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Extrapair fertilizations vary with female traits and pair composition, besides male attractiveness, in barn swallows

Alessandra Costanzo [a, *], Roberto Ambrosini [b], Manuela Caprioli [a], Emanuele Gatti [c], Marco Parolini [a], Andrea Romano [a], Diego Rubolini [a], Luca Gianfranceschi [c], Nicola Saino [a]

[a] *Department of Environmental Science and Policy, University of Milan, Milan, Italy*
[b] *Department of Earth and Environmental Sciences (DISAT), University of Milano Bicocca, Milan, Italy*
[c] *Department of Biosciences, University of Milan, Milan, Italy*

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Reproductive promiscuity, whereby females are fertilized by extrapair mates, is common. The frequency of extrapair fertilizations (EPFs) depends on at least three sources of variation. First, females may differ in their proneness to being fertilized by extrapair males. Second, males may differ in traits that affect realized promiscuity of females. Third, EPF decisions depend on the combined effects of the identity of social mates. Here, we relied on extensive genetic parentage analysis of the offspring of a socially monogamous bird, the barn swallow, *Hirundo rustica*, to assess which of the above sources of variation predict the occurrence of EPFs. When we controlled for pair composition and social mate attractiveness, EPFs covaried with morphological and coloration traits of feathers in females. As expected, females mated with highly ornamented, long-tailed males had fewer EPFs. The composition of the breeding pair also accounted for variation in EPFs, implying that the ability of individual males to secure genetic parentage varies between female mates. These results show that females differ in promiscuity, and phenotypic traits of females that are visible to males are associated with promiscuity, potentially serving as cues to prospecting males. Hence, contrary to common interpretations of the negative relationship between male sexual attractiveness and female promiscuity, it can be speculated that larger genetic parentage by highly ornamented males results from their ability to secure the less promiscuous mates rather than from females being less promiscuous when mated to them. Moreover, our study shows that EPFs also depend on the composition of the social pair, as expected if a component of female promiscuity decisions depends on genetic or behavioural compatibility with the social male mate. Our study emphasizes that female promiscuity and its phenotypic correlates, and composition of the social pair, deserve closer attention in studies of sexual selection mediated by EPFs.

Reproductive promiscuity is the rule, rather than the exception, in many plant and animal taxa. Even in animals with strong (monogamous or polygamous) sociosexual bonds between the sexes, a batch of ova from a single female may be fertilized both by her social and by extrapair males (Griffith, Owens, & Thuman, 2002; Petrie & Kempenaers, 1998; Westneat & Stewart, 2003). Reciprocally, a single male may fertilize ova from multiple females, including extrapair ones, during a single breeding episode (i.e. season; Griffith et al., 2002; Petrie & Kempenaers, 1998).

Promiscuity is adaptive for males, if the advantages of enhanced individual reproductive output via extrapair fertilizations (EPFs) are not overwhelmed by any costs of paternity loss of the males' own social progeny or by the costs associated with extrapair mating behaviour (e.g. search costs; infection by horizontally transmitted parasites; Birkhead & Møller, 1992). Variation in the frequency of EPFs and in paternity (i.e. the proportion of social offspring that are also biological offspring of a focal male) is often found to be nonrandom with respect to male phenotypic and genetic traits, depending on the expression of male sexual ornaments (Jennions & Petrie, 1997; Wong & Candolin, 2005), position in the social dominance hierarchy (Qvarnström & Forsgren, 1998; Smith, 1988) or timing of arrival at the breeding sites (Griffith et al., 2002; Stutchbury, 1998). Such variation has consequences for sexual selection as well as for population genetic variability ultimately because asymmetric competition for genetic parentage among males can affect the variance in realized reproductive success (Clutton-Brock, 1988; Partridge, 1989).

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* Correspondence: A. Costanzo, Department of Environmental Science and Policy, University of Milan, Via Celoria 26, I-20133 Milan, Italy.
E-mail address: alessandra.costanzo@unimi.it (A. Costanzo).

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A number of adaptive evolutionary explanations of female promiscuity have been proposed. These hypotheses posit that females acquire either direct benefits (Birkhead & Møller, 1992; Nakamura, 1998; Sheldon, 1994) or indirect genetic benefits for their progeny, if the extrapair male is of superior genetic quality than the social mate (Jennions & Petrie, 2000; Møller & Ninni, 1998; Yasui, 1998). An alternative view is that females choose as extrapair mates those that carry 'compatible' genes (Colegrave, Kotiaho, & Tomkins, 2002; Mays, Albrecht, Liu, & Hill, 2008; Tregenza & Wedell, 2000) or show behavioural compatibility (Ihle, Kempenaers, & Forstmeier, 2015; Patrick, Chapman, Dugdale, Quinn, & Sheldon, 2012). For example, females may be expected to choose males that are genetically dissimilar to them because this will provide fitness benefits in terms of offspring heterozygosity at genes where heterozygosity enhances fitness (Griffith & Immler, 2009; Griffith et al., 2002; for a review, see Jennions & Petrie, 2000), like the MHC genes (Juola & Dearborn, 2012). EPFs may therefore be a tool to circumvent the social constraints on optimal choice of social mates that are either of superior genetic quality or carry compatible genes to those of the choosy female. If the female's decision to be promiscuous depends on 'absolute' quality of the social mate, all females should be less promiscuous when mated to a male displaying reliable phenotypic signals of superior quality, such as large sexual ornaments (Griffith et al., 2002; Petrie & Kempenaers, 1998). If, on the other hand, this decision depends on genetic compatibility, independent of sexual ornamentation of their mate, females should differ in fidelity to different males and, reciprocally, a given male should experience different promiscuity by different female mates.

