

NEWS AND VIEWS

PERSPECTIVE

Piecing together female extra-pair mate choice: females really do prefer more ornamented males

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Evolutionary biologists have long been fascinated by extravagant male traits that abound across the animal kingdom and yet convey no apparent benefits to survival. From isopods to elephants, from armaments to ornaments, researchers have spent decades studying male–male competition and female mate choice in an effort to understand the significance of these secondary sexual characteristics. Among socially monogamous species, a frequently proposed explanation for the existence of male ornaments is that they are indicators of male genetic quality subject to female extra-pair mate choice. However, despite over two decades of extensive research into extra-pair paternity (EPP), the evidence that females actually choose more ornamented extra-pair sires is surprisingly scant. Consequently, whether EPP and female choice have contributed to the evolution of male ornaments in socially monogamous species, and what fitness benefits (if any) they signal to females, remains unclear. Progress in this field has been hampered by the challenge of dissociating clear female choice for ornamentation from confounding factors. In this issue of *Molecular Ecology*, Whittingham & Dunn (2016) use an experimental approach in a bird species with very high rates of EPP to tease apart these correlative effects. In doing so, they demonstrate clearly that male ornamentation is subject to female extra-pair mate choice. Their findings further suggest that EPP can be adaptive for females, and represent an important step forward in validating the role of EPP as an evolutionary driver of ornamental elaboration in socially monogamous species.

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Extra-pair paternity occurs when females mate with males outside the social pair-bond and produce clutches of mixed paternity. Before research into EPP became mainstream, sexual selection was considered to be relatively weak in socially monogamous species. However, we now know that extra-pair mating can significantly increase variance in male reproductive success. Nowhere is this more obvious than in birds, where EPP is commonplace and where many species exhibit elaborated coloration or ornamentation. In socially monogamous species, EPP is now purported to be a principle driver of male ornamentation. This view has, to some degree, been validated by comparative work finding positive correlations between the rate of EPP and level of sexual plumage dichromatism between species (Owens & Hartley 1998).

Consequently, in species where males have extravagant plumage, females are generally expected to demonstrate extra-pair mating preferences for more ornamented males. Because extra-pair males usually provide only sperm for females, male ornaments are hypothesized to signal indirect (good genes) benefits for offspring. Such intuitively appealing theoretical predictions and corroborative interspecific evidence endorses a rather tidy framework of sexual selection. It is therefore surprising that after decades of research, support for good genes benefits remains equivocal (Hsu *et al.* 2015) and few studies have demonstrated that EPP creates selection pressures on male traits.

That is not to say that significant progress has not been made. For example, positive correlations between male ornamentation and EPP success have been found in yellowhammers, *Emberiza citronella* (Sundberg & Dixon 1996), yellow warblers (Fig. 1a), *Setophaga petechia* (Yezerinac & Weatherhead 1997), collared flycatchers, *Ficedula albicollis* (Sheldon & Ellegren 1999), and scarlet rosefinches, *Carpodacus erythrinus* (Albrecht *et al.* 2009). Recently, Wells *et al.* (2015) demonstrated that in the tui, *Prosthemadera novaezealandiae*, another bird species with a very high rate of EPP, males with large throat feather ornaments (Fig. 1b) gained both greater within-pair and extra-pair paternity. The authors suggested that this creates selection pressures that have led to sexual size dimorphism in the ornament. Nevertheless, there are many other species with elaborate plumage where no such correlations are found (reviewed in Hsu *et al.* 2015).

Because the above studies are all correlational, however, the relationship between EPP success and ornamentation cannot easily be dissociated from many potential confounds. Male age is arguably the most common confounding factor because in many species older males are more elaborated (Hsu *et al.* 2015). Furthermore, it is sometimes argued that extra-pair mating is purely a male reproductive strategy (Arnqvist & Kirkpatrick 2005) and that

