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Short communication

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

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The question of why socially monogamous females engage in extra-pair behaviour is long-standing in evolutionary biology. Due to a lack of empirical support among passerine birds, recent work has moved away from the indirect-benefits hypothesis to explain extra-pair mating behaviour by females, instead favouring the hypothesis that this is the result of a pleiotropic effect. That is, a trait under strong positive selection in either or both sexes are genetically linked with another, potentially unrelated, trait. For example, genes beneficial to female fecundity (that promote within-pair solicitation of mating from a male partner) might also lead to extra-pair behaviour (by also promoting solicited copulations from extra-pair males). Here, we test two predictions from this hypothesis: We test the prediction that female divorce, measured as the number of social mates within a given year, is linked with 1) the number of extra-pair males engaged by the female and 2) the proportion of the female's offspring that are extra-pair. Our results show that females who divorce their social partner are more likely to produce extra-pair offspring than those who maintain social monogamy, supporting the pleiotropy hypothesis. However, those females did not also have a higher proportion of extra-pair offspring. The number of broods initiated was also positively correlated with the number of extra-pair males that sired a female's offspring, probably through increased opportunity for extra-pair males to sire offspring over a longer breeding season. Our results support the intrasexual pleiotropy hypothesis as a driver of female extra-pair behaviour.

Keywords: divorce, extra-pair paternity, genetic pedigree, GLMM, house sparrow

Background

Since extra-pair paternity was first demonstrated using genetic profiling to allocate parentage to a house sparrow *Passer domesticus* (hereafter sparrow/s, Burke and Bruford 1987), the question of why females in socially monogamous breeding systems engage in promiscuous behaviour has puzzled evolutionary biologists (Brouwer and Griffith 2019, Griffith et al. 2002). Sexual selection dictates that females should choose a reproductive

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partner to maximize the fitness benefits for her or her offspring. He can provide benefits either directly (Møller 2000, Mennerat et al. 2018, Brouwer and Griffith 2019) or indirectly to her via offspring with high-quality genes (Arnqvist and Kirkpatrick 2005, Brouwer and Griffith 2019).

Direct benefits to females may involve parental care, access to resources or defence against predation (Møller 2000, Nakagawa et al. 2007a,b, Kempenaers and Schlicht 2010, Mennerat et al. 2018, Brouwer and Griffith 2019, Krams et al. 2022). Likewise, female extra-pair paternity has been suggested to insure against death (Petrie and Kempenaers 1998), infertility (Wetton and Parkin 1991, Sheldon 1994, Santema et al. 2020, Vedder 2022, Table 1) or genetic incompatibility of her social partner (Hansson et al. 2004, Arct et al. 2015). Although such direct benefits will indeed provide a fitness advantage, the effect is likely weak and unlikely to fully explain the frequency of extra-pair paternity observed in the wild (Arnqvist and Kirkpatrick 2005, Charmantier and Sheldon 2006, Mennerat et al. 2018). Likewise, whether these benefits derive from extra-pair paternity or some other proximal behaviour also remains contentious (Nakagawa et al. 2015, Eliassen et al. 2022, Lifjeld and Slagsvold 2022).

More often, extra-pair males, those from outside an established pair bond, only have the potential to provide indirect benefits to females. That is, extra-pair males sire offspring without investing in costly parental care (Arnqvist and Kirkpatrick 2005, Lebigre et al. 2013, Raj Pant et al. 2022, Table 1). The good-genes hypothesis predicts that extra-pair males should therefore signal a better (Hamilton and Zuk 1982, Birkhead 1995, Kirkpatrick and Barton 1997), or more compatible (Blomqvist et al. 2002, Griffith and Immler 2009, Ihle et al. 2015), genetic proposition than the 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 in passerine birds, the most studied systems for this question (Charmantier and Sheldon 2006, Hsu et al. 2015, Grinkov et al. 2022). This is highlighted by multiple meta-analyses on the topic, (Akçay and Roughgarden 2007, Arct et al. 2015), and subsequent discussion in the field (Drobniak et al. 2015, Griffith 2015, Nakagawa et al. 2015, Reid 2015, Brouwer and Griffith 2019). Further, several empirical studies have suggested costs, rather than benefits, to extra-pair offspring (Schmoll et al. 2009, Sardell et al. 2012, Hsu et al. 2014), and to promiscuous females (Forstmeier 2007, Matysioková and Remeš 2013, Schroeder et al. 2016). Yet, despite clear costs, females actively seek extra-pair copulations (Lifjeld and Robertson 1992, Forstmeier 2007, Girndt et al. 2018), and the mechanism that drives these behaviours in females remains unresolved.

