

Extrapair paternity alongside social reproduction increases male lifetime fitness

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Within breeding years, male birds vary in their reproductive strategy. While some maintain monogamy with a social partner, others also engage with extrapair partners, while others forgo monogamy altogether in favour of exclusively seeking extrapair paternity. Although theory predicts that extrapair paternity is beneficial to males, which sire extrapair offspring without investing in costly parental care, empirical examples from wild populations are sparse. We used 17 years of data from a closed population of house sparrows, *Passer domesticus*, with a complete genetic pedigree, to test the hypothesis that extrapair paternity increases male lifetime reproductive success. We compared a mixed strategy of within-pair (or social) and extrapair paternity with total genetic monogamy and total extrapair paternity. We demonstrate that males who combine within-pair and extrapair paternity have increased reproductive success against the other two groups. Our results also suggest that males that exclusively seek extrapair paternity have the lowest lifetime fitness. Overall, we provide an empirical demonstration of the theory, showing that where males can sire extrapair offspring alongside within-pair offspring, extrapair paternity is beneficial to male lifetime fitness.

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Male reproductive success varies in the wild, underpinned in part by differences in reproductive strategy over time. In socially monogamous but genetically promiscuous species, a male that has a social partner but also produces offspring with other females is expected to produce more offspring than a genetically monogamous male (Brouwer & Griffith, 2019; Jennions & Petrie, 2000; Raj Pant et al., 2022). Therefore, from an evolutionary perspective, siring extrapair offspring (resulting in extrapair paternity; EPP) is predicted to be adaptive for males (Eliassen & Kokko, 2008; Kempenaers et al., 1992; Reid & Wolak, 2018), which may produce offspring without investment in costly parental care (Lebigre et al., 2013; Raj Pant et al., 2022; Trivers, 1972). This assumes that extrapair and social (hereafter within-pair) offspring are recruited (i.e. survive to the point of reproduction) equally well; i.e. that there

are no fitness costs specific to extrapair offspring (Bateson & Bateson, 1983; Clutton-Brock, 1988; Hsu et al., 2014). However, empirical data on male mating strategies and the subsequent link with lifetime fitness benefits are still poorly understood (Raj Pant et al., 2022; Schmoll et al., 2009).

Testing this relationship between male mating strategy and lifetime fitness requires that (1) all offspring in a population are assigned genetic parentage and (2) some males adopt the same reproductive strategy across their lifetime, allowing for comparison. These requirements represent a methodological challenge because sampling all offspring in an open wild population is often difficult, and so, seemingly monogamous males may have unobserved extrapair offspring (Maldonado-Chaparro et al., 2018; Raj Pant et al., 2022). Thus, defining male reproductive strategy with any certainty is often difficult, which likely explains why the theoretical prediction that male extrapair fertilizations are adaptive (Parker, 1990) is

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seldom empirically demonstrated in the wild (Brouwer & Griffith, 2019; Raj Pant et al., 2022; Reid et al., 2014; Reid & Wolak, 2018).

