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Brief Communication

Indirect genetic effects increase heritability estimates for male and female extra-pair reproduction

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Abstract

The question of why females engage in extra-pair behaviors is long-standing in evolutionary biology. One suggestion is that these behaviors are maintained through pleiotropic effects on male extra-pair behaviors (genes controlling extra-pair reproduction are shared between sexes, but only beneficial to one sex, in this case, males). However, for this to evolve extra-pair reproduction must be both heritable and positively genetically correlated between sexes. Previous studies have suggested low heritability with no evidence for between-sex genetic correlations in extra-pair reproduction. However, these have not considered indirect genetic effects (derived from the behavior of others, IGEs) from the social partner, the influence of the social partner's genotype on the phenotype of an individual, despite the potential of IGEs to uncover hidden heritable variation. Using data from a closed-house sparrow population with a genetic pedigree spanning two decades, we tested the influence of social partner IGEs on heritable variation and genetic correlation estimates of extra-pair reproduction. We found that the inclusion of IGEs resulted in larger heritable genetic variance for both male and female extra-pair heritability. While IGEs did not change between-sex genetic correlations, we found they reduced uncertainty in those estimates. Future studies should consider the effect of IGEs on the mechanisms of sex-specific extra-pair reproduction.

Keywords: quantitative genetics, indirect genetic effects, reproduction, house sparrow, genetic pedigree, extra-pair reproduction

Background

The question of why females engage in extra-pair behaviors has long puzzled evolutionary biologists (Brouwer & Griffith, 2019; Griffith et al., 2002). Extra-pair behaviors (hereafter extra-pair reproduction) occur outside of an established social pair bond, from copulation to realized paternity of extra-pair offspring, and are common in socially monogamous passerine birds (Cockburn, 2006; Griffith et al., 2002). Extra-pair reproduction between species has been linked to phylogenetic variation (Brouwer & Griffith, 2019), suggesting a genetic basis for the trait, but the mechanism of selection is unclear and may vary between sexes. The benefits of engaging in extra-pair behavior for the male are siring more offspring without investing in costly parental care (Lebigre et al., 2013; Raj Pant et al., 2022; Trivers, 1972)—but this is not the case for females, who can only replace within-pair offspring with extra-pair offspring, and risk associated costs (Albery et al., 2021; Dixon et al., 1994; Matysioková & Remeš, 2013; Poiani & Wilks, 2000; Schroeder et al., 2016; Trivers, 1972; Valera et al., 2003). Yet, females actively seek extra-pair copulation (Forstmeier, 2007; Girndt et al., 2018; Lifjeld & Robertson, 1992).

Adaptive hypotheses explain female participation in extra-pair behaviors with indirect benefits—genetic fitness benefits to her offspring. However, evidence for the indirect benefits hypotheses are sparse (Arct et al., 2015). In fact, empirical studies either fail to identify indirect benefits, or suggest costs, to extra-pair offspring (Akçay & Roughgarden, 2007; Grinkov et al., 2022; Hsu et al., 2014, 2015; Sardell et al., 2012; Schmoll et al., 2009) and to promiscuous females (Forstmeier, 2007; Matysioková & Remeš, 2013; Schroeder et al., 2016). An alternative, non-adaptive, hypothesis posits that variation in female extra-pair behaviors is maintained instead through intersexual pleiotropy (Forstmeier et al., 2014; Halliday & Arnold, 1987). Intersexual pleiotropy may drive female extra-pair behavior, where the trait is genetically linked to another trait under positive selection in males, for instance, male extra-pair reproduction (Halliday & Arnold, 1987; Reid & Wolak, 2018). However, empirically testing the intersexual pleiotropy hypothesis is challenging because any study must demonstrate that male extra-pair reproduction is beneficial, that extra-pair reproduction is heritable, and that it is positively genetically correlated between sexes (Forstmeier et al., 2014; Reid et al., 2011a).

