

# Divorce is linked with extra-pair paternity in a monogamous passerine

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May 24, 2023

## Abstract

The question of why socially monogamous females engage in extra-pair behaviour is long-standing in evolutionary biology. Recent theoretical work has moved away from the indirect-benefits hypothesis to explain female extra-pair behaviours, instead favouring suggestions that they are the result of pleiotropic effects. That is, a trait under strong positive selection in either or both sexes are genetically linked to another, often unrelated, trait. For example, where genes beneficial to female fecundity (contributing to within-pair solicitation of her social partner) are linked with extra-pair behaviour (soliciting copulations from extra-pair males). Here, we test two predictions from this hypothesis: We test the prediction that female divorce, measured from the number of social mates within a given year, is linked with (1) the number of extra-pair males and (2) the proportion of her offspring that are extra-pair. Our results suggest that females who frequently divorce social partners are more likely to produce extra-pair offspring than those who maintain social monogamy. However, by contrast, those females do not also have a higher proportion of extra-pair offspring. The number of broods initiated was also positively correlated with extra-pair males, probably through increased opportunity for extra-pair males to sire offspring over a longer breeding season. Our results provide an empirical example of a behavioural trait, beneficial to female fecundity, that is linked with extra-pair behaviour. These empirical results support the intrasexual pleiotropy hypothesis as a driver of female extra-pair behaviour.

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Here, we test two predictions from this hypothesis: We test the prediction that female divorce, measured from the number of social mates within a given year, is linked with (1) the number of extra-pair males and (2) the proportion of her offspring that are extra-pair. Our results suggest that females who frequently divorce social partners are more likely to produce extra-pair offspring than those who maintain social monogamy. However, by contrast, those females do not also have a higher proportion of extra-pair offspring. The number of broods initiated was also positively correlated with extra-pair males, probably through increased opportunity for extra-pair males to sire offspring over a longer breeding season. Our results provide an empirical example of a behavioural trait, beneficial to female fecundity, that is also linked with extra-pair behaviour. These empirical results support the intrasexual pleiotropy hypothesis as a driver of female extra-pair behaviour.

## Background

Since extra-pair paternity was first demonstrated using genetic finger-printing to allocate parentage to a house sparrow *Passer domesticus* (hereafter sparrow, Burke, and Bruford 1987), the question of why females in socially monogamous breeding systems engage in promiscuous behaviour still presents a challenge to evolutionary biologists (Griffith, Owens and Thuman 2022; Brouwer and Griffith 2019). Sexual selection dictates that females should choose a reproductive partner to maximize the fitness benefits he provides either directly to them, through parental care, or through a high-quality breeding territory (Møller 2000; Nakagawa et al. 2007; Brouwer and Griffith 2019). Other benefits can be incurred indirectly, by providing offspring with high-quality genes from the male. However extra-pair males, those from outside an established pair bond, can only provide indirect benefits to females. That is, extra-pair males may sire offspring without investing in costly parental care (Lebigre, Arcese, and Reid 2013; Raj Pant et al. 2022; Table 1), the good genes hypothesis predicts that they should signal a better (Hamilton and Zuk 1982; Birkhead 1995; Kirkpatrick and Barton 1997), or more compatible (Blomqvist et al. 2002; Ihle, Kempenaers, and Forstmeier 2015; but also see Griffith and Immler 2009) proposition than her social partner.

However, these predictions – that offspring produced by extra-pair matings, and extra-pair males themselves, are of superior quality than within-pair offspring, and within-pair males, respectively – are not well supported by empirical evidence (Hsu et al. 2015; Grinkov et al. 2022). This is highlighted by multiple meta-analyses on the topic, (Akçay and Roughgarden 2007; Arct, Drobniak, and Cichoń 2015), and subsequent discussion in the field (Drobniak, Arct, and Cichoń 2015; Griffith 2015; Nakagawa, Schroeder, and Burke 2015; Reid 2015; Brouwer and Griffith 2019). Further, several empirical studies have suggested costs rather than indirect benefits, to extra-pair offspring (Schmoll et al. 2009; Sardell et al. 2012; Hsu et al. 2014), and to promiscuous females (Forstmeier 2007; Matysiuková and Remeš 2013; Schroeder et al. 2016). Yet, females actively seek extra-pair copulations (Lifjeld and Robertson 1992; Forstmeier 2007; Girndt et al. 2018), and to date, the mechanism that drives these behaviours in females remains unresolved.