In passerine birds, extrapair paternity is common (Brouwer & Griffith, 2019), achieved mainly by males that survive beyond their first breeding year (Cleasby & Nakagawa, 2012; Hsu et al., 2015, 2017; Schlicht & Kempenaers, 2023) and are successful at forming pair bonds (Birkhead & Møller, 1992; Gibbs et al., 1990). Theory predicts that extrapair males should represent a genetically superior (Birkhead & Møller 1995; Hamilton & Zuk, 1982; Kirkpatrick & Barton, 1997) or more compatible (Blomqvist et al., 2002; Ihle et al., 2015; Jennions & Petrie, 2000; but also see Griffith & Immler, 2009; Rekdal et al., 2023) prospect than the female's social partner, because extrapair males provide no direct benefit other than sperm; that is, they are only able to provide indirect benefits to offspring via their genes, rather than providing direct benefits to the female (reviewed in Jennions & Petrie, 2000; Kempenaers & Schlicht, 2010; Søraker & Dunning, 2023). However, empirical evidence for such 'good genes' hypotheses are scarce (Arct et al., 2015; Krokene et al., 1998) and studies more often contradict the theory, either finding no benefit or suggesting costs (Akçay & Roughgarden, 2007; Badás et al., 2020; Grinkov et al., 2022; Hsu et al., 2014, 2015; Matysioková & Remeš, 2013; Schmoll et al., 2009; Schroeder et al., 2016; Søraker & Dunning, 2023). For example, seeking extrapair paternity may increase an individual's exposure to sexually transmitted diseases (Badás et al., 2020; Poiani & Wilks, 2000) or reduce parental care of offspring (Hsu et al., 2014; Schroeder et al., 2016; Søraker & Dunning, 2023). From the female perspective, the benefits are difficult to identify (Liffield & Slagsvold, 2022; Maldonado-Chaparro et al., 2018; Sardell et al., 2012; Søraker & Dunning, 2023) and costs are magnified (where extrapair behaviour also potentially carries direct costs to parental care; Hsu et al., 2014; Schroeder et al., 2016; Søraker & Dunning, 2023). Thus, the drivers of extrapair paternity are the subject of intense debate (Arct et al., 2015; Griffith, 2015; Nakagawa et al., 2015; Reid, 2015). In the absence of evidence, female extrapair mating may instead be explained by benefits to male offspring through linked behaviours controlled by the same set of genes; that is, where the cost of extrapair paternity to the female is small against the benefit attained by her male offspring (Dobson et al., 2023; Dunning et al., 2023; Forstmeier et al., 2014; Wang et al., 2020). While the benefits of extrapair paternity to males are clear in the short term (Albrecht et al., 2007; Webster et al., 2007; Yezerinac et al., 1995), relatively few studies have tested whether extrapair paternity increases male lifetime fitness (Raj Pant et al., 2022).

Previous studies have tested the effect of extrapair paternity on variance in lifetime reproductive success (e.g. Germain et al., 2021; Grunst et al., 2019; Lebigre et al., 2013), or how fitness differs between extrapair and within-pair offspring (e.g. Gerlach et al., 2012; Hsu et al., 2014; Sardell et al., 2012). Studies that have compared lifetime fitness with male mating strategies found either the expected relationship between extrapair behaviours and good genes, where great reed warblers *Acrocephalus arundinaceus*, with large song repertoires benefited through extrapair paternity (Hasselquist, 1998), or more recently, no association (Herényi et al., 2012). A recent study found positive covariance between copulations within- and outside-group paternity in a cooperative breeding Seychelles warbler, *Acrocephalus sechellensis* (Raj Pant et al., 2022; where outside-group paternity is considered equivalent to extrapair paternity), corroborating similar findings in another cooperative breeder, splendid fairy-wren, *Malurus splendens* (Webster et al., 2007). However, the scarcity of molecular paternity assignment and lifetime fitness corrected for longevity in noncooperative breeding systems limits further study of male reproductive strategy.

Here, we used 17 years of lifetime fitness data from a broadly closed (with minimal movement to or from) resident, nonmigratory island population of house sparrows, *Passer domesticus* (hereafter sparrow(s)), with a complete genetic pedigree. Using this system overcomes the aforementioned methodological challenges. We quantified lifetime reproductive fitness for three male mating strategies and measured associated benefits by restricting our analysis to males who followed the same strategy across their lifetime: (1) extrapair males that engaged in both within-pair and extrapair paternity; (2) monogamous (within-pair) males with no extrapair paternity; (3) floating males with no social partner that engaged in extrapair paternity. We use these data to test the hypothesis that males who engage in both within- and extrapair paternity produce the most lifetime offspring and subsequent recruits, followed by monogamous and floating males, even after accounting for differences in male longevity.