Multiple studies have found support for the idea that male extra-pair behaviors contribute to male lifetime reproductive success, including research by Albrecht et al. (2009), Baldassarre and Webster (2013), Lebigre et al.

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(2013), Losdat et al. (2015), Webster et al. (2007), and Raj Pant et al. (2022). However, heritability estimates for these behaviors are often low or without robust estimation (Grinkov et al., 2020; Reid & Wolak, 2018; Reid et al., 2011a, 2011b). Additionally, so far, empirical studies have not found conclusive evidence for between-sex correlation in extra-pair behavior in either captive (Wang et al., 2020) or wild populations (Reid & Wolak, 2018; Zietsch et al., 2015). However, these studies did not consider indirect genetic effects (IGEs). IGEs refer to the variance explained by shared genetic variance of interacting conspecifics (Maldonado-Chaparro et al., 2018; see Table 1). If present, IGEs can strongly mediate trait expression and therefore have the potential to reveal "hidden" heritable variation (Bijma, 2010; Wolf et al., 1998). For example, female extra-pair reproduction may be influenced by genetic variation that determines the mate-guarding behavior of her social partner, which in-turn limits her access to extra-pair males (Maldonado-Chaparro et al., 2018).

Despite the potential of IGEs to contribute to heritable genetic variance, most quantitative genetic estimates for extra-pair behaviors only consider direct genetic effects (Table 1). Yet, extra-pair behavior is inherently social and relies on the interplay of up to four individuals—the focal individual, the social partner, and the extra-pair partners of both the focal individual and social partner, thus not including IGEs may underestimate the total genetic variance in traits (Kruuk & Wilson, 2018; Schroeder et al., 2019). Moreover, IGEs can facilitate evolution in the presence of positive genetic covariance between the focal individual and their partner, even when heritability is low (Bailey et al., 2018; Bijma, 2010; Schroeder et al., 2019).

Here, we tested for social partner IGEs and between-sex genetic correlation of extra-pair reproduction using a closed and intensively monitored wild island passerine population, with a genetic pedigree spanning two decades.

Methods

Study population

We have monitored the sedentary and closed population of house sparrow *Passer domesticus* (hereafter sparrow/s) breeding on Lundy Island in the Bristol Channel, UK (51°10′N, 4°40′W), systematically since 2000 (see Dunning et al., 2022; Ockendon et al., 2009; Schroeder et al., 2012a, b). All sparrows are marked with a unique sequence of three colored leg rings and a BTO metal ring to allow identification of social parents at nesting boxes (for details, see Nakagawa et al., 2007). Annually, nearly all present sparrows are identified by observation and capture, without bias (Simons et al., 2015). We collected DNA samples from nestlings at the natal site and from recaptured adults and used 22 microsatellite loci

Table 1. Quantitative genetic terms used in this study, their definitions and key references.

