

Age-dependent trajectories differ between within-pair and extra-pair paternity success

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Abstract

Reproductive success is associated with age in many taxa, increasing in early life followed by reproductive senescence. In socially monogamous but genetically polygamous species, this generates the interesting possibility of differential trajectories of within-pair and extra-pair siring success with age in males. We investigate these relationships simultaneously using within-individual analyses with 13 years of data from an insular house sparrow (*Passer domesticus*) population. As expected, we found that both within- and extra-pair paternity success increased with age, followed by a senescence-like decline. However, the age trajectories of within- and extra-pair paternity successes differed significantly, with the extra-pair paternity success increasing faster, although not significantly, in early life, and showing a delayed decline by 1.5 years on average later in life compared to within-pair paternity success. These different trajectories indicate that the two alternative mating tactics should have age-dependent pay-offs. Males may partition their reproductive effort between within- and extra-pair matings depending on their current age to reap the maximal combined benefit from both strategies. The interplay between these mating strategies and age-specific mortality may explain the variation in rates of extra-pair paternity observed within and between species.

Introduction

Age-dependent paternity success, a change with age in the number of offspring sired by a male, has been described in many taxa (Hoikkala *et al.*, 2008; Carazo *et al.*, 2011; Schroeder *et al.*, 2012; Tarof *et al.*, 2012; Lebigre *et al.*, 2013). Generally, male reproductive success increases with age and then declines later in life (Mauck *et al.*, 2004; Willisch *et al.*, 2012; Froy *et al.*, 2013). In a socially monogamous but genetically polygamous system, the costs and benefits of within- and

extra-pair matings to males probably differ, such that these two avenues to paternity success might have different age trajectories. However, this possibility has only been indirectly investigated once (Lebigre *et al.*, 2013; but see below for further discussion), with the remaining studies either focusing on other mating systems (Auld *et al.*, 2013; Froy *et al.*, 2013; Hayward *et al.*, 2013; Zhang *et al.*, 2015; Caudill *et al.*, 2016), in systems where extra-pair mating is rare and thus being neglected (Aubry *et al.*, 2009; Bouwhuis *et al.*, 2012; Zabala & Zuberogitia, 2015), or mixing within-pair and extra-pair paternity successes instead of estimating them separately (Hatch & Westneat, 2007; Schroeder *et al.*, 2012; Froy *et al.*, 2013; Harris *et al.*, 2016).

Both within-pair and extra-pair paternity success are expected to increase with age ('Age-related increase hypothesis'). However, this increase might occur for

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different reasons in each case. For example, an increase in a male's within-pair paternity success with age might result from female preference of older males, as older males are more resourceful and experienced, and thus able to invest more into parental care than younger males (Williams, 1966; Trivers, 1972; Forslund & Part, 1995; Riechert *et al.*, 2012). Notably, because males provide no resources or paternal care to extra-pair offspring, the above-outlined female preference can only apply to within-pair paternity success. In addition, older males might have higher extra-pair paternity success than younger males because older males, through experience, may be better at attracting or forcing females to engage in extra-pair mating (Westneat & Stewart, 2003; Poesel *et al.*, 2006). Furthermore, the age-related increase in paternity success may result from older males being of high genetic quality, as evidenced by their viability (Fisher, 1930; Hamilton & Zuk, 1982; Brooks & Kemp, 2001). High genetic quality can result in higher offspring fitness, and thus, females may choose these older males as social and genetic sires for their offspring. The prediction of age-related increase in paternity success is consistent with the robust pattern supported by meta-analyses that, in birds, extra-pair fathers tend to be older than within-pair fathers (Akçay & Roughgarden, 2007; Cleasby & Nakagawa, 2012; Hsu *et al.*, 2015).