METHODS

Study Population

We used data from the Lundy Island (off the southwest coast of England, 51°10'N, 4°40'W) sparrow population. Sparrows show biparental care and are multibrooded and socially monogamous but genetically promiscuous (Anderson, 2006). This population has been the subject of intense study since 1991 when the first 80 sparrow nestboxes were erected. The genetic assignment of parentage and the first genetic proof of extrapair paternity was demonstrated in a house sparrow chick (Burke & Bruford, 1987; also see Wetton & Parkin, 1991), and this method of parental assignment has become central to the Lundy study.

Sparrows on Lundy are captured and resighted throughout the breeding (April – August) and nonbreeding period (November – February). Before fledging from the nest, we fitted all chicks with a unique sequence of coloured leg rings, a uniquely coded British Trust for Ornithology metal leg ring and a unique subcutaneous passive integrated transponder tag (PIT tag; Schroeder et al., 2011). We took DNA samples from adults, hatchlings (alive or dead) and unhatched eggs. We used 22 microsatellite loci to genetically assign parentage (Dawson et al., 2012) and used these data to assemble a genetic pedigree. We identified social parents at the nestbox using their unique sequence of colour rings or PIT tags. The rate of individual resightings varied between 91% and 96% between years (Schroeder, Burke et al., 2012; Schroeder, Nakagawa et al., 2012; Simons et al., 2015).

Ethical Note

All sparrows were captured using mist nets, or at the nestbox, and were extracted, ringed and sampled by experienced bird ringers. We monitored the influence of PIT tags on individual fitness throughout our study and found no correlation (Schroeder et al., 2011). Blood samples (~0.5–20 µl) were taken from the ulnar vein by experienced and licensed field workers. All fieldwork was carried out, including tissue collection for DNA extraction, with the permission of the Lundy Company and Field Society and under appropriate permits from the U.K. Home Office (PP7009092 and PP5873078) and British Trust for Ornithology (S:6308).

Data Extraction

We estimated lifetime fitness as the number of genetic offspring sired and how many of these were recruited into the population of breeding birds between 2000 and 2016. The number of lifetime

recruits accurately represents lifetime fitness in this population (Alif et al., 2022). We only included birds for which we had both social and genetic parentage information, which we recorded using the identification of individual colour rings of parent birds at nestboxes and DNA from blood samples, respectively.

To assign male reproductive strategies, we used all hatchlings and unhatched eggs with known social fathers and genetic sires (6280 offspring, 73.2% of all eggs laid between 2000 and 2016). The remaining 2298 offspring for which parentage was uncertain were either unhatched eggs or dead chicks from which we could not extract DNA of sufficient quality due to tissue autolysis. We then categorized all offspring as either within-pair offspring, sired by a female's social partner, or extrapair offspring sired by a different male to that of her social partner. We categorized all adult males, which only used one reproductive strategy across their lifetime, into one of three reproductive strategies: (1) extrapair males, who sired within-pair and extrapair offspring during their lifetime; (2) monogamous males, who only sired within-pair offspring during their life; (3) floating (or floater) males, who only sired extrapair offspring, without having a social partner (see Moreno, 2016). Although most males in our system vary their reproductive strategies over their lifetime, such birds were not included in our analysis (Fig. 1).

Because males born before 1999 may have bred before 2000, and those alive after 2016 may have continued reproducing, we restricted the male data set to males born between 1999 and 2015, but who died before 2016, to aid precise lifetime fitness estimation. To calculate when a male was last seen alive, we combined 38 218 individual observations collected from 2000 to 2019, including captures ($N = 27\,810$), recordings of RFID tags ($N = 3878$; see Dunning et al., 2024; Sánchez-Tójar et al., 2017), resightings of colour rings ($N = 3047$), parentage assignments ($N = 1957$) and dominance interactions observed at a feeder ($N = 1526$; Sánchez-Tójar et al., 2017).

Our final data set included 396 males (mean [range] life span = 2.4 [1–8] years) with complete information on lifetime fitness that used a single reproductive strategy ($N = 192$ extrapair males, 139 monogamous males, 65 floaters). Note that house sparrow breed from their first year, and so each year represents a potential breeding event for all sparrows in our study.

