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► To cite this version:

Tim Schmoll. A review and perspective on context-dependent genetic effects of extra-pair mating in birds. *Journal für Ornithologie = Journal of Ornithology*, 2011, 152 (S1), pp.265-277. 10.1007/s10336-011-0683-4 . hal-00685386

HAL Id: hal-00685386

<https://hal.science/hal-00685386>

Submitted on 5 Apr 2012

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A review and perspective on context-dependent genetic effects of extra-pair mating in birds

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Abstract

The evolutionary origin and the maintenance of extra-pair mating in birds has been a major field of study in the last decades, but no consensus has been reached on the adaptive significance of this behaviour for female birds. The genetic benefit hypothesis proposes that extra-pair sires provide alleles of superior quality and/or better compatibility compared to the social mate, resulting in offspring of higher reproductive value. One frequently adopted approach to test this idea compares the performance of maternal half-siblings in broods with multiple paternity. However, results from such comparisons are inconsistent. Here I discuss the idea that the magnitude of genetic fitness benefits from extra-pair mating depends on the environmental context. Context-dependent genetic effects in maternal half-sibling comparisons have been demonstrated for only five passerine bird species up to date. In none of the studies were the crucial environmental conditions experimentally manipulated and the potentially confounding effects of differential maternal investment in relation to paternity were mostly not accounted for either. A number of high-quality data sets on fitness consequences of extra-pair mating behaviour are available that could be (re-) analysed for context-dependence given relevant gradients of the environment have been recorded and their use is well justified *a priori*. Such relevant variation may include, for example, the time of breeding in temperate regions, hatching order, but also offspring sex. Primarily, however, experimental approaches are required that systematically and gradually vary fitness-relevant environmental gradients like food availability or parasite abundance and analyse the resulting differential fitness effects while controlling for differential investment. Context-dependence of genetic effects of extra-pair mating behaviour may offer an opportunity for reconciling conflicting results from different extra-pair paternity studies within and across species. More generally, it could allow better understanding under which environmental conditions selection may act to maintain a female mating bias towards extra-pair males with potentially far-reaching implications for the ecology and evolution of mating preferences and the maintenance of genetic variation in (sexually) selected traits.

Keywords

compatible genes; context-dependence; differential investment; extra-pair paternity; genotype-by-environment interaction; good genes; fitness consequences; half-sibling comparison; multiple mating.

Introduction

Extra-pair paternity (EPP) arises when female birds engage in extra-pair copulations (EPC) with males other than their social mates, frequently resulting in broods with multiple paternity which contain offspring sired by the social male (within-pair offspring, WPO) and offspring sired by extra-pair males (extra-pair offspring, EPO). A large and solid body of evidence has impressively demonstrated that EPP is the rule rather than the exception in birds (especially in passerines), and a number of synthetic contributions have reviewed this field with its various ramifications over the last two decades (e.g. Westneat et al. 1990; Birkhead and Møller 1992; Petrie and Kempenaers 1998; Griffith et al. 2002; Westneat and Stewart 2003; Akçay and Roughgarden 2007).

As EPP is so widespread and so common and because it must be considered a powerful source of pre- as well as postcopulatory sexual selection, no comprehensive understanding of avian mating systems and sexual selection in birds seems possible without understanding the evolutionary causes and consequences of this phenomenon. However, despite the very substantial research effort in the field, there is still no consensus on a number of fundamental questions related to this topic. For example, there is sustained debate about which sex is actually in control of EPC behaviour and, particularly, about the adaptive significance of extra-pair mating behaviour for female birds (e.g. Griffith et al. 2002; Westneat and Stewart 2003; Arnqvist and Kirkpatrick 2005; Griffith 2007; Akçay and Roughgarden 2007; Griffith and Immler 2009). A number of different hypotheses have been put forward to explain why female birds mate extra-pair, which are discussed in more detail in the reviews mentioned above. In this contribution I will focus on the idea that has gained most attention and stimulated the most intense and most controversial debate in the past, i.e. that genetic benefits from a mating bias towards extra-pair sires select for extra-pair mating behaviour in females (for a more general review and discussion of genetic benefit models of mate choice see e.g. Jennions and Petrie 2000; Mays and Hill 2004; Neff and Pitcher 2005).