Term	Definition	Key References
Additive genetic variance (V_A)	The component of phenotypic variance in a trait, among individuals in a population, attributed to the additive effects of inherited alleles.	Falconer and MacKay (1996); Charmantier et al. (2014)
Direct genetic effects (DGE)	The effect of an individual's own genes on their own trait expression. For example, the black badge of the male house sparrow is the result of his own genes, with no outside influence.	Wolf et al. (1998); Bijma (2011)
Indirect genetic effects (IGE)	The effect of individual/s genes on the expression of another individual's trait, i.e., male mate guarding behaviour, a direct genetic effect of his own genotype, prevents a female from copulation with another male, an expression of her own phenotype. The male's genotype directly effects the expression of the female's phenotype.	Wolf et al. (1998); Bijma (2011)
Genetic correlations (r_g)	The magnitude and direction to which the expression of two traits are influenced by the same set of genes, ranging from (−1, genetic variation fully influences both traits in opposite directions) to (1, both traits are fully influenced in the same direction).	Charmantier et al. (2014)
Pleiotropic effects	Pleiotropy describes a single gene, or set of genes, that influence multiple unrelated traits, where r_g describes the magnitude and direction of correlation, pleiotropy describes a mechanism underlying the correlation between traits.	Halliday & Arnold (1987)
Heritability (h^2)	The proportion of phenotypic variance in a trait that is due to additive genetic variance from additive direct genetic effects only, ranging from (0, direct additive genetic variance accounts for no phenotypic variation in a trait) to (1, direct additive genetic variance fully determines phenotypic variation in a trait).	Wilson et al. (2010); Charmantier et al. (2014); Schroeder et al. (2019)
Total heritable variation (t^2)	The proportion of phenotypic variance in a trait that is due to genetic variation from direct and indirect genetic effects, and their covariance.	Bijma (2011); Schroeder et al. (2019)
Individual Permanent environment (PE)	Environmental effects on an individual's phenotype that are constant across (or common to) repeated measures on that individual. For example, sparrows with nests in noisy environments provisioned offspring less often than those in quieter breeding locations.	Kruuk and Hadfield (2007); Charmantier et al. (2014)
Social permanent environment (SE)	Environmental effects (see above; PE) on an individual's phenotype that are constant across (or common to) repeated measures on a conspecific (in this case, the social partner). For example, how much parental care a social partner provides to a brood may change the amount of parental care provided by the focal individual.	Maldonado-Chaparro et al. (2018)

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to allocate paternity (Dawson et al., 2012). Female house sparrows are socially monogamous, but genetically promiscuous (Schroeder et al., 2016), and, on Lundy, our sparrows instigate a mean of 2.3 (*SD* 1.04) broods and lay a mean of 9.1 (*SD* 4.9) eggs annually (Westneat et al., 2014). Previous studies have described extra-pair behavior but found no evidence for adaptive benefits to females of extra-pair behavior in this system (Hsu et al., 2014, 2015; Ockendon et al., 2009; Schroeder et al., 2016). Changing social partners is common, with 47% of individuals having more than one social partner across their lifetime (Schroeder et al., 2016).

We used these data to construct a genetic pedigree (Schroeder et al., 2015) spanning 20 years from 2000 to 2019 and comprised of 8,151 individuals. We identified extra-pair offspring where the genetic sire differed from the social partner in the pedigree. We defined an extra-pair reproduction event differently from the perspective of each social partner: a male extra-pair reproduction event was measured by the count of extra-pair offspring he sired in other nests while he maintained his own social brood elsewhere. We did this by defining the start and end date of each social brood and checking the paternity of offspring against the list of present males. For females, the number of extra-pair offspring she can raise is limited by her egg production. Thus, we measured a female extra-pair reproduction event as a binary trait (extra-pair offspring present in brood, 1, or absent, 0). We considered all eggs in her nest to be her own, as our pedigree shows no nest parasitism (egg-dumping) as a strategy in our house sparrow system.

To avoid pseudo-replication and to measure male and female extra-pair reproduction using different scales in our models, we considered the perspective of both social parents separately in our models. Because each individual may be involved in several broods over the course of their lifetime, the number of extra-pair samples exceeds the total number of unique individuals and initiated broods. Thus, each social brood was measured twice, once from the social female's perspective and once, separately from the social male's perspective.

Heritability and IGE models

We estimated within-sex heritability and between-sex genetic correlations of extra-pair reproduction using animal models. Animal models use a genetic pedigree within a mixed-effect model to differentiate between environmental and genetic influences on a phenotypic trait (Wilson et al., 2010). We ran a series of animal models using MCMCglmm (Hadfield, 2010) in R, v3.6.3 (R Core Team, 2023).

We used a series of univariate and bivariate models with different random effects to determine whether social partner IGEs detected genetic variance within-sex extra-pair reproduction. We then used the same approach to test for genetic correlations between male and female extra-pair behavior (see Tables 2 and 3 for model specifications). To improve confidence in our models, we repeated each using multiple sets of priors, which confirmed the results qualitatively (Supplementary Table S1). We modeled male extra-pair reproduction as a Poisson trait and female extra-pair reproduction as a threshold trait (i.e., presence, 1, or absence, 0, of extra-pair offspring within a brood). To reflect the increased likelihood of older males siring extra-pair offspring, we included age as a fixed effect across all models (Girndt et al., 2018). We did not include fine-scale environmental or social effects, which can potentially bias heritability estimates in closed systems (Germain et al., 2016; Grinkov et al., 2022).