Several alternative hypotheses have sought to explain why female extra-pair behaviours persist. For example, insurance against the death- (Petrie and Kempenaers 1998) or infertility (Wetton and Parkin 1991; Sheldon 1994; Vedder 2022; Table 1) of a social partner may motivate females to seek extra-pair copulations, maintained through indirect selection (Kempenaers and Schlicht 2010). The social environment may be another mediator of extra-pair behaviour (Maldonado-Chaparro et al. 2018; Table 1), where individuals with high sociality - their propensity to associate with others – likely have more opportunity to choose partners from larger pools of potential mates. Accordingly, the number (Oh and Badyaev 2010; Dunning et al. 2023) and quality (Firth and Sheldon 2016; Beck, Farine, and Kempenaers 2021) of social associations were empirically shown to be linked to reproductive success, including extra-pair mate choice (Beck, Farine, and Kempenaers 2020). Empirical studies generally find that extra-pair partners are more likely to be close neighbours (Westneat and Sherman 1997; Schlicht, Valcu, and Kempenaers 2015; Mingju et al. 2017; Beck, Farine, and Kempenaers 2020; Beck, Valcu, and Kempenaers 2020), adding weight to the role of opportunism in extra-pair copulation (as empirically demonstrated by Fossøy, Johnsen, and Lifjeld 2006; and theoretically by Brommer et al. 2007; 2010).

Alternatively, the benefits of female extra-pair behaviour may be explained by non-adaptive hypotheses, for example through antagonistic pleiotropy (Halliday and Arnold 1987; Arnqvist and Kirkpatrick 2005), where extra-pair behaviours are controlled by linked sets of genes and selected for in one or both sexes. The intersexual (between-sex) antagonistic pleiotropy hypothesis (Halliday and Arnold 1987; Reid and Wolak 2018; Table 1) posits that female extra-pair behaviours are controlled by sets of genes present in both sexes and selected where the benefit to one sex outweighs the cost to the other (Halliday and Arnold 1987; Reid and Wolak 2018; Wang et al. 2020). For example, where the benefit of extra-pair copulations for males, outweighs the cost of the behaviour in females who inherit the genes from their fathers. Intersexual antagonistic pleiotropy is a common driver of behavioural traits (Poissant, Wilson, and Coltman 2010). Early empirical studies into non-adaptive explanations for female extra-pair behaviour suggested a role for intersexual pleiotropy (Forstmeier et al. 2011), but subsequent work from the same system later suggested

that intrasexual (or within-sex) pleiotropic effects may better explain female extra-pair behaviour (Wang et al. 2020).

Similarly, the intrasexual antagonistic pleiotropy hypothesis posits that a trait under selection is genetically linked to another trait in the same sex, where the benefits of one trait outweigh the cost of the other trait (Halliday and Arnold 1987; Forstmeier et al. 2014; Wang et al. 2020; Table 1). In this case, female extra-pair behaviour could be pleiotropically linked with female fecundity. This would be the case, for example, where female responsiveness to male courtship is pleiotropically linked with increased solicitation of copulations, enhancing fertilization success also in a within-pair context, and extra-pair behaviour may persist (suggested by Wang et al. 2020; Bolund, Schielzeth, and Forstmeier 2012)

Although quantitative genetic evidence for the antagonistic pleiotropy hypotheses is described from captive experiments (Forstmeier et al. 2011; Wang et al. 2020), evidence from wild systems is scarce. Reid et al. (2018) found no relationship between genes beneficial to male reproductive success and female extra-pair behaviour (an example of intersexual antagonistic pleiotropy). Further, quantitative approaches to understanding pleiotropic effects on female extra-pair behaviours have resulted in inconclusive effect sizes, for two reasons: First, the heritability of male and female promiscuity is closely related to fitness, masking any evidence of pleiotropy effect (Reid et al. 2011; Reid 2015; Dobson et al. 2023); And second, studies with genetic pedigrees from wild populations are scarce and have few generations, resulting in inconclusive effect sizes (Reid et al. 2011; Moiron, Charmantier, and Bouwhuis 2022; Dobson et al. 2023), even where prevalence of extra-pair behaviour is high. However, if pleiotropic effects are driving female extra-pair behaviour, then the expression of two linked behaviours should be empirical – if not genetically – detectable in wild systems.

