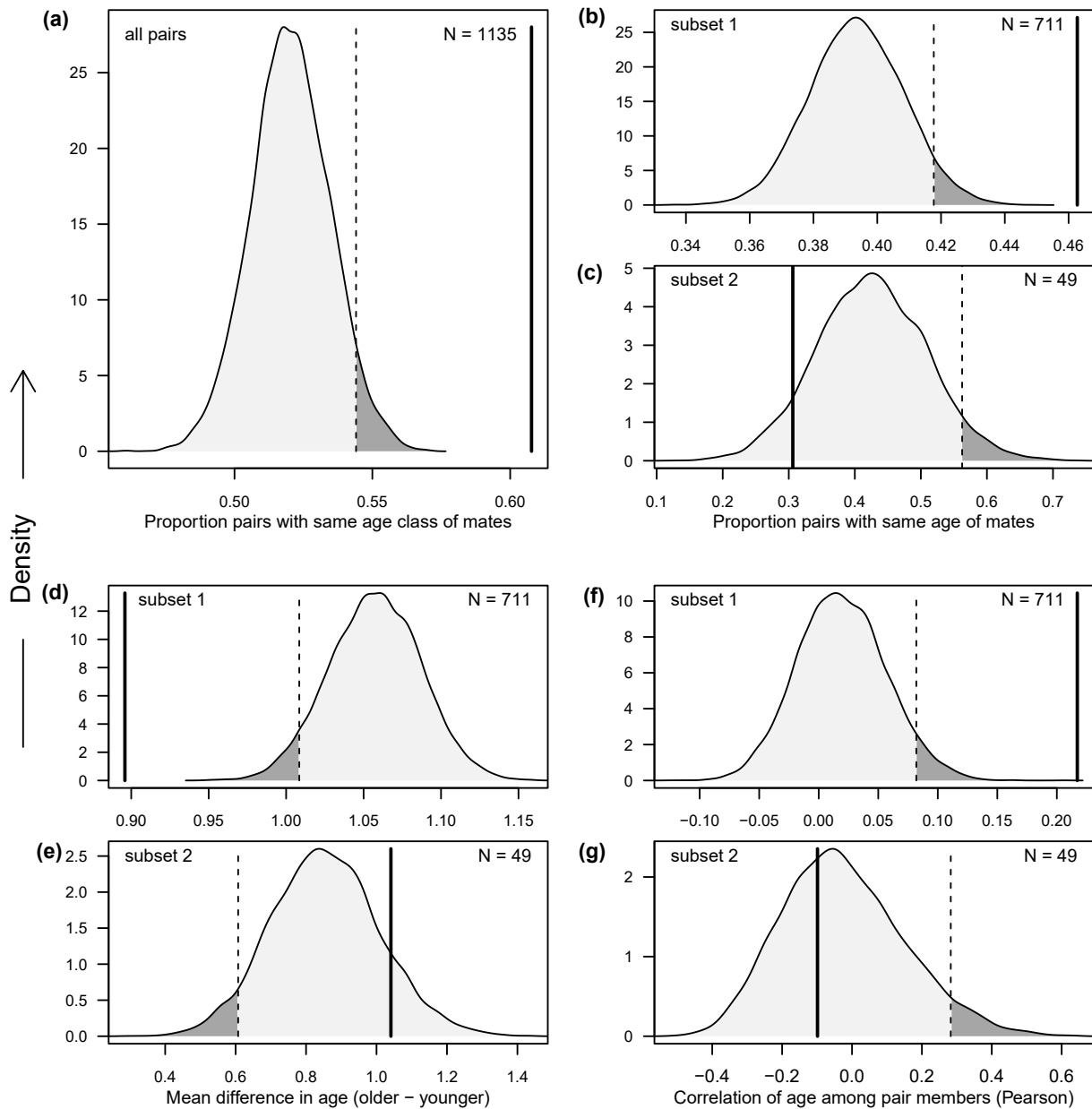


Figure S4. Relationships between the age of social pair members. We compare the realized value with simulated values under random mating for the proportion of pairs for which the age class (yearling or older) is the same for both pair members (a), the proportion of pairs for which the exact age (in years) is the same for both pair members (b, c), the mean age difference (in years) between pair members (d, e) and the correlation (Pearson's r) of age (in years) among pair members (f, g). Shaded areas show the density distribution obtained from 10000 random pairings of individuals among breeding pairs of the same year (see Supplementary Methods S5). The dashed vertical line in each panel indicates the location of the top or bottom 5% of simulated values; the bold line indicates the realized value. In panels (b-g,) only data from 2011 onwards were included (see Supplementary Methods S5). Panels (b), (d) and (f) are based on pairs with exact age known for both pair members (subset 1, $N = 711$). Panels (c), (e) and (g) are based on pairs for which the exact age was known for both pair members and both were older than yearlings (subset 2, $N = 49$). Similar to results of previous studies (Hund & Prinzinger 1985; Black & Owen 1995; Martin 1995; Cézilly et al. 1997; Potti 2000; Fasola et al. 2001; Ferrer & Penteriani 2003; McCleery et al. 2008; Auld et al. 2013; Hsu et al. 2017; blue tit: Auld & Charmantier 2011; great tit *Parus major*: Roth et al. 2019) the simulation suggests that the age class and the age of pair members was correlated (a, f). Because yearlings were more often mated to each other than expected under random mating, the frequency of pair members with the same age was higher (b) and the absolute age difference between pair members lower (d) than expected under random mating. When only considering social pairs where both pair members were older than yearlings, no indication of age-assortative mating was found (c, e, g).

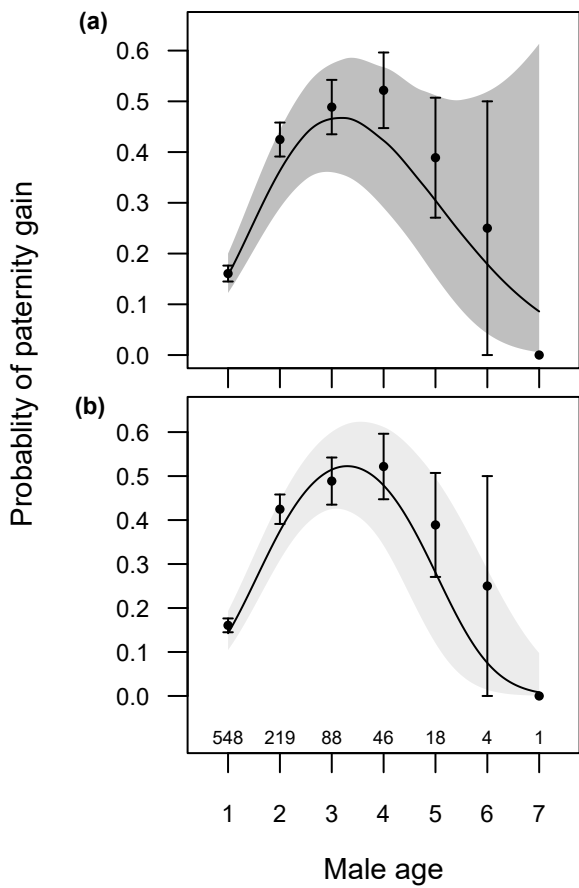


Figure S5. Graphical representation of GAMM (a) and polynomial GLMM (b) model results for the effect of male age on the probability of paternity gain, where the polynomial GLMM supported a second-order polynomial. Both panels show the cross-sectional raw data as means (points) with standard errors (error bars) and the predictions (lines) with their 95% CI (shading). Sample sizes are indicated at the bottom. Model fits are from the GAMM (a, dark grey) and from the polynomial regression (b, light grey). Note the similarity of the predictions between the two modelling approaches (see Table S6 for details on model fit).

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