Statistical Analyses

We tested whether extrapair males had more lifetime offspring and recruits than monogamous males and floaters. We fitted two univariate generalized linear mixed-effect models with the same fixed and random effect structure using Bayesian Markov–Monte Carlo methods in the package 'MCMCglmm' version 2.29 in R version 4.0.4. (Hadfield, 2010; R Core Team, 2023). The respective response variables were the number of lifetime offspring (modelled with a zero-truncated Poisson error distribution) and recruits (Poisson error distribution). In both models, male lifetime mating strategy was added as a three-level categorical fixed effect (levels: extrapair, monogamous, floater) and male longevity as a continuous linear and nonlinear (squared) fixed effect. Longevity was included in the model to account for the increased reproductive opportunity over a lifetime, and we median-centred it to facilitate model convergence and interpretation (Korner-Nievergelt et al., 2015). Longevity positively affects lifetime reproductive success, even if there is senescence later in life (Hubbell & Johnson, 1987; Jensen et al., 2004). Cohort (male's birth year: 1999–2015) was fitted as the only random effect.

We interpreted statistical significance where 95% credible intervals did not overlap zero. We ran 3 million iterations with a burn-in period of 550 000 and a thinning of 3000 for the zero-truncated model and 4.5 million iterations with a burn-in period of 550 000 and a thinning of 4500 for the lifetime recruits model as the response variable. We assessed the convergence of Markov