Later in life, within-pair paternity success and extra-pair paternity success are both expected to decline due to senescence ('senescence hypothesis'). Reduced physiological functioning with age is expected to result in lower survival and reproductive performance of males (Williams, 1957; Kirkwood, 1977; Kirkwood & Austad, 2000). Because male physiological function declines with age, and old males might sire offspring of lower quality, females are expected to prefer males of younger or intermediate age (Beck & Promislow, 2007). Furthermore, through germline senescence, fertility and hence paternity success via both mating pathways are expected to decrease with age (Catry *et al.*, 2006; Pizzari *et al.*, 2008; Sierra *et al.*, 2013; Johnson *et al.*, 2015; Schroeder *et al.*, 2015). Because males provide different resources in within- and extra-pair matings, the costs of senescence in these two mating strategies are likely to be different. We therefore predict a difference in optimal allocation to both strategies and the resulting rate of senescence-associated decline in within- vs. extra-pair paternity success later in life.

According to the age-related increase hypothesis and the senescence hypothesis, we expect to see an increase in early life followed by a senescence-related decline in later life for both within- and extra-pair paternity successes, but resulting from different underlying causes and therefore potentially at different rates. However, we do not know how this pattern differs between the two classes of paternity success. Through quantifying the age-related trajectories of different mating strategies,

we can extend our understanding of how the maintenance of different mating strategies within the same mating system evolved. Some studies have investigated both components of male reproductive success, but often tested at the population level instead of individual level (Tarof *et al.*, 2012; Lebigre *et al.*, 2013). However, to understand age trajectories of paternity success of individual males, it is crucial to separate the effects of age at the individual level (i.e. a within-individual or longitudinal effect of age) from the effects of age at the population level (i.e. a between-individual or cross-sectional effect of age; van de Pol & Verhulst, 2006; Bouwhuis *et al.*, 2009). For example, an age-related increase in paternity success can be caused by (i) males with shorter lifespan always siring fewer offspring (i.e. selective disappearance), or (ii) a combination of both within- and between-individual effects of age (Cam *et al.*, 2002; van de Pol & Verhulst, 2006; van de Pol & Wright, 2009).

The Lundy Island house sparrow (*Passer domesticus*) system is exceptional for a data set on wild animals, because it provides complete information on within-pair and extra-pair paternity success at each exact age (Hsu, 2014; Hsu *et al.*, 2015). Furthermore, we have previously shown age-dependent productivity with evidence of senescence (Schroeder *et al.*, 2012). This combination makes this population ideal for testing the hypothesized age-related associations between within- and extra-pair paternity success (Table 1). Here, we explicitly tested for differences in age trajectories of within-pair and extra-pair paternity success at an individual and population level, to gain novel insights into how these processes, resulting from different underlying causes, might maintain variation in mating strategies within one species.

Materials and methods

Field data collection

We used data from a house sparrow population on Lundy Island, which is located 19 km offshore in South-West England. This population has been systematically monitored since 2000 (Ockendon *et al.*, 2009). We fitted almost all adult birds with a uniquely numbered metal ring supplied by the British Trust for Ornithology and with a unique colour ring combination (Schroeder *et al.*, 2012). During the breeding season from April to August, we located active nests in nest boxes and other sites, and we monitored each nest from egg laying to offspring fledging. To monitor survival and to ensure that all birds were registered, we captured adults throughout the year. Through these efforts, we have near-complete life-history information on each individual. We collected tissue samples from individuals for paternity analysis. We used a total of 13 microsatellite loci to assign genetic parents to offspring

Table 1 The posterior means (and 95% credible intervals) from generalized linear mixed models with Poisson errors explaining the effects of age on within-pair and extra-pair paternity success (the annual number of respective offspring) of Lundy island house sparrow males.

	Within-pair paternity success	Extra-pair paternity success
Fixed effects		
Intercept	−1.56 (−2.69 to −0.36)	−2.07 (−3.40 to −0.73)
Within-individual effects of age		
Linear coefficient	0.19 (−0.19 to 0.57)	1.56 (1.07 to 2.06)
Quadratic coefficient	−1.04 (−1.63 to −0.46)	−1.84 (−2.55 to −1.09)
Between-individual effects of age		
Linear coefficient	3.96 (1.65 to 6.17)	1.70 (−0.94 to 4.22)
Quadratic coefficient	−0.89 (−2.03 to 0.18)	0.05 (−1.25 to 1.32)
Terminal effect	−0.31 (−0.68 to 0.03)	0.12 (−0.30 to 0.52)
Random effects		
Individual identity	0.15 (0.00 to 0.43)	0.17 (0.00 to 0.41)
Cohort	0.03 (0.00 to 0.10)	0.06 (0.00 to 0.19)
Focal year	0.20 (0.02 to 0.48)	0.12 (0.00 to 0.31)
Mother identity	0.05 (0.00 to 0.16)	0.20 (0.00 to 0.49)
Social father identity	0.03 (0.00 to 0.11)	0.10 (0.00 to 0.32)
Genetic father identity	0.05 (0.00 to 0.17)	0.07 (0.00 to 0.24)
Dispersion	1.13 (0.80 to 1.47)	0.58 (0.27 to 0.90)