In models measuring heritability, we included the focal individuals' identity twice as random effects. The first random effect was used to estimate the effect of the individual permanent environment and the second one was linked to a pedigree-based inverse relatedness matrix to estimate DGE (Table 2, Models 1.1 + 1.2). This separates environmental and genetic causes of variance in extra-pair reproduction (Kruuk & Hadfield, 2007). In models measuring total heritable variation, considering both DGE and IGE, we also included the identity of the social partner twice: first to estimate the social partner permanent environment and then to a generate a pedigree-based relatedness matrix linked to the partner, to estimate the IGE. In univariate models, we also modeled covariation between DGEs and IGEs, but we could not do this in bivariate models due to MCMCglmm package constraints (Table 2). We constrained the covariance to zero for all non-genetic effects in bivariate models because extra-pair reproduction as we defined them, cannot be expressed in the same individual from the male and female perspective (Table 2). Initial analysis included year as a random effect, but as it accounted for a little variation and did not change quantitative genetic estimates across multiple models. Therefore, it was removed from further analysis (Supplementary Table S2).

To estimate the additive genetic variance of non-Gaussian traits, we used an associated link function in the GLMM (de Villemereuil et al., 2016). We used natural log and probit link functions for male and female models, respectively, using the Poisson and threshold families in the MCMCglmm package (Hadfield, 2010). This means that the estimates are on "latent" scale, transformed by the link function, and no longer on the same scale of the observed data. Therefore, any variance estimates (and hence heritabilities and genetic correlation estimates) from the model will also be on the latent scale (de Villemereuil et al., 2016). Following de Villemereuil et al. (2018), it may be more appropriate to interpret heritability and genetic correlation estimates on the observed scale by back-transforming model outputs. However, due to the influence of fixed effects in estimating quantitative genetic parameters in non-Gaussian models, most studies only report the heritability of non-Gaussian traits on latent scales (latent scale quantitative genetic estimates). We used the R package QGglmm (de Villemereuil et al., 2016) to back-transform quantitative genetic variance estimates (and therefore heritability, IGEs, total heritable variation, and genetic correlations) on the observed scale (Supplementary Table S3). We included both latent and observed scale estimates to aid comparability (Supplementary Table S3). All models were deemed to have converged when autocorrelation was less than 0.1, trace and density plots were unimodal, and effective sample sizes for each effect were >1,000 (Hadfield, 2010). We considered heritability and variance estimates to be non-zero to where the lower credible interval did not span zero (≥0.001).

Results

Prevalence of extra-pair reproduction

We recorded 1,787 initiated broods with complete parental data, involving 776 individual house sparrows, 410 females and 366 males. The total number of offspring in the

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Table 2. Model specifications for extra-pair events in univariate models (1.1–4.2).