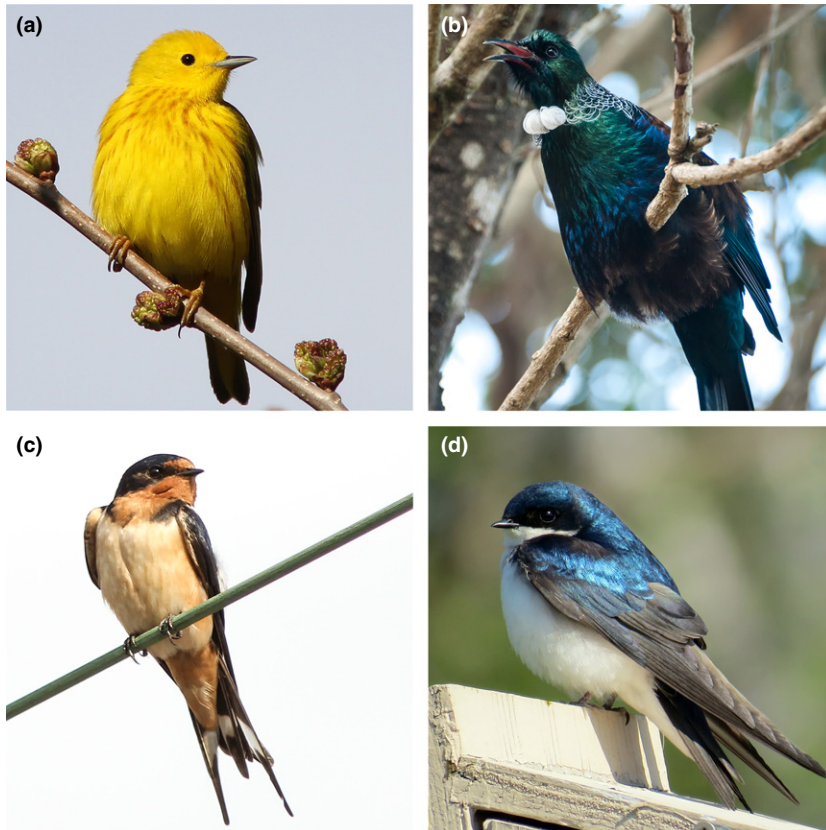


Fig. 1 Correlations between extra-pair paternity (EPP) success and male plumage traits have been found in (a) the amount of red breast streaking of yellow warblers and (b) the size of the white throat feather plumes of the tui. In (c) barn swallows, rufous ventral plumage colouration has been experimentally demonstrated to influence within-pair paternity. In this issue of *Molecular Ecology*, Whittingham & Dunn (2016) demonstrate experimentally that the iridescent blue dorsal plumage colouration of (d) tree swallows strongly determines EPP success. Credits: (a, c) David D. Beadle; (b) Sarah J. Wells; (d) Peter O. Dunn.

females are coerced into multiple mating by older, more dominant males (Westneat & Stewart 2003). Consequently, experimental studies are necessary to ascertain whether the paternity successes of more ornamented males are a direct result of female choice for the ornament. One of the few studies to achieve this is a study of within-pair paternity in barn swallows, *Hirundo rustica* (Fig. 1c). By experimentally manipulating male plumage coloration before and after consecutive breeding attempts, and thereby controlling for the same social mate and nest site, Safran *et al.* (2005) showed that females facultatively adjust paternity according to perceived male quality. While this study provides insight into the potential for EPP to drive selection on male ornamentation, the evolutionary significance of female multiple mating remains unclear because no experimental study has definitively identified the male phenotypic traits subject to female extra-pair mating preferences.

It is for this reason that the Whittingham & Dunn (2016) study is significant. The tree swallow (Fig. 1d), *Tachycineta bicolor*, is a socially monogamous passerine with iridescent blue-green dorsal plumage possessed by both sexes. Previous work has shown that in males, this plumage is associated with EPP success (Bitton *et al.* 2007). However, because plumage and paternity are also related to age and condition, Whittingham & Dunn (2016) conducted an experiment to identify whether female choice specifically targets ornamentation. Using an ink marker, they experimentally dulled the iridescent plumage of male tree swallows and found that dulled males had lower EPP

success, and therefore lower total reproductive success, than sham control and untreated males. To exclude the possibility that paternity success was driven by experienced older males coercing females into extra-pair mating, the authors randomly chose males for their experimental treatment, which controlled for age and other variables. Finally, they confirmed their results under natural conditions because among untreated males, dull males again sired fewer extra-pair young than bright males, and extra-pair males had significantly brighter plumage than the within-pair males they cuckolded. As a consequence, they show that the dorsal plumage in male tree swallows is under direct female extra-pair mate choice.