Because extra-pair behaviours are common in passerine birds (Griffith, Owens, and Thuman 2002; Cockburn 2006; Smith 1988; Forstmeier 2007), they are an excellent model system for testing hypotheses relating to sexual selection and extra-pair behaviour. Here, we used a wild house sparrow population with a twenty-year genetic pedigree to test the prediction that extra-pair behaviours are correlated with social mate choice (suggested by Wang et al. 2020), an assumption of the intrasexual antagonistic pleiotropy hypothesis. Sparrows have high rates of extra-pair paternity (Hsu et al. 2014; Hsu et al. 2015; Girndt 2018) and are considered a model organism for studies on behaviour, life history, and sexual selection (Sánchez-Tójar, Schroeder, and Farine 2018; Hanson et al. 2020). In this study, we test that female propensity to switch social partners within a breeding year (hereafter, divorce), a trait with a potential genetic basis (Germain, Wolak, and Reid 2018) and a proxy for mate choice, is linked with extra-pair behaviour. First, we tested that divorce is linked with the number of extra-pair offspring, then with extra-pair males. We carried out our study in a closed house sparrow system, with a near-complete genetic pedigree spanning 20 years.

Table 1. Hypotheses referenced in this manuscript, see Brouwer and Griffith (2019) for a comprehensive review.

Referenced Hypotheses	Description
Good genes	Extra-pair partners that signal a greater genetic proposition to
Fertility insurance	Extra-pair copulations are sought to protect against infertility
Sociality as a mediator of variation in extra-pair behaviour	The social environment provides a mechanism for extra-pair b
Intersexual antagonistic pleiotropy	Non adaptive female extra-pair mating derived of alleles where
Intrasexual antagonistic pleiotropy	Female extra-pair behaviour is derived of alleles traits benefici

## Methods

### System

We systematically monitored a population of house sparrows *Passer domesticus* on Lundy Island in the Bristol Channel, UK (51.11N, 4.40W), since 2000 (see Nakagawa et al. 2007; Ockendon, Griffith, and Burke

2009; Schroeder et al. 2012; Dunning et al. 2023). The sparrows on Lundy breed in nesting boxes, arranged into neighbourhoods broadly defined by building infrastructure or linear features. Females are socially monogamous, but genetically promiscuous (Schroeder et al. 2016), and, on Lundy, most have 2-3 broods of 4-5 eggs per breeding season (Westneat et al. 2014).

We collected tissue samples from nestlings at the natal site and from recaptured birds post-fledging and used the DNA extracted from those to allocate paternity with the help of >22 microsatellite loci (Dawson et al. 2012). We then constructed a near-complete genetic pedigree (see Schroeder et al. 2015), spanning 19 years, 2000 - 2019. All sparrows are fitted with a unique sequence of three coloured leg rings and a British Trust for Ornithology (BTO) coded metal ring (for details see Simons et al. 2015), which allowed us to later identify social pairs at the nest box. Dispersal to and from Lundy Island is limited. This, and our systematic and thorough monitoring, allowed us to determine the exact age of birds in years, and to know when they died, either from the rings of birds found dead or, defined as when ringed birds were not observed for more than two years (see Simmons et al 2015).

To measure female divorce, we first excluded females that only had a single brood, and thus, no opportunity to divorce their social mate. We also excluded 17 females that divorced mates following the death of their social partner, where the death of a social male occurred during the female breeding year. We removed offspring whose parents (either social or genetic) were missing or uncertain. We defined a divorce event where a female paired socially with a new male to that of her previous social partner, between broods but within years. This resulted in 353 female breeding years. These female years represented 920 broods by 190 females, 205 social fathers and 309 genetic sires between 2004 and 2019.

We defined a chick as extra-pair where they survived to the point of sampling on day two and the confirmed social- differed from the genetic father (the sire) in our pedigree. We counted the number of extra-pair offspring and the number of both social and extra-pair fathers within females within years (female years).

## Models and permutations

To empirically test if females that divorce more often were also more likely to produce extra-pair offspring, as implied by intrasexual antagonistic pleiotropy theory, we ran two GLMM models with Bayesian Markov Monte-Carlo simulations, using MCMCglmm in R (Hadfield 2010; R Core team 2023):

**The association of divorce with extra-pair paternity** - To examine the link between female year divorce and extra-pair paternity, and because MCMCglmm cannot easily deal with proportion data, we ran a multinomial model with the number of extra-pair and social offspring per female year as response variables (see Hadfield 2010). We fitted female divorce, measured as the number of social partners within a female year, the number of broods she initiated, to control for increased opportunity for extra-pair offspring, and her age in years since hatching, to compensate for the effect of age on reproductive value (Hsu et al. 2017), as fixed effects. We also included Female ID and breeding year as random effects on the intercept to account for variation within those groups.