After briefly introducing the genetic benefit hypothesis of extra-pair mating and the advantages and potential problems of using maternal half-sibling comparisons to test it, I will outline the idea that the magnitude of genetic benefits of extra-pair matings may depend on

environmental context and illustrate potential consequences for the evolution of female mating preferences and the maintenance of genetic variation for traits under selection. Then I will briefly summarise and review the main results of the few empirical studies that have demonstrated context-dependent genetic effects of extra-pair matings and suggest potential directions for future research in this field. In line with other recent conceptual contributions (e.g. Greenfield and Rodriguez 2004; Bussière et al. 2008; Ingleby et al. 2010), this paper aims at promoting an approach that puts work on sexual selection more explicitly into the ecological context within which it operates.

Genetic benefit hypothesis of extra-pair mating – good and/or compatible alleles

The principal idea behind the genetic benefits hypothesis is that, by engaging in extra-pair matings, females express a mating preference that is otherwise constrained, for example because social monogamy precludes many females from mating with the few top genetic quality males in a population or because the best social and the best genetic mate for any individual female are not identical. This hypothesis therefore assumes that female birds have a substantial degree of control over extra-pair fertilizations through either pre-copulatory extra-pair mate choice and/or cryptic postcopulatory mechanisms that bias paternity in favour of (particular) extra-pair sires. In the following, I will subsume both these possibilities under the term "mating preference" (for extra-pair males), which does therefore not necessarily imply classic precopulatory mate choice. A further assumption of the genetic benefit hypothesis is that extra-pair mating behaviour is costly for females and needs to be balanced by some sort of fitness benefit. This benefit may lie in the higher viability or fecundity and/or sexual attractiveness of offspring sired through EPCs with males that are of higher genetic quality or of better genetic compatibility compared to the respective social mate. The proposed genetic benefits may therefore be assumed to be additive genetic (acquisition of "good alleles") or represent non-additive effects presupposing an interaction of maternal and paternal genotype (acquisition of "compatible alleles" sensu Kempenaers 2007, i.e. broadly defined as alleles that increase fitness contingent on the genetic make-up of the choosing individual). Thus, a mating preference for mates with compatible alleles may, for example, include biasing paternity to maximise offspring heterozygosity, minimise the risk of close inbreeding, or optimise immunogenetic complementarity. Both types of benefits are not mutually exclusive but could also operate in concert.

Revealing paternal genetic effects on offspring traits by maternal half-sibling comparisons

The most straightforward test of the genetic benefit hypothesis of extra-pair mating is a comparison of the performance of maternal half-siblings from multiply sired broods (Sheldon et al. 1997). Here, potentially confounding, non-genetic effects of a common environment of sire and offspring as well as maternal effects on offspring fitness-related traits are controlled for (but see paragraph on differential maternal investment below). Maternal half-siblings share, by definition, on average half of their maternally inherited nuclear genes and experience the same early environment, including, for example, the same parenting skills of the respective social parents or exposure to the same parasite load in the shared nest. Therefore, any systematic differences in phenotypic traits between the two maternal half-siblings can only be attributed to the differential paternal genetic contribution (differential paternity hereafter) of the respective genetic sires. A consistently superior performance of EPO compared to their WPO maternal half-siblings is thus considered strong evidence in favour of the genetic benefit hypothesis (Sheldon et al. 1997; Griffith et al. 2002). In principal, this statement is true regardless of whether the proposed genetic benefits are assumed to represent additive or non-additive effects (but see Griffith and Immler 2009).

Extra-pair paternity and genetic benefits – inconsistent results

Evidence for a genetic type of benefit based on maternal half-sibling comparisons is rather mixed across studies. Some highly cited landmark studies spectacularly support the genetic benefit hypothesis. For example, in Collared Flycatchers *Ficedula albicollis*, EPO were in better body condition near fledging compared to their maternal half-siblings (Sheldon et al. 1997), and nestling condition has been shown to positively affect recruitment in this species (Lindén et al. 1992). Furthermore, the difference in mean body condition between half-siblings was predicted by the difference in size of an at least partly intersexually selected male ornament of the respective sires (the white forehead patch, Sheldon et al. 1997). In Bluethroats *Luscinia svecica*, EPO nestlings showed better cellular immunocompetence than their maternal and, notably, also their paternal half-siblings, suggesting not only a genetic benefit from an extra-pair mating preference, but also an interaction effect