The terminal effect indicates whether or not an individual died before the subsequent breeding season (with survived as the reference). Fixed effects statistically different from '0' are marked in bold.

in a pedigree framework (Dawson *et al.*, 2012; Schroe-der *et al.*, 2012; Hsu *et al.*, 2015).

Data selection

We used data collected between 2000 and 2012 in this study. Males were included if they hatched between 2000 and 2011. Paternity success was defined as the total number of annual offspring sired by a male in each year of his life. We defined a social pair as a male and female that we observed incubating the eggs and/or feeding the chicks in the focal nest, additionally confirmed by genetic parentage assignments. Within-pair paternity success consisted of those offspring in a brood that a male genetically sired with his social mate for that brood. Extra-pair paternity success of a male was defined as the number of offspring he sired with females that were not his social mate. Hatched chicks and unhatched eggs, where we succeeded in obtaining DNA samples, were counted as offspring (for the details of sampling and paternity assignments, see Supplementary Information in Hsu *et al.*, 2015). Further details of data selection are presented in Fig. S1 and Appendix S1.

Age variables

Within-subject centring was used to distinguish the within-individual effects of age from the between-individual effects of age on paternity success (van de Pol & Verhulst, 2006; van de Pol & Wright, 2009). Four independent variables of age (in years) were assessed after we scaled and centred the raw age data: (i) the within-individual linear coefficient, modelled as a male's linear increase of paternity success as a function of age. This was calculated by subtracting a male's age in a specific year from the mean age across the years he is present in the data set (Δage). (ii) The within-individual quadratic coefficient, which modelled a male's quadratic relationship between paternity success and age (Δage^2). (iii) The between-individual linear coefficient, which modelled a population-level linear increase of paternity success as a function of age, demonstrated as the mean age of an individual ($\overline{\text{age}}$), and (iv) the between-individual quadratic coefficient, modelled as a population-level quadratic relationship between paternity success and age ($\overline{\text{age}}^2$) (van de Pol & Verhulst, 2006; van de Pol & Wright, 2009).

Reproductive performance might change drastically shortly before death, and could either decline due to a terminal illness or improve due to terminal investment (Coulson & Fairweather, 2001; Bonneaud *et al.*, 2004; Bowers *et al.*, 2012). A terminal effect would be different from a more gradual decline due to senescence. However, terminal effects can potentially confound age-related effects and thus must be accounted for (Simons *et al.*, 2016). We therefore modelled the terminal effect with a binary variable indicating whether an individual died between the current and following breeding seasons (died = 1, survived = 0). To separate terminal effects from the within-individual effects of age, we also ran all analyses with individuals with at least 3 years of breeding records (see Appendix S1 and Table S1 for data description). The results qualitatively agreed with the results from the main data set presented here.

Statistical analysis

All analyses were conducted in R version 3.0.2 (R Core Team), 2013 and fitted Bayesian generalized linear mixed models (GLMMs) with Markov Chain Monte Carlo methods with the R package *MCMCglmm* (Hadfield, 2010). We employed separate GLMMs with Poisson errors with the annual within-pair and extra-pair paternity successes as the response variables, respectively. We present the means of posterior distributions and their 95% credible intervals (95% CIs) as parameter estimates for each model. A fixed effect was considered as statistically significant if its 95% CI excluded zero. Details of MCMC setting are described in Appendix S1.