**The effect of divorce on extra-pair male engagement** - To examine the link between female divorce and engagement of extra-pair partners, we used a bivariate model structure, with the number of extra-pair partners within a given female year as the response variable. We again fitted female divorce, the number of broods initiated and her age in years since hatching as fixed effects. Female ID and breeding year were again modelled as random intercepts to account for variation within those groups. We first ran models using a Poisson distribution and logit link function, but those models failed to converge. Instead, we used a Gaussian distribution and link function and output estimates between the Poisson and Gaussian models were equivalent.

For all models, we used the default priors of the MCMCglmm package, and ran over 343,000 iterations, with a burn-in of 34,000 and a thinning interval of 200. We checked the posterior trace plots to ensure that autocorrelation was below 0.1 and that the effective sample sizes ranged between 1,000 and 2,000. The

fixed effects were considered statistically significant when the 95% credible interval (CI) of its posterior distribution did not span zero.

To test that our results were biologically meaningful, and not the outcome of random chance, we ran a series of permutations. We removed the link between female ID and reproductive traits by building random matrices between males and females to re-run our models. First, we simulated 1000 breeding events, by shuffling the number of offspring and extra-pair offspring between females while maintaining age structure. We then repeated these steps to simulate the number of extra-pair partners for each female. For each permutation, we ran an identical GLMM model to those described above. We dropped the bottom 2.5% of the lower credible intervals, and the top 2.5% of the upper credible intervals, to leave 95% of the 1000 credible intervals. We then extracted the minimum lower and maximum upper credible interval and the mean estimate. We interpreted significance – that is, our results were unlikely to have occurred by chance – where the observed posterior mean fell outside the span of the permuted credible intervals.

## Results

From 533 female breeding years, we identified 4963 offspring of known social and genetic parentage including 932 extra-pair offspring, 1.7 per female year (0 – 11, sd: 1.77), from 1403 broods (2.6 per female year, sd: 0.68). Females who engaged in extra-pair behaviour had a mean of 2.5 extra-pair offspring per female year (1 – 11, sd: 1.6). Within female breeding years, 120 females divorced their social partners on at least one occasion (110 once, and 10 twice, 1.24 per social partners female year: sd 0.47), where 413 remained faithful to a single social partner over multiple broods within a female year.

Neither the number of social fathers nor the number of broods was significantly linked with the proportion of extra-pair offspring that hatched within a female year. However, the number of social fathers and the number of broods per female year were positively linked to the number of extra-pair partners she chose within a breeding year. The log odds of having an extra-pair partner increased by 0.43, or 1.54 extra-pair partners, per social partner, and by 0.24, or 1.27 extra-pair partners per brood respectively (Figure 1). Female age was not linked to either the proportion of extra-pair offspring or the number of extra-pair sires.

Neither the number of broods nor the number of social fathers was associated with the number of extra-pair partners in our randomizations. The observed estimates all fell outside of the simulated confidence intervals (Figure 1). Observed posterior means fell outside of simulated 95% confidence intervals for both broods (0.27, -1.29 – 0.13) and social fathers (0.81, -0.00 – 1.86), implying that our results are not the result of chance. Our results support the hypothesis that females who divorce social partners regularly also engage more extra-pair males than those who maintain social monogamy.

## Hosted file

image1.emf available at <https://authorea.com/users/622021/articles/645321-divorce-is-linked-with-extra-pair-paternity-in-a-monogamous-passerine>

Figure 1. We interpreted significance in GLMM model outputs where 95% credible intervals did not span zero (red bars; otherwise black bars denote non-significant results), and points denote posterior mean. Our observed results (A1-2) suggest that female birds who divorce social partners regularly engage with more extra-pair males than those who maintain social monogamy. Likewise, the number of broods initiated also significantly predicted an increase in extra-pair males, without affecting the proportion of extra-pair offspring, presumably by virtue of opportunity (A2; red bars). Simulated breeding events (B1-2), where extra-pair males and extra-pair offspring were permuted between females in our system were not significant. Random effects are given in the shaded box (Dam and Cohort) for each model. Intercept and residuals for each model are not shown in the figure: A1, intercept -1.65 (-2.12 – -1.1), residuals 0.61 (-2.11 – 0.92); A2, intercept -1.65 (-2.11 – -1.8), residuals 0.53 (3.47 – 0.72); B1, intercept -0.5 (-8.78 – -0.14), residuals 0.81 (6.54 – 0.95); B2, intercept 1.26 (8.53 – 1.66), residuals 1.06 (9.37 – 1.2).