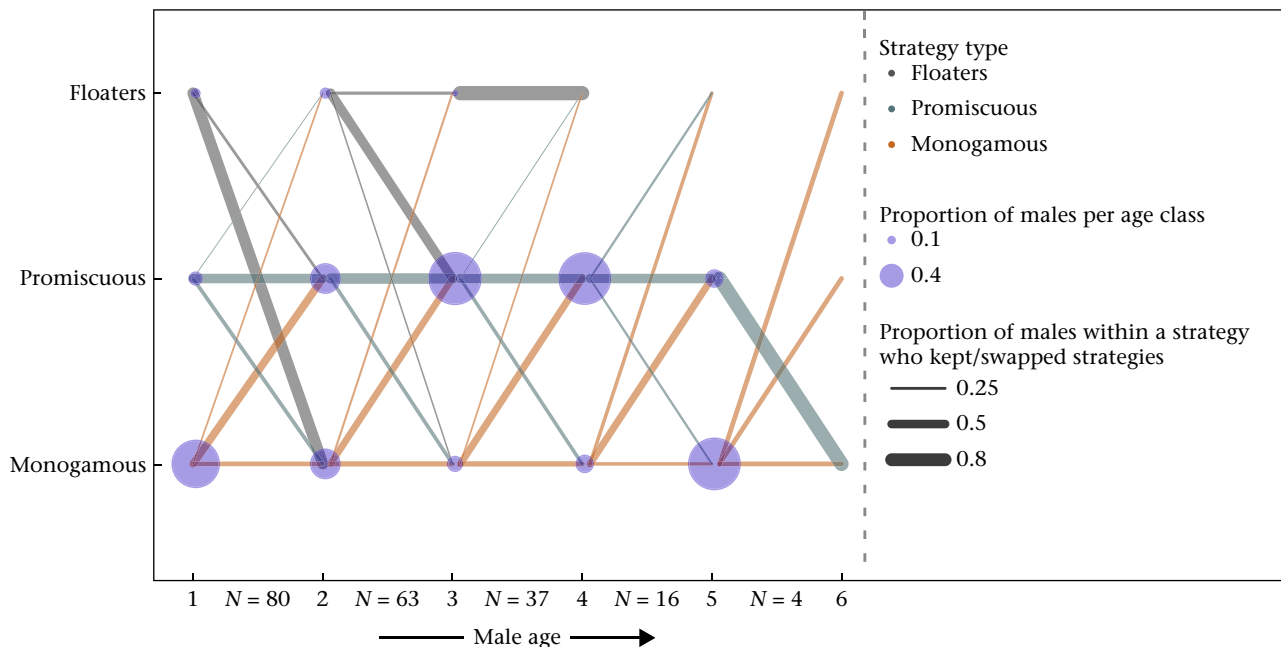


Figure 1. Male mating strategy over time. Most male birds in our study did not follow the same mating strategy over a lifetime, instead switching in response to their environmental circumstance. For example, floating as a mating strategy is most common in first-year birds and decreases as birds age, and floaters often switch to a monogamous mating strategy in their second or third year. To understand the fitness benefits associated with each strategy, in this study, we confined our analysis to birds that used a single mating strategy over their lifetime. The size of points corresponds to the proportion of males per mating strategy and the width to the proportion of males within a category that swapped or continued with a given strategy.

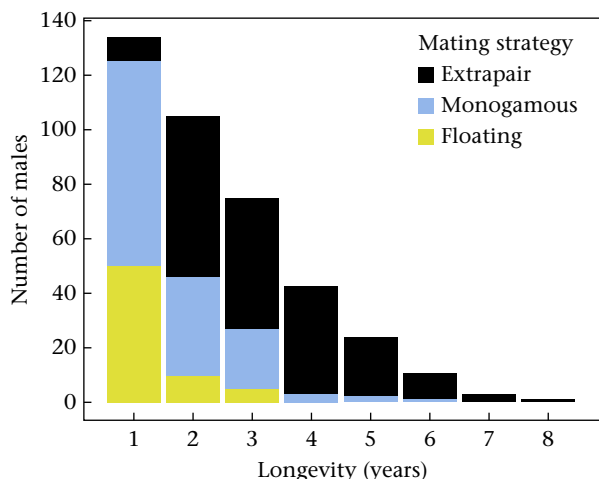


Figure 2. Number of males of a particular mating strategy per age (longevity) class. Extrapair paternity becomes the dominant male mating strategy in a population of house sparrows, some of which will continue to breed until 8 years of age. Floaters are predominantly first-year breeders, but some survive until 3 years of age. Note that floating is predominantly a strategy of young birds who fail to attract a social mate, whereas a great proportion of older males are more likely to engage in extrapair behaviours.

chains visually from trace plots. We used the Geweke and Heidelberg diagnostic with the package ‘coda’ (Plummer et al., 2006), which was also used to ensure low (< 0.1) autocorrelation of successive iterations.

RESULTS

Males included in our study bred for a maximum of 8 years, and on average, males that sired extrapair offspring were longer-lived (mean $\pm$ SD = 3.3 ± 1.4 years) than monogamous (1.7 ± 1.0 years) and floating (1.3 ± 0.6 years) males. Most males had extrapair offspring in their second year of breeding (Figs 1 and 2), supporting earlier results from this same population (Hsu et al., 2017). Males

included in our study produced a maximum of 14 lifetime recruits (2.0 ± 2.9 recruits), but 43.9% failed to recruit offspring at all.

Our model results suggest that the numbers of lifetime offspring and lifetime recruits were highest for extrapair males (Fig. 3, Table 1). After accounting for differences in longevity, extrapair males sired, on average, 29% more lifetime offspring and 45% more lifetime recruits than monogamous males, whereas floating males had the lowest lifetime fitness (Figs 2 and 3, Table 1). The variance explained by the fixed effects (R^2_{marginal} ; defined by Nakagawa & Schielzeth, 2013) was 80% and 72% for lifetime offspring and lifetime recruits, respectively (Table 1).

DISCUSSION

As predicted by sexual selection theory, we found a positive relationship between fitness and male extrapair paternity in a large longitudinal data set with exact estimates of lifetime fitness and male mating strategy. Even after accounting for longevity, males that sired extrapair offspring produced more lifetime recruits than monogamous and floating males. We previously showed in this population that the recruitment probability of extrapair offspring was slightly less than that of within-pair offspring (Hsu et al., 2014). Together with the presented results, this suggests that the benefits of extrapair mating while pair-bonded brings a quantitative, numerical fitness advantage for male sires.