However, many studies have failed to identify any obvious net advantage to females arising from reproductive promiscuity (Arnqvist & Kirkpatrick, 2005; Griffith, 2007). This has led to speculation that female promiscuity can also arise as a consequence of genetic constraints on female sexual behaviour (Forstmeier, Nakagawa, Griffith, & Kempenaers, 2014). Such constraints may operate at the between-sexes level, with genes that promote adaptive sexual promiscuity in male offspring also having positive pleiotropic effects on promiscuity in daughters (Forstmeier, Martin, Bolund, Schielzeth, & Kempenaers, 2011), or at the within-sex level, with females that are genetically more responsive to courtship by their social mate being also more responsive to courtship by extrapair males (Patrick et al., 2012).

The hypotheses on the evolution of female promiscuity rest on the implicit assumption that females can differ in promiscuity (Forstmeier, 2007), that is, that there are females that are more prone to engage in extrapair copulations/fertilizations than others, and such individual variation is the target of selection driven by the benefits and costs of extrapair copulations/fertilizations and of the genetic constraints on female mating behaviour (Forstmeier et al., 2014). However, the evidence that females differ in realized promiscuity is typically confounded by the effects of the (largely undocumented) variation in female proneness to engage in EPFs with social effects such as variation in mate quality, which are both expected to affect the frequency of EPFs (e.g. Dyrcz et al., 2002). One approach to test whether individual females differ in promiscuity is to analyse the covariation between realized female promiscuity and female phenotypic traits while controlling for social effects such as those of the identity and of the ornamental traits of their male social mates that may affect availability of females for EPFs.

Variation in female promiscuity, in turn, is likely to have a major impact on several evolutionary processes. First, it can affect the outcome of male–male competition for genetic parentage by affecting paternity and the access of males to EPFs, and the consequent sexual selection processes (Birkhead, 2000). Second, particularly in species with relatively large paternal investment in reproduction, males may prefer females with low promiscuity as social mates because of reduced risks of incurring the fitness costs of loss of paternity in their social broods (Sheldon & Ellegren, 1998). Third, reliable signals of female promiscuity may evolve in species in which females actively solicit extrapair copulations, as females that reliably signal high promiscuity will have easier access to preferred extrapair male mates (Bouwman & Komdeur, 2005; Whittingham & Dunn, 2010). These signals, in addition, may be the target of adaptive choice by males of females with low promiscuity as social mates. Finally, at the population level, variation in female promiscuity will be a major determinant of population parameters that depend on individual variation in realized reproductive success. Variation in female promiscuity can thus be expected to have pervasive effects on sexual selection and population genetic processes. Yet, the extent of variation in female promiscuity and the traits of females that covary with it are only very sparsely known.

Some studies have hinted at little consistency in female 'fidelity' across breeding episodes (e.g. Forstmeier, 2007; Weatherhead, 1999). These studies, however, did not control for potentially confounding social effects such as the identity and the ornamentation of the social mate or the composition of the breeding pair, and therefore do not allow inferences on the propensity of females to engage in EPFs. In a study of coal tits, *Parus ater*, for example, females were not consistent in their level of promiscuity across breeding episodes, except when mates remained the same, suggesting that promiscuity depended on the combined effects of female and male identity (Dietrich, Schmoll, Winkel, Epplen, & Lubjuhn, 2004). In a manipulative study of blue tits, *Cyanistes caeruleus* (Jong et al., 2017), females that were treated with testosterone were less promiscuous than controls. Because testosterone levels may differ between females, this study provides a mechanistic explanation for individual level consistency in promiscuity of females (Jong et al., 2017). In the pied flycatcher, *Ficedula hypoleuca*, females with longer wings had a smaller proportion of extrapair offspring in their brood, when the effects of age and male coloration were controlled for, providing evidence for an association between promiscuity and wing morphology independent of confounding effects (Moreno et al., 2015). Interestingly, in a study of the aquatic warbler, *Acrocephalus paludicola*, the opposite pattern was found, with females with longer wings being more promiscuous (Dyrcz et al., 2002). In the same study, females with relatively short bills were also found to be more promiscuous. In a study of great tits, *Parus major*, EPFs were found not to be related to exploratory behaviour of females, suggesting that variation in female promiscuity does not depend on genetic linkage with other, potentially related behavioural traits (Patrick et al., 2012). Female promiscuity has also been shown to vary with age (Røskaft, 1983; Stutchbury et al., 1997), although the proximate causes in terms of social effects (e.g. age-dependent variation in mate quality), ontogenetic variation in female behavioural traits related to mating (e.g. ability to escape/resist forced copulation attempts) or viability selection mediated, for example, by horizontal parasite transmission remain unclear.

In the present study we capitalized on extensive genetic parentage analysis of a population of the socially monogamous barn swallow, *Hirundo rustica*, with moderate frequency (ca. 15% of the nestlings; 29% of the broods) of EPFs (Costanzo et al., 2017; see Results) and where a moderate percentage (ca. 30%, see Results) of individuals change mate between breeding episodes/breeding seasons, to address the following questions.

First, do phenotypic traits of females exist that are correlated with their promiscuity? Evidence for such an association while controlling statistically for the identity and sexual ornamentation of the male mates would lend support to the hypothesis that females differ in