## Discussion

We empirically tested an assumption of the intrasexual antagonistic pleiotropy hypothesis - that extra-pair behaviour is linked to another trait beneficial to female fecundity, in this case, solicitation of social partners (Halliday and Arnold 1987; Wang et al. 2020), which we measured as the rate of divorce within years. Our results suggested that female divorce is linked with females engaging more extra-pair males. However, we found no effect of divorce on the proportion of extra-pair offspring. We also found a link between the number of broods initiated and female engagement of extra-pair males, which we consider a by-product of the opportunity for more extra-pair paternity over a longer breeding period.

Opportunity has been demonstrated to increase extra-pair behaviour in several systems (see Maldonado-Chaparro et al. 2018), including empirical studies suggesting that extra-pair copulations may be obligate, where they are facilitated by opportunity (Fossøy, Johnsen, and Lifjeld 2006). Liker, Freckleton, and Székely (2014) suggested that the sex ratio of the wider social environment also influences the divorce rate, driven by female-biased sex ratios and infidelity, by male-biased sex ratios (but also Culina, Hinde, and Sheldon 2015). However, opportunity cannot explain what drives extra-pair decision-making, instead, that must come from selective advantage to those who engage in extra-pair copulations. Our results support the suggestion by Wang et al. (2020) that female social solicitation behaviours are linked with extra-pair mate solicitation, and therefore, support intrasexual antagonistic pleiotropy as a mechanism for female extra-pair behaviour. However, we suggest that other, probably post-copulatory, processes control the proportion of extra-pair offspring born to females within a breeding year. Equivalent attention has also been given towards intersexual pleiotropic effects, where female extra-pair behaviour may be linked with a trait which benefits male reproductive success, these studies have found little support in captivity (Wang et al. 2020), or in wild populations (Zietsch et al. 2015; Reid and Wolak 2018). Where quantitative genetic studies have sought to demonstrate a heritable basis for male extra-pair behaviour, required for intersexual pleiotropy to drive female extra-pair behaviour, estimates are low (Reid et al. 2011; Reid and Wolak 2018; Grinkov et al. 2020). However, Dobson et al. (2023) found that the inclusion of social partner indirect genetic effects (those derived from the behaviour of another) improved model fit for the heritability of both male and female extra-pair behaviour, implying a role for the wider social environment in the plasticity of extra-pair behaviour.

We used divorce rate within a female breeding year, between multiple broods, as a measure of solicitation, but not between breeding years - more akin to a classic definition of divorce behaviour. Divorce is more broadly defined as where both partners are alive, and at least one of them has paired with a new social partner (Black and Hulme 1996; but also see Culina, Radersma, and Sheldon 2015). However, the motivations for female sparrows to divorce social partners between broods may be like those described elsewhere for divorce, which has been demonstrated to represent an adaptive strategy between sexes across monogamous birds (Choudhury 1995; Culina, Radersma, and Sheldon 2015; Mercier, Yoccoz, and Descamps 2021; Wilson, Nguyen, and Burley 2022). Previous works have also considered divorce and extra-pair behaviours as linked traits in the context of indirect benefits (Cezilly and Nager 1995; Choudhury 1995), that is, both provide females with a mechanism to improve the quality of their social partner, by divorcing or cuckolding, lesser quality males. However, empirical evidence for indirect benefits derived from extra-pair behaviours is scarce (Akçay and Roughgarden 2007; Arct, Drobnjak, and Cichoń 2015), and multi-paternity broods were not linked to the divorce rate Ramsay et al. (2000).

Although we consider our data to be near-complete, our phenotypic study is still subject to some bias (Hadfield 2008). For example, we sampled chicks for paternity at day two, (see Dunning et al. 2023), but this may still exclude an invisible fraction of those pairs, females (Kidd et al. 2015) or eggs (Yuta et al. 2018; Assersohn et al. 2021) who fail early. As a result, our study measures extra-pair paternity, and not extra-pair copulations, which could be more frequent than is reflected in paternity analysis (Fossøy, Johnsen, and Lifjeld 2006; Girndt 2018). Females that exhibit extra-pair behaviours may not always produce extra-pair offspring, but their within-pair offspring will inherit her genes, which may determine the extra-pair behaviour. Future work may support intrasexual pleiotropy as a mechanism for female extra-pair behaviour by either including measures of copulation attempts (rather than paternity) or, through further quantitative genetic methods.

We demonstrate that females who swap mates more frequently within breeding years engage more extra-

pair males, but do not have greater proportions of extra-pair offspring. Our study contributes an empirical example to the growing body of research that supports non-adaptive phenomena as mechanisms for why females engage in extra-pair behaviours.

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