For each model, the four age variables and the terminal effect were fitted as fixed effects. In addition, we noted that male within-pair paternity success might increase with the age of their social females, which showed age-associated effects on clutch size (Hatch & Westneat, 2007; Westneat *et al.*, 2009). Nevertheless, we have previously found assortative mating for age in this population (M. J. P. Simons, I. S. Winney, Y.-H. Hsu, J. Schroeder, S. Nakagawa & T. Burke, unpublished manuscript). The male age is therefore associated with female age and thus the clutch size, which may further influence male within-pair paternity success. The female age is therefore an intermediate factor in the association between male age and male within-pair paternity success, and should not be fitted as a fixed effect in statistical models because it might otherwise confound our estimates of male age effects on paternity success (Schisterman *et al.*, 2009). Nevertheless, we ran a set of analyses including female age as a fixed effect, and the results showed our findings in the main text are robust (Appendix S2).

The following variables were included as random effects on the intercept: the individual identity of each male to account for pseudo-replication, the focal year, the cohort in which the male was born, and the identity of the mother, social father and genetic father of the focal male. Because we previously detected maternal effects on annual productivity (Schroeder *et al.*, 2012), and paternal effects on offspring phenotypes have been suggested to affect offspring reproductive success (Rando, 2012; Soubry *et al.*, 2014), we conservatively included identities of the parents as random effects. To test for overparameterization, we ran the main models without any parental identities, but the results agree with the results from the main models. We therefore kept the parental identities for biological reasons. To test whether the within-individual age trajectory differed between within-pair and extra-pair paternity successes, we conducted *post hoc* (contrast) analyses to compare the Bayesian posterior distributions of (i) the quadratic coefficient of the estimated effects of age and (ii) the age at which the paternity success reached maximum, estimated as $(-\text{linear coefficient}) / (2 \times \text{quadratic coefficient})$ (or the first derivative = 0 of the fixed part of the model), between within-pair and extra-pair paternity success.

Results

Descriptions of the recorded paternity success

The paternity success of 284 male house sparrows that sired at least one offspring, either extra-pair or within-pair, was recorded. Among these males, 52.1% ($N = 148$) survived to the age of two and 28.5% ($N = 81$) lived for three breeding seasons or more. In total, we assessed the paternity of 3194 offspring, of

which 2637 were within-pair offspring and 557 (17.4%) were extra-pair offspring. In their first year, 69.7% of males sired at least one offspring (either within-pair or extra-pair, or both; Fig. S2). For males that survived to the age of five, all individuals sired at least one offspring at the age of five or older. Among all males, 51.4% sired at least one within-pair offspring in their first breeding season, whereas 73.7% of all males that survived to age two sired at least one within-pair offspring in their second breeding season (Fig. S2). As expected, fewer males sired extra-pair offspring, with only 27.8% of all males siring at least one extra-pair offspring at age one, rising to 48.7% by the age of two and to 100% by the age of five.

Age dependency in within-pair and extra-pair paternity success

Within-pair paternity success

The within-individual linear coefficient of age on within-pair paternity success was not different from zero, but the within-individual quadratic coefficient of age was significantly negative (Table 1 & Fig. 1). Note that because within-subject centring was used, the non-significant linear coefficient suggests that the age at which within-pair paternity success reached its maximum was not significantly different from zero, that is the individual mean age. In addition, there was a positive between-individual linear coefficient of age (Table 1), but no significant between-individual quadratic coefficient of age on annual within-pair paternity success (the linear effect of age was positive after removing the quadratic term; Table S2). Furthermore, there was a nonsignificant terminal effect of age: a male tended to sire fewer within-pair offspring in breeding seasons immediately prior to his death.

Extra-pair paternity success

Age had a significant within-individual linear coefficient and within-individual quadratic coefficient (Table 1 & Fig. 1) on extra-pair paternity success. There were no significant between-individual effects of age on extra-pair paternity success, but the linear effect of age was significantly positive after removing the quadratic term (Table S2). There was no terminal effect on extra-pair paternity success (Table 1; but see Appendix S3 for the age-independent terminal effects).