Model	Random terms	V_{PE}	V_{ADGE}	V_{AIGE}	V_{SE}	Cov (V_{ADGE}, V_{AIGE})	h^2_{obs} or t^2_{obs}	h^2_{lat} or t^2_{lat}
Males as focal individuals								
1.1	Male DGE + male PE	**0.675 (0.323–1.04)**	0.058 (<0.001–0.234)	-	-	-	0.004 (<0.001–0.016)	0.024 (<0.001–0.1)
2.1	Male DGE + male PE + female partner PE female DGE	0.363 (<0.001–0.71)	0.098 (<0.001–0.324)	-	**0.614 (0.243–0.983)**	-	0.006 (<0.001–0.02)	0.04 (<0.001–0.13)
3.1	Male DGE + male PE + female partner PE + female partner IGE	0.355 (<0.001–0.7)	0.102 (<0.001–0.344)	0.38 (<0.001–0.82)	0.275 (<0.001–0.702)	-	0.028 (<0.001–0.056)	**0.14 (0.016–0.29)**
4.1	cov(male DGE + female partner IGE) + male PE + female partner	0.284 (<0.001–0.67)	0.152 (<0.001–0.408)	0.434 (<0.001–0.84)	0.244 (<0.001 –0.638)	−0.149 (−0.423–0.044)	0.017 (<0.001–0.040)	**0.114 (0.001–0.28)**
Females as focal individuals								
1.2	Female DGE + female PE	**0.171 (0.065–0.28)**	0.024 (<0.001–0.082)	-	-	-	0.012 (<0.001–0.042)	0.02 (<0.001–0.07)
2.2	Female DGE + female PE + male partner PE	**0.15 (0.031–0.27)**	0.029 (<0.001–0.087)	-	0.053 (<0.001–0.133)	-	0.014 (<0.001–0.044)	0.023 (<0.001–0.07)
3.2	Female DGE + female PE + male partner PE + male partner IGE	**0.149 (0.032–0.27)**	0.032 (<0.001–0.094)	0.012 (<0.001–0.04)	0.048 (<0.001 – 0.123)	-	0.022 (<0.001–0.056)	0.035 (<0.001–0.09)
4.2	PE cov(female DGE + male partner IGE) + female PE + male partner PE	**0.149 (0.037–0.26)**	0.029 (<0.001–0.09)	0.012 (<0.001–0.04)	0.051 (<0.001–0.129)	−0.0017 (−0.025–0.019)	0.019 (<0.001–0.052)	0.029 (<0.001–0.08)

Note. Random effects parameters included direct genetic effects (DGE), individual permanent environment (PE), social partner permanent environment (SE) and social partner indirect genetic effects (IGE). cov() denotes models where covariation between male and female parameters was allowed to take on any value, otherwise, covariation between male and female parameters was fixed to 0. Individual permanent environment (V_{PE}), additive genetic variance due to direct genetic effects (V_{Adge}), additive genetic variance due to indirect genetic effects ($V_{Aige)}$, social partner permanent environment (V_{SE}), observed scale heritability (h^2_{obs}), observed scale heritability (h^2_{lat}), observed scale total heritable variation (t^2_{obs}), latent scale total heritable variation (t^2_{obs}), from the posterior means of extra-pair event models using prior 1. Cov() denotes where covariation between variances was measured. Heritability estimates (h^2) are derived from models 1 and 2, while total heritable variation estimates (t^2) are derived from models 3 and 4. Heritability, total heritable variation and variance component estimates where CIs were ≥0.001 are highlighted in bold. Residual variance, intercept and fixed effect estimates can be found in Supplementary Table S5. Fixed effect specifications are universal across all models.

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Table 3. Model specifications for bivariate covariance models (5–7).

Covariance models

Model	Random terms	Male V_{ADGE}	Female V_{ADGE}	Male V_{AIGE}	Female V_{AIGE}	COV (V_{ADGE})	COV (V_{AIGE})	Male h^2_{obs} or t^2_{obs}	Male h^2_{lat} or t^2_{lat}	Female h^2_{obs} or t^2_{obs}	Female h^2_{lat} or t^2_{lat}	r_{gobs}	r_{glat}
5	cov(male DGE + female DGE) + idh(male PE + female PE)	0.056 (<0.001–0.2)	0.024 (<0.001–0.084)	-	-	0.003 (–3.28e^{-02}–0.046)	-	0.003 (<0.001–0.011)	0.02 (<0.001–0.07)	0.007 (<0.001–0.024)	0.021 (<0.001–0.074)	0.09 (–0.84–0.94)	0.089 (–0.84–0.943)
6	cov(male DGE + female DGE) + idh(male PE + female PE) + idh(female partner PE + male partner PE)	0.096 (<0.001–0.332)	0.027 (<0.028–0.093)	-	-	0.003 (–4.23e^{-02}–0.057)	-	0.006 (<0.001–0.02)	0.039 (<0.001–0.125)	0.008 (<0.001–0.026)	0.024 (<0.001–0.073)	0.045 (–0.81–0.97)	0.045 (–0.81–0.97)
7	cov(male DGE + female DGE) + idh(male PE + female PE) + idh(female partner PE + male partner PE) + cov(female partner IGE + male partner IGE)	0.102 (<0.001–0.336)	0.029 (<0.001–0.098)	0.374 (<0.001–0.797)	0.012 (<0.001–0.04)	0.0001 (–5.5e^{-02} –0.05)	–0.01 (–8.92e^{-02}–0.042)	**0.032 (0.004–0.064)**	**0.138 (0.02–0.24)**	0.021 (<0.001–0.057)	0.032 (<0.001–0.085)	0.066 (–0.67–0.55)	0.066 (–0.68–0.55)