The social environment is increasingly recognized as an important mediator of extra-pair behaviour (Maldonado-Chaparro et al. 2018, Raj Pant et al. 2019, Dobson et al. 2023, 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. 2023a) and quality (Firth and Sheldon 2016, Beck et al. 2021) of social associations were shown to be linked to reproductive success, including extra-pair mate choice (Beck et al. 2020a). Extra-pair partners are more likely to be close neighbours, and extra-pair paternity increases as a function of population density (Westneat and Sherman 1997, Schlicht et al. 2015, Mingju et al. 2017, Mennerat et al. 2018, Beck et al. 2020a, b), adding weight to the role of opportunity in extra-pair copulation (as empirically demonstrated by Fossøy et al. 2006, and theoretically by Brommer et al. 2007, 2010).

Alternatively, female extra-pair behaviour may instead 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 for 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

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

Referenced hypotheses	Description	References
Good genes	Extra-pair partners that signal a greater genetic proposition than the social male is sought to provide indirect benefits to her offspring	Hamilton and Zuk (1982), Birkhead (1995)
Fertility insurance	Extra-pair copulations are sought to protect against infertility in her own social partner, with or without phenotype cues	Wetton and Parkin (1991), Sheldon (1994), Vedder (2022)
Sociality as a mediator of variation in extra-pair behaviour	The social environment provides a mechanism for extra-pair behaviour through increased mate-choice	Maldonado-Chaparro et al. (2018)
Intersexual antagonistic pleiotropy	Non-adaptive female extra-pair mating derived of alleles where the cost of extra-pair behaviour to females is small relative to the benefit to males	Halliday and Arnold (1987), Forstmeier et al. (2014), Wang et al. (2020)
Intrasexual antagonistic pleiotropy	Female extra-pair behaviour is a trait beneficial to female fecundity, for example solicitation of social partners (considered here)	Forstmeier et al. (2014), Wang et al. (2020)

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 et al. 2010). Early empirical studies into non-adaptive explanations for female extra-pair behaviour indeed 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), so the jury is still out.

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 (and subsequent mate-switching, i.e. divorce) 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 Bolund et al. 2012, Wang et al. 2020). Divorce in wild birds is defined as where both partners are alive, and at least one of them has paired with a new social partner (Black and Hulme 1996, Culina et al. 2015, Chen et al. 2023). Previous works have considered divorce and extra-pair behaviours to be linked traits in the context of indirect benefits (Cezilly and Nager 1995, Choudhury 1995, Culina and Brouwer 2022); that is, both provide females with a mechanism to overcome the issue of low quality of their social partner, by divorcing or cuckolding males of lesser quality.

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 and Wolak (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 often near zero, and closely related to fitness, potentially 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 et al. 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 empirically – if not genetically – detectable in wild systems.

Because extra-pair behaviours are common in passerine birds (Smith 1988, Griffith et al. 2002, Cockburn 2006, 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 20 year genetic pedigree to test the prediction that extra-pair behaviours are correlated with the solicitation of social mates (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 et al. 2018) and are considered a model organism for studies on behaviour, life history, and sexual selection (Sánchez-Tójar et al. 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 et al. 2018) and a proxy for mate choice, is linked with extra-pair behaviour. First, we tested if divorce is associated 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.

Material and 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 (Nakagawa et al. 2007a, b, Ockendon et al. 2009, Schroeder et al. 2012, Dunning et al. 2023a). The sparrows on Lundy breed in nesting boxes, arranged into neighbourhoods broadly defined by building infrastructure or linear features. Boxes are mostly internal (inside farm buildings), with a median distance of 7.8 m (SE = 0.52) between boxes within neighbourhoods. Sparrows are territorial and non-cooperative during the breeding period. Females are socially monogamous but genetically promiscuous (Schroeder et al. 2016), and, on Lundy, most have 2 to 3 broods of 4 to 5 eggs per breeding season (Westneat et al. 2014). There are no native nest predators on Lundy.

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 (Schroeder et al. 2015), spanning 19 years, 2000–2019. All sparrows were fitted with a unique sequence of three coloured leg rings and a British Trust for Ornithology (BTO) coded metal ring (Simons et al. 2015), which allowed us to later identify social pairs at the nests. Dispersal to and from Lundy Island is limited (Schroeder et al. 2015). 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 (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 switched mates following the death of their social partner, where the death of a social male occurred during the breeding season. We removed offspring whose parents (either social or genetic) were missing or uncertain. We defined a divorce event as when 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 when it survived to the point of sampling on day two, and the confirmed social father 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). Likewise, social fathers were defined as where they were the genetic sire of chicks that survived to day two.