The comparison between within-pair and extra-pair paternity success

Comparing the within-individual effects of age, the difference between the quadratic coefficient of extra-pair paternity success was slightly smaller than that of within-pair paternity success, although the difference was not statistically significant (*post hoc* comparisons: posterior mean = 0.80, 95% CI = -0.15 to 1.73). In addition, the point at which the within-individual

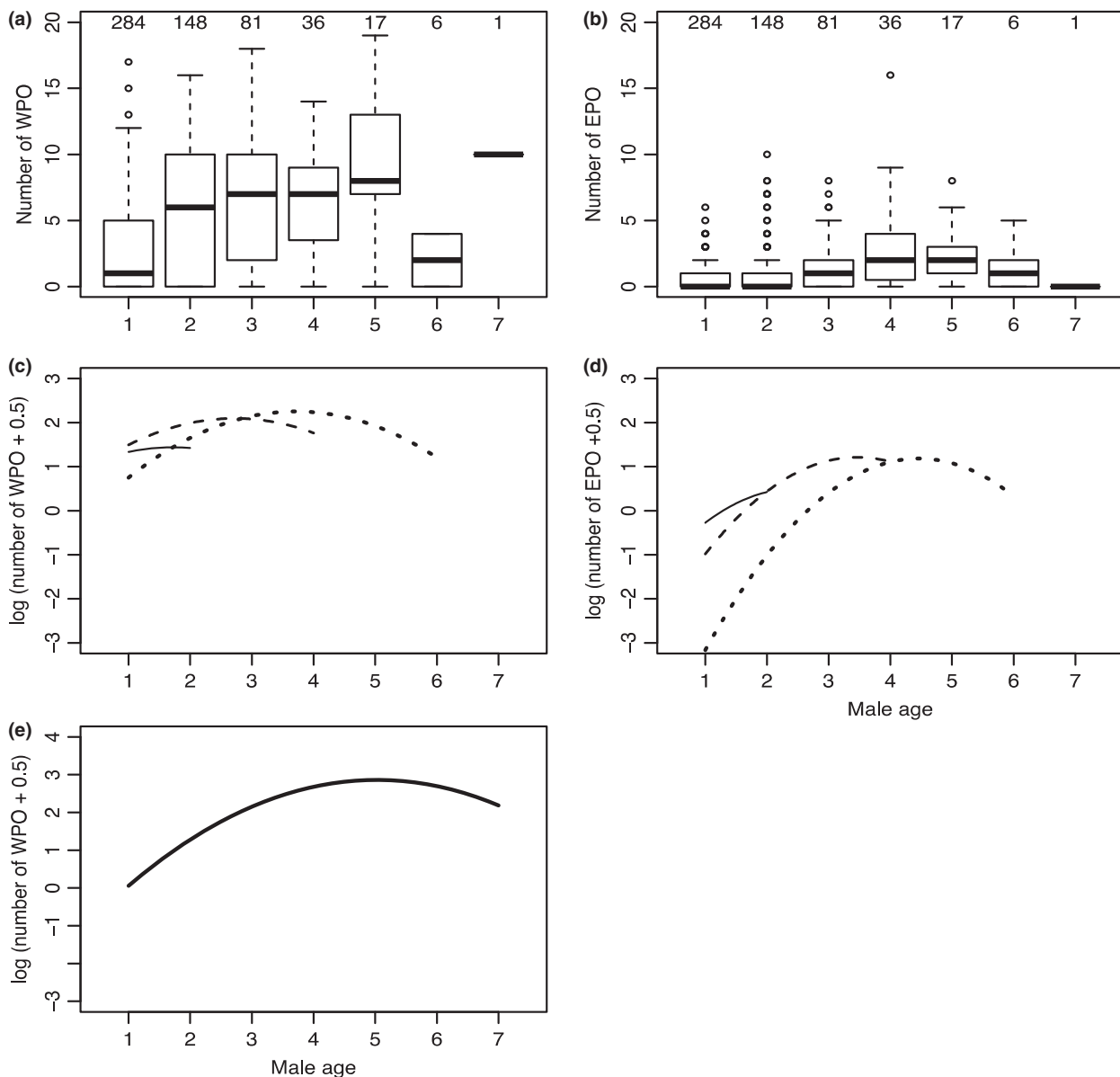


Fig. 1 Within-pair (a, c, e) and extra-pair (b, d) paternity successes in house sparrows on Lundy Island. (a, b) Box plots representing the distribution of annual paternity success from the raw data, and thus representing trends at the population level. The sample size of each age group is presented above each box. (c, d) The within-individual effect of age on the original scale, shown for individuals that lived up to and died at 2, 4 and 6 years old, respectively. (e) The between-individual effect of age on within-pair paternity success on the original scale. The within- and between-individual effects of age presented here were obtained by rerunning the statistical models with the same combination of fixed and random effects on the original data scale, instead of using scaled and centred age data.