Note. Random effects parameters included direct genetic effects (DGE), individual permanent environment (PE), social partner permanent environment (SE) and social partner indirect genetic effects (IGE). cov() denotes models where covariation between male and female parameters was allowed to take on any value, otherwise, covariation between male and female parameters was fixed to 0. Individual permanent environment (V_{PE}), additive genetic variance due to direct genetic effects (V_{ADGE}), additive genetic variance due to indirect genetic effects (V_{AIGE}), social partner permanent environment (V_{SE}), observed scale heritability (h^2_{obs}), observed scale heritability (h^2_{lat}), observed scale total heritable variation (t^2_{obs}), latent scale total heritable variation (t^2_{obs}), observed scale genetic correlation (r_{gphen}) and latent scale genetic correlations (r_{glat}) from the posterior means of extra-pair event models using prior 1. Cov() denotes where covariation between variances was measured. Heritability estimates (h^2) are derived from models 5 and 6 while total heritable variation estimates (t^2) are derived from model 7. Heritability, total heritable variation and variance component estimates where CIs were ≥0.001 are highlighted in bold. Residual variance, intercept and fixed effect estimates can be found in Supplementary Table S5. Fixed effect specifications are universal across all models.

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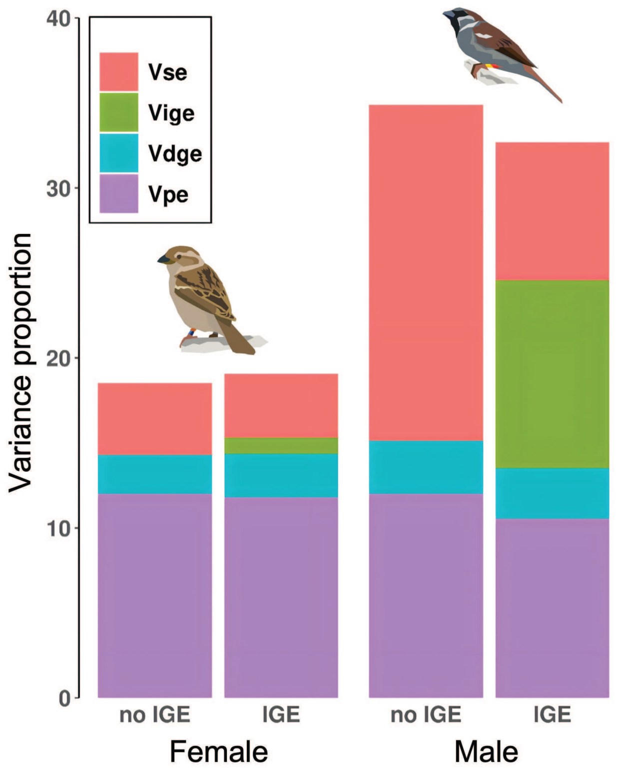