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, www.r-project.org):

1) **The association of divorce with extra-pair paternity** – To examine the link between divorce within a female year and extra-pair paternity, we ran a multinomial model with the number of extra-pair and social offspring per female year as response variables (Hadfield 2010). We fitted female divorce, measured as the number of social partners within a female year, the number of broods the female initiated to control for the 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, Michálková et al. 2019, Schlicht and Kempenaers 2023), as fixed effects. We also included Female ID and breeding year as random effects on the intercept to account for variation within those groups.
2) **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 1000 and 2000. 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 (mean 1.7 per female year, range 0–11, SD 1.77), from 1403 broods (2.6 per female year, SD 0.68). Females that 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 partner female year, SD 0.47), while 413 engaged with 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 associated with the number of extra-pair partners that fathered some of the female's offspring within a breeding year. The log odds of having an extra-pair partner increased by 1.54 extra-pair partners, per social partner, and 1.27 extra-pair partners per brood, respectively (Fig. 1). Female age was not linked with 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 (Fig. 1). Observed posterior means fell outside of the 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 explained by chance. Our results support the hypothesis that females who divorce engage with more extra-pair males than those who display social monogamy.

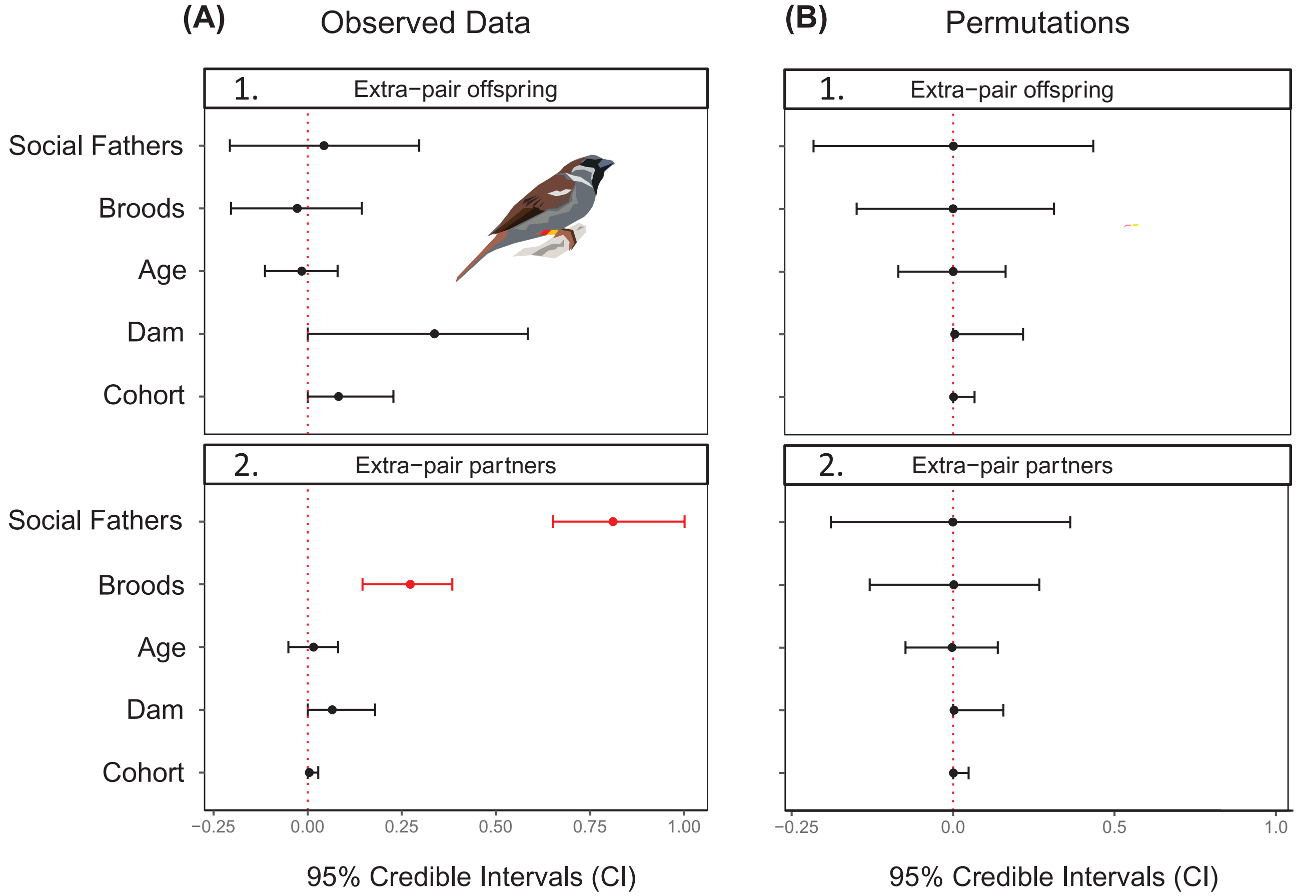

Figure 1. Females that divorce more often had more extra-pair partners than monogamous females. Our observed results (A1–2) suggest that female birds who divorced social partners engaged with more extra-pair males than those who maintained social monogamy. Likewise, the number of broods initiated also significantly (red bars) 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 insignificant (black). 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 to −1.1), residuals 0.61 (−2.11 to 0.92); A2, intercept −1.65 (−2.11 to −1.8), residuals 0.53 (3.47–0.72); B1, intercept −0.5 (−8.78 to 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 suggest 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 to be a by-product of the opportunity for extra-pair behaviours over an extended breeding period.

Our results support the suggestion by Wang et al. (2020) that female social solicitation behaviours are linked with extra-pair mate solicitation and, therefore, may support intrasexual antagonistic pleiotropy as a mechanism for female extra-pair behaviour. 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) suggested 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. The social environment is likely to influence the expression of extra-pair behaviours (Maldonado-Chaparro et al. 2018) and within-pair divorce rates (Liker et al. 2014, Culina et al. 2015) through increased access to potential extra-pair partners (Fossøy et al. 2006, Plaza et al. 2019).

Recent studies have suggested that females may benefit directly from extra-pair paternity through enhanced nest defence by extra-pair males (Mennerat et al. 2018, Eliassen et al. 2022, Krams et al. 2022, Lifjeld and Slagsvold 2022 for discussion). Such direct benefits may be difficult to untangle from neighbour effects (Maldonado-Chaparro et al. 2018, Mennerat et al. 2018, Beck et al. 2020a) or disturbance to activity cycles (Santema and Kempenaers 2023, Schlicht et al. 2023), both of which result in increased extra-pair paternity.