Floater males are nonterritorial males (Moreno, 2016) that often remain undetected in wild populations (Sardell et al., 2010). Theory predicts (Rubenstein, 1980) and previous studies suggest (Kempnaers et al., 2001; Sergio et al., 2009; Smith & Arcese, 1989) a poorer reproductive performance of floating than pair-bonded males. Nevertheless, our study is the first to show that floaters that remain floaters, on average, have the lowest lifetime fitness. Floating thus might represent a best-of-a-bad-job strategy. As floaters are predominantly young males (Fig. 2), they compete with older territory holders to take over nestboxes (Sánchez-Tójar et al., 2017). Finally, it is unclear how floaters achieve extrapair paternity: whether through forced copulations, as they might be selected to harass females more than territory holders (Moulton et al., 2013), or

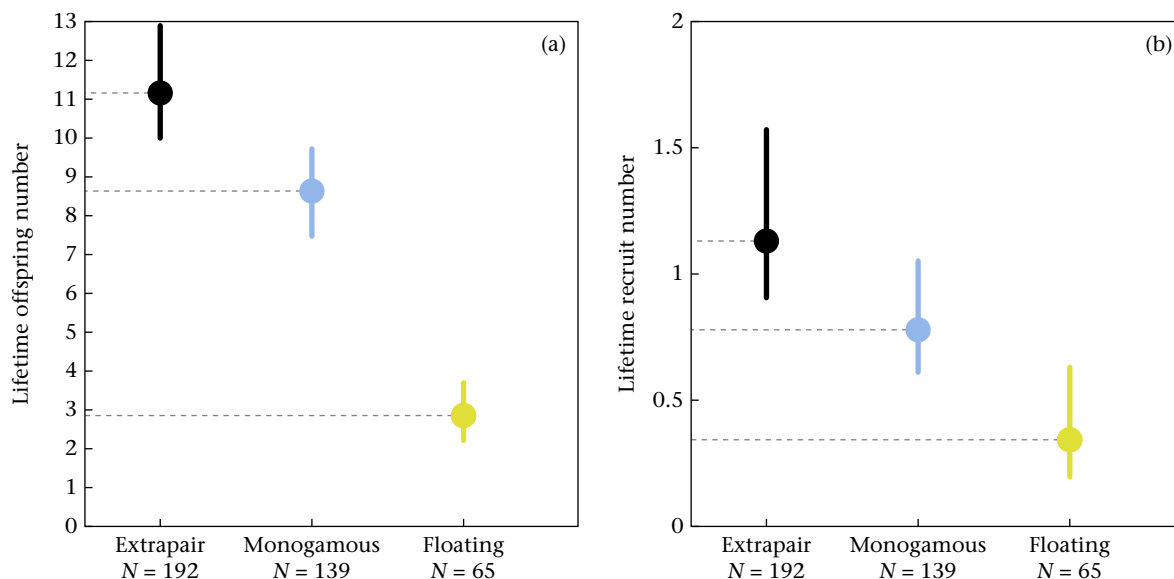


Figure 3. Lifetime fitness for each male mating strategy (extrapair males, monogamous males and floaters) in a wild population of house sparrows: (a) lifetime offspring number and (b) lifetime recruit number. Dots represent backtransformed posterior modes from a zero-truncated Poisson (a) and a Poisson (b) mixed-effects model, and vertical bars show the 95% credible intervals.