Figure 1. The proportion of the variance explained in male and female extra-pair reproduction by different variance components with and without the inclusion of social partner indirect genetic effects. Variance components including social partner permanent environment variance (Vse), additive genetic variance estimated from direct genetic effects (Vdge), additive genetic variance estimated from indirect genetic effects (Vige), and permanent environment variance (Vpe). In bars without IGEs variance proportions are estimated from model 2.1 for females and 2.2 for males. In bars with IGEs variance proportions are calculated from models 3.1 for females and 3.2 for males. All variances shown were estimated on latent scales. The proportion of variance due to fixed effects is not shown here.

pedigree was 6,774, with 18.95% (1,283) being sired by a male different from their social father. From these data, we identified 3,233 extra-pair reproduction samples for our models from the female (1,721) and the social male (1,512) perspectives.

Heritability and IGE models

Model outputs did not differ qualitatively between models using different priors (Tables 2 and 3; Supplementary Tables S4–S6). Direct additive genetic variance for male and male and female extra-pair reproduction were close to zero (Table 2). However, the addition of social partner IGEs increased the total genetic variance available for males and females by a factor of 4.91 and 1.52, respectively (Figure 1; Tables 2 and 3).

Male and female extra-pair reproduction were mostly explained by IGEs and permanent environment, respectively (Table 2), accounting for 12% and 11% of total phenotypic variance (Figure 1; Table 2). All models detected high levels of residual variation for both male and female extra-pair reproduction (Supplementary Table S5).

Male and female heritability

Both latent and observed scale heritability estimates were close to zero for male and female extra-pair reproduction (Table 2). Social Partner IGEs slightly increased female total heritable variation estimates, but increased male total heritable variation substantially; however, CIs were still close to zero for both males and females (Table 2). Covariation between direct and indirect genetic effects for male and female extra-pair behaviors were both negative but overlapped 0, reducing total heritable variation estimates (Table 3).

Genetic correlation estimates between male and female extra-pair reproduction

Genetic correlations between male and female extra-pair reproduction estimated from direct genetic effects were positive, but CIs greatly overlapped zero (Table 3). Both models including the addition of social IGEs produced close to zero correlation, and CIs still overlapped zero but reduced the uncertainty in those estimates (Table 3). Quantitative genetic parameters did not differ between different priors, nor between univariate and bivariate models (Table 3, Supplementary Tables S4–S6).

Discussion

Our results suggest that additive genetic variance and heritability for extra-pair reproduction are increased with the inclusion of social partner IGEs in both sexes, but particularly in males, where total genetic variation reached 14%. However, the addition of IGEs also increased uncertainty in variance. Although that uncertainty may be linked to increased model complexity, simulation studies suggest (Bijma, 2013) that 793 breeding pairs are sufficient to consider our estimates reliable. Our results support those of other systems, which find marginal heritability in extra-pair reproduction with high residual variation, implying that male and female extra-pair reproduction may be inherently flexible traits (Beck et al., 2020; Forstmeier et al., 2011, Grinkov et al., 2020; Reid et al., 2011a, 2011b; Wang et al., 2020; Zietsch et al., 2015).

Extra-pair reproduction may be driven by genes that control copulation and solicitation (Dixon et al., 1994; Matysioková & Remeš, 2013; Schroeder et al., 2016) and by the behavior of neighbors (Beck et al., 2020, 2021). However, despite extra-pair copulations likely commonly occurring (Fossøy et al., 2006), not all copulations result in extra-pair offspring, due to mate guarding (Forstmeier et al., 2011) and post-copulatory processes (Girndt et al., 2019; Knief et al., 2017). These processes are difficult to account for in wild populations (Beck et al., 2020), and may contribute to unexplained variation in both male and female reproduction, consequently resulting in smaller additive genetic variance and heritability estimates for extra-pair reproduction (Beck et al., 2020; Forstmeier et al., 2014). This has been demonstrated in captive zebra finches *Taeniopygia* sp., where heritability of copulation behaviors is substantial (Forstmeier et al., 2011; Wang et al., 2020), but equivalent data is extremely difficult to collect in the wild (Beck et al., 2020). Also, the numbers of extra-pair copulations may not predict the numbers of extra-pair offspring produced (Girndt et al., 2018), confounding the issue further. Despite this, because genes are only passed on to the next generation through the recruitment of extra-pair offspring, extra-pair behavior measurements in the wild have evolutionary relevance when compared with captive systems that may miss population scale processes. Such processes, like assortative mating, may skew heritability estimates for both extra-pair copulations and successful reproduction (Reid & Wolak, 2018; Wang et al., 2020).