extra-pair paternity success peaked was estimated to be marginally larger than that of within-pair paternity success, suggesting that the peak age of extra-pair paternity success was on average 1.5 years later than that in within-pair paternity success (*post hoc* comparisons: posterior mean = -0.34 , 95% CI = -0.70 to 0.01). These results were supported through sensitivity analysis based on five different sub-data sets (Table S3).

Discussion

We observed that, as predicted by the age-related increase hypothesis, both within-pair and extra-pair paternity success initially increased with age. In addition, as predicted by the senescence hypothesis, both components of paternity success showed a senescence-related decline later in life. Notably, we have

demonstrated that extra-pair and within-pair paternity success showed different trajectories relative to age within individuals (Fig. 1), resulting in a greater proportion of annual paternity success being achieved via extra-pair offspring as males age, while within-pair paternity declined (Appendix S4). Note that the effects of age occurred within individuals, and were not driven by differences between individuals. Nevertheless, the age trajectory of paternity success in our study may only be apparent in individuals that lived for 4 years or more, because short-lived individuals will only experience a limited change in paternity success (Fig. 1). We detected a marginal terminal decline in within-pair (but not in extra-pair) paternity success, which could be caused by a decline in physiological condition (Coulson & Fairweather, 2001; Hammers *et al.*, 2012; Simons *et al.*, 2016). This result was consistent with a previous study on the same population, in which we detected a terminal decline in annual productivity (Schroeder *et al.*, 2012).

There were two differences between the longitudinal age trajectories of within-pair and extra-pair paternity success: (i) the increase and decline in extra-pair paternity success was steeper than for within-pair paternity success, although this difference in steepness was not statistically significant (Table 1), and (ii) the age-dependent decline started 1.5 years earlier in within-pair than in extra-pair paternity success assuming a male individual survived sufficiently long (Fig. 1). The direction and strength of effects were consistent in our results from all six data sets with different sample sizes (Table S3), suggesting the directions of these relationships were robust. The rapid, within-individual increase in extra-pair paternity is characterized by relatively low extra-pair paternity success at the age of one, so that across their lifetimes males have room for improvement as they age. Indeed, 51% of male sparrows sired within-pair offspring in their first year and this increased to 1.25 times at age two, whereas only 28% of them sired extra-pair offspring in their first year, which doubled by age two (Fig. S2). In socially monogamous but genetically polyandrous species, female mate choice in within-pair mating may be constrained by the availability of unpaired males. However, the constraint can be relaxed in an extra-pair context. At any given time, a male usually pairs up with only one within-pair female (but see Anderson, 2006), but may copulate with multiple extra-pair females. This flexibility in extra-pair mating may enable the rapid increase in extra-pair paternity success with age that we observed here.

The different timing of senescence-related declines in within-pair and extra-pair paternity success might be explained by senescence acting differently on female preferences, on male performance at either attracting or coercing females, or both (Nussey *et al.*, 2013). Each mechanism will have differential effects on the two

forms of paternity success (Catry *et al.*, 2006; Pizzari *et al.*, 2008; Sierra *et al.*, 2013). From a female's perspective, the costs associated with male senescence are likely to be higher for within-pair than extra-pair mating, because both the direct costs (e.g. reduced resource and paternal care) and indirect costs (e.g. reduced germline quality) may affect within-pair mating, while only indirect costs are involved in extra-pair mating. The indirect benefits of old males, if there are any (e.g. genetic Kokko & Lindstrom, 1996), can potentially outweigh these indirect costs (*cf.* Schroeder *et al.*, 2015). Therefore, the potential indirect benefits may contribute to a later decline in extra-pair paternity success, which is likely to be a result of female choice.