Table 1

The effect of extrapair paternity on lifetime fitness in a wild house sparrow population ($N = 396$ males)

	Estimate [lower and upper CrI]
Lifetime offspring number^a	
(Intercept, i.e. extrapair)	2.42 [2.31, 2.54]
Monogamous	−0.30 [−0.46, −0.15]
Floater	−1.35 [−1.63, −1.11]
Longevity	0.52 [0.47, 0.64]
Longevity ²	−0.05 [−0.08, −0.03]
Random effects	
Cohort	0 [0, 0.06]
Residual	0.21 [0.17, 0.27]
R^2_{marginal}	79.67 [75.48, 83.91]
Lifetime recruit number^b	
(Intercept, i.e. extrapair)	0.17 [−0.11, 0.42]
Monogamous	−0.40 [−0.71, −0.13]
Floater	−1.13 [−1.77, −0.65]
Longevity	0.67 [0.52, 0.87]
Longevity ²	−0.07 [−0.11, −0.02]
Random effects	
Cohort	0.10 [0, 0.24]
Residual	0.33 [0.21, 0.52]
R^2_{marginal}	72.02 [61.24, 82.22]

Results from two univariate mixed-effects models with longevity as a median-centred continuous linear and nonlinear (squared) fixed effect. Posterior modes and 95% credible intervals (CrI) are shown.

^a Zero-truncated Poisson error distribution.

^b Poisson error distribution.

through female choice. In captive sparrows, extrapair copulation attempts initiated by females are, on average, 17 times more likely to lead to copulation than extrapair copulation attempts started by males (Girndt et al., 2018). Females might thus be soliciting extrapair copulations from floaters for reasons that remain to be studied (but see Maldonado-Chaparro et al., 2018).

We also showed previously that the numbers of lifetime offspring and recruits increase until middle age (Alif et al., 2022; Hsu et al., 2017; Schroeder, Burke et al., 2012; Schroeder, Nakagawa et al., 2012) and decline after that. Although it is difficult to disentangle this effect from senescence and selective disappearance of individuals (Nussey et al., 2009), if, for instance, higher-quality individuals are long-lived, the initially positive relationship between lifetime fitness and longevity might not be explained by a mechanism such as the increased opportunity for mating or age-specific fecundity, but by the absence of lower-quality individuals in older age classes (Bouwhuis et al., 2009). Age-specific fecundity has been described in our population, both within and between males (Hsu et al., 2017; Schroeder, Burke et al., 2012; Schroeder, Nakagawa et al., 2012), with a typical within-individual increase in reproductive success followed by a decline, evidencing reproductive senescence. Our findings emphasize the need to account for nonlinear longevity effects when testing for differences between male mating strategies in lifetime fitness (Herényi et al., 2012).

To the best of our knowledge, our study is the first to test the hypothesis of a fitness benefit from extrapair paternity on a noncooperative breeder, using a data set that overcomes the usual limitations of studying wild populations. We confirmed that males that mix monogamous and extrapair breeding achieved higher lifetime fitness than ‘faithful’ and floating males, demonstrating the theoretical expectation that male extrapair paternity increases fitness.

Author Contributions

J. Dunning: Writing – Original draft, Writing – Review & editing, Data curation. **A. Girndt:** Conceptualization, Methodology, Software, Validation, Formal analysis, Data curation, Writing – Original draft, Writing – Review & editing, Visualization, Project administration. **A.**

Sánchez-Tójar: Conceptualization, Methodology, Software, Validation, Formal analysis, Data curation, Writing – Original draft, Writing – Review & editing, Visualization, Investigation. **I. Winney:** Writing – Review & editing, Investigation. **Y.-H. Hsu:** Writing – Review & editing, Investigation. **S. Nakagawa:** Writing – Review & editing, Investigation. **T. Burke:** Writing – Review & editing, Resources, Funding acquisition. **J. Schroeder:** Conceptualization, Methodology, Writing – Review & editing, Investigation, Project administration, Resources, Funding acquisition.

Data Availability

All data used in this manuscript are available via the Zenodo repository (<https://doi.org/10.5281/zenodo.8320269>).

Declaration of Interest

The authors declare that the research was conducted without any commercial or financial relationships that could be construed as a potential conflict of interest.

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