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Between-sex genetic correlations are notoriously difficult to estimate in wild populations due to the requirement of large sample sizes (Lynch, 1999; Bonduriansky & Chenoweth, 2009), resulting in uncertainty in existing estimates (this study; Forstmeier et al., 2011; Reid & Wolak, 2018). This is likely due to the small genetic variances estimated for both male and female extra-pair reproduction (Travers et al., 2016). Estimating between-sex genetic correlations between direct measures of male and female extra-pair copulation behavior may yield more precise estimates (Forstmeier et al., 2014). The inclusion of social IGE effects in male and female extra-pair copulation behavior measurements may reduce uncertainty even further. However, a high degree of uncertainty may also possibly hide existing weak positive or negative genetic correlations between female and male extra-pair reproduction (Reid & Wolak, 2018). Future work could consider simulations to aid in answering these questions (Reid & Wolak, 2018), while in field studies, sample sizes increase with subsequent generations.

Past selection on male reproductive success may also have depleted additive genetic variation in male extra-pair reproduction, and in females through positive genetic correlations with males; resulting in low heritability estimates in both male and female extra-pair reproduction and high uncertainty in genetic correlation estimates. In this case, although past correlations between male and female extra-pair reproduction might have existed in this population, we are no longer able to detect them. However, female extra-pair reproduction may not be maintained by positive genetic correlations with male extra-pair reproduction even if positive between-sex genetic correlations previously existed, as partaking in extra-pair reproduction may not necessarily increase lifetime reproductive success for males. For example, in pursuit of extra-pair copulations males may reduce mate guarding, with a gain in extra-pair offspring resulting in fewer within-pair offspring and no overall change to lifetime reproductive success (Harts & Kokko, 2013; Møller & Birkhead, 1993; Møller & Ninni, 1998; Reid & Wolak, 2018). This combined with low extra-pair offspring fitness (Hsu et al., 2015) could result in decreased male lifetime reproductive success. It is also possible that female extra-pair reproduction persists through additional pleiotropic effects that benefit female fecundity (Forstmeier et al., 2014). Positive genetic correlations between female solicitation behavior and female fecundity have been described in captive populations (Wang et al., 2020), but yet, empirical evidence from wild systems is lacking.

Our study explored the genetic basis and role of the social partner on male and female extra-pair reproduction, to better understand how such behaviors are maintained in socially monogamous populations. We found no support for the notion that female extra-pair reproduction are maintained in socially monogamous populations through antagonistic intersexual pleiotropy. However, we suggest that social partner IGEs can uncover hidden genetic variation, especially for males. Social partner IGEs contributed substantially more to total male extra-pair heritability, accounting for more total additive genetic variance than male direct genetic effects and explained the largest proportion of phenotypic variation. We demonstrate the importance of IGE inclusion in quantitative models exploring aspects of animal behavior. Future studies into why female extra-pair reproduction persist in socially monogamous populations should consider the intrasexual antagonistic pleiotropy hypothesis and, where sample size allows, should include social partner IGEs when estimating heritabilities.

Supplementary material

Supplementary material is available online at *Evolution*

Author contributions

S.D., J.D., and J.S. developed research direction. S.D., J.D., and H.Y.J.C. worked on methods and interpretation of results. S.D. and J.D. prepared manuscript. All authors contributed to data collection and writing and editing of this manuscript.

Data availability

A copy of the data and code used in this project can be found at https://github.com/Sazz01/CMEECourseWork/tree/master/research_project.

Conflict of interest: The authors declare no conflicts of interest.

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