We used divorce rate within a female breeding year between multiple broods as a measure of solicitation, but not between breeding years. The motivations for female sparrows to divorce social partners between broods may be those described elsewhere for divorce, which has been demonstrated to represent an adaptive strategy between sexes across monogamous birds (Choudhury 1995, Culina et al. 2015, Mercier et al. 2021, Culina and Brouwer 2022, Wilson et al. 2022). Previous studies into the link between divorce and extra-pair behaviour are few and often conflicting (Ramsay et al. 2000), but a recent meta-analysis across species suggested that the rate of divorce is significantly linked with male, but not female, promiscuity (Chen et al. 2023). The male perspective on divorce and extra-pair paternity was beyond the scope of this study (Lebigre et al. 2013, Girndt et al. 2018, Raj Pant et al. 2022).

Our results also support the hypothesis that divorce and extra-pair mating behaviour are linked, possibly where weak pair bonds result in both behaviours (Cezilly and Nager 1995). However, more recent studies have failed to find a link (Botero and Rubenstein 2012, Culina and Brouwer 2022). The absence of an identified association may mean that different processes drive divorce and extra-pair paternity, or that one either of these might be non-adaptive (Culina and Brouwer 2022).

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, (Dunning et al. 2023a), 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) that failed early. As a result, our study measures extra-pair paternity, and not extra-pair copulations, which might be more frequent than is reflected in paternity analysis (Fossøy et al. 2006, Girndt et al. 2018). A female that exhibits extra-pair behaviours may not always produce extra-pair offspring, but her within-pair offspring will inherit her genes, which may determine their extra-pair behaviour. Future work to test for intrasexual pleiotropy as a mechanism for female extra-pair behaviour in an equivalent wild system could potentially include measures of copulation attempts (rather than paternity) or through further quantitative genetic methods (Forstmeier et al. 2014). Further studies should also consider how non-adaptive phenomena translate into lifetime reproductive success (Raj Pant et al. 2019).

We demonstrate that females who swap mates more frequently within breeding years engage more extra-pair males but do not produce a greater proportion of extra-pair offspring. Our study contributes an empirical example to the growing body of research that supports non-adaptive phenomena to explain females engaging in extra-pair behaviours.

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Author contributions

Jamie Dunning: Conceptualization (equal); Data curation (equal); Formal analysis (equal); Investigation (equal); Methodology (equal); Validation (equal); Visualization (equal); Writing – original draft (equal); Writing – review and editing (equal). **Terry Burke**: Funding acquisition (equal); Methodology (equal); Project administration (equal); Supervision (equal); Writing – review and editing (equal). **Julia Schroeder**: Conceptualization (equal); Data curation (equal); Investigation (equal); Methodology (equal); Project administration (equal); Supervision (equal); Writing – original draft (equal); Writing – review and editing (equal).

Transparent peer review

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Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.8pk0p2ntx (Dunning et al. 2023b).

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