Three aspects of the Whittingham & Dunn (2016) study render their conclusions particularly robust. First, their study was conducted on a wild, naturally breeding population, and the experimental manipulation applied to male plumage is within the natural range of coloration for the species. These factors ensure that effect sizes generated by the study are realistic and meaningful to the species. Second, the study was conducted on a species with one of the highest rates of EPP, where the selection pressures and effect sizes on male ornamentation created by female extra-pair mate choice should be detectable. Third, the ability to identify extra-pair males and draw pairwise phenotypic comparisons with their within-pair counterparts provide a particularly strong case for direct female preference.

Whittingham & Dunn (2016) provide important evidence of female extra-pair mate choice for an ornamental trait

independent of age. Nevertheless, their findings do not preclude that any benefits received from ornamented males are attributable to age. For example, female preference genes could be in linkage disequilibrium with genes controlling age-related fitness benefits. The authors offer a potential framework through which this could occur. Because older male tree swallows are known to provide greater quantities of more motile sperm, they suggest that sperm quality is signalled by the condition-dependent plumage. The authors thus invoke the old, but frequently overlooked, fertility insurance hypothesis (Sheldon 1994) that could help reconcile why the good genes benefits argued to be signalled by male ornaments remain elusive; females could instead gain direct fertility benefits from extra-pair mating. Indeed, a recent comparative study that revived this hypothesis found a positive correlation between rates of EPP and hatching success (Reding 2015).

However, genetic linkage to a phenotypic trait is not a requirement of the fertility hypothesis, and the results of Whittingham & Dunn (2016) also bear resemblance to the 'good-genes-as-heterozygosity' hypothesis (Brown 1997). This hypothesis predicts correlations between the expression of sexually selected traits and male heterozygosity that provides fitness benefits to females in the form of enhanced offspring viability (e.g. Marshall *et al.* 2003). Older males are still predicted to gain EPP because, if viability is positively related to heterozygosity, then older males should be more heterozygous on average than younger males (Weatherhead *et al.* 1999). Under the good-genes-as-heterozygosity hypothesis, females stand to gain direct as well as indirect benefits if enhanced offspring viability manifests as increased fertility or hatching success. These two hypotheses highlight some interesting avenues for future research into potential direct benefits associated with extra-pair mating.

While the study of Whittingham & Dunn (2016) represents an important piece of the EPP puzzle, it also incites further questions. For example, if female choice creates selection pressures on male ornamentation, why are female tree swallows also ornamented? Ornamentation is likely to be particularly costly for females if it has evolved in response to genetically correlated sexual selection on males, as opposed to direct selection on female competition for mates or resources (Amundsen 2000). Intriguingly, tree swallows exhibit atypical female-biased delayed plumage maturation (DPM), where first-year breeding females exhibit a considerably duller brown plumage. DPM is commonly associated with costly sexually selected traits and in tree swallows is argued to reduce competition among young breeding females (Coady & Dawson 2013). However, the presence of female-biased DPM hints at an important function to ornamentation in older females. Thus, despite the clear indication of female preference for more ornamented extra-pair males, there is obviously more to the story.

Whittingham & Dunn's (2016) well-designed study has resolved some definitive support of a long-standing hypothesis: females really do prefer highly ornamented

extra-pair partners. In tree swallows, females control extra-pair copulations and thus the hypothesis that females are coerced into multiple mating by males can be refuted. However, it remains to be determined whether extra-pair mating is generally adaptive for females, as female mating behaviours can arise through intersexual genetic constraints resulting from selection in males (Forstmeier *et al.* 2014). Yet, Whittingham & Dunn's (2016) evidence of female preference for a phenotypic trait associated with male quality lends weight to the adaptive alternative.

Deep insight into the benefits of extra-pair mating to females can only result from rigorous experimental or cross-fostering studies that control for the influence of maternal effects on offspring fitness. Moreover, strategies that can test direct and indirect benefits simultaneously will likely provide the most powerful approach. For example, the direct benefits fertility hypothesis could be experimentally tested by inseminating females with a mix of sperm from males of different phenotypic quality (Sheldon 1994; see also Thuman & Griffith 2005 for a robust nonexperimental treatment of sperm competition). Cross-fostering of the resulting offspring and examining their performance and lifetime reproductive success could then identify potential indirect benefits. Until such studies are achieved, behavioural ecologists can nevertheless sigh a breath of relief, in the knowledge that Whittingham & Dunn (2016) have shown that we have not spent the past few decades entirely chasing our tail feathers.

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