Male manipulation (Westneat & Stewart, 2003; Poessel *et al.*, 2006) might also explain the delayed decline in extra-pair paternity success. Age-dependent male manipulation is probably more effective in the context of extra-pair than within-pair mating because males might be able to persuade a momentary copulation, but not a pair bond. Incidentally, but importantly, the delayed decline in extra-pair paternity success resulted in older males showing an increase in extra-pair paternity success, yet simultaneously with a decrease in within-pair paternity success. This result might explain the robust finding of extra-pair males being older in house sparrows (Wetton *et al.*, 1995; Ockendon *et al.*, 2009; Hsu *et al.*, 2015) and, as a general pattern, across bird species in meta-analyses (Cleasby & Nakagawa, 2012; Hsu *et al.*, 2015).

The different age-dependent trajectories of within-pair and extra-pair paternity success suggest that within-pair and extra-pair mating could be viewed as alternative reproductive tactics (defined as behavioural phenotypes following Dominey, 1984) that bear different age-dependent payoffs. Alternative reproductive tactics usually refer to intrasexual competitors within one species finding different solutions to reproductive competition (Taborsky *et al.*, 2008). A typical example would be different males adopting different mating strategies (e.g. a dominant or sneaker) where the payoff of these strategies is frequency dependent; in a few cases the strategies are genetically determined (e.g. Kupper *et al.*, 2016) but usually they are facultative (Alonzo, 2008). In house sparrows, however, a male can participate in both within- and extra-pair mating at the same time. Therefore, these alternative reproductive tactics are not mutually exclusive, and the degree of investment in one mating tactic over the other can vary over time. Our result on the age-dependent increase in the proportion of extra-pair paternity strongly supports this view (Appendix S4). One might argue that, although the proportion increased with age, the net paternity gain might not increase due to the potential trade-off between pursuing extra-pair copulations and mate-guarding of a male's own female (Hill *et al.*, 2011). However, we recently reported that the likelihood

of a male house sparrow being cuckolded declined with age (Schroeder *et al.*, 2016). Also, there was no association between a male's extra-pair paternity success and his annual paternity loss due to cuckoldry (Appendix S5), suggesting that any trade-off, if there is one, could be mediated by other variables.

To maximize their fitness, male house sparrows might follow an age-contingent reproductive strategy, allocating their reproductive effort between within- and extra-pair matings in accordance with the relative opportunities at each age. Selection on age-dependent mating effort will be shaped by the interaction between optimal reproductive investment and mortality (McNamara *et al.*, 2009). Nevertheless, extrinsic mortality (e.g. predation risk) may differentially affect within- and extra-pair paternity success. For example, if a socially monogamous population is subject to high adult mortality, making future reproductive benefits unlikely, males might increase the effort that they put into extra-pair mating to maximize their current benefits (Botero & Rubenstein, 2012). Because the rate of extrinsic mortality (and variation therein) and the cost of reproduction vary among populations and across species, the optimal distribution of male mating effort with age might similarly vary among populations and species. This interplay between population-specific and species-specific mortality and selection can therefore potentially explain the high variation in the proportion of extra-pair paternity among different populations and species (*cf.* Griffith *et al.*, 2002).

In conclusion, we have identified an age-related increase in paternity success early in life and an age-related decline later in life for both within-pair and extra-pair paternity success. The differences between these two age-related trajectories suggest that there is selection on males to allocate their mating effort between these two classes of mating differentially at different ages. This selection pressure on the partitioning of mating effort could be influenced by the rate of extrinsic mortality and variation in the costs of reproduction. The population-specific and species-specific dynamics among the two mating pathways, mortality and the costs of reproduction can potentially explain the high variation in the proportions of extra-pair paternity observed within and across species.

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Supporting information

Additional Supporting Information may be found online in the supporting information tab for this article:

Appendix S1 Supporting information concerning the Methods and Results in tests of age-dependency of within-pair and extra-pair paternity success.

Appendix S2 Testing age-dependent trajectories on paternity success after considering the assortative mating for age.

Appendix S3 Evaluating age-independent senescence and terminal effects.

Appendix S4 Testing for age-dependency on the annual proportion of extra-pair paternity gain.

Appendix S5 Testing the age-dependency of the annual proportion of within-pair paternity loss.

Appendix S6 Testing age-dependent trajectories paternity success in males sired at least one within-pair offspring through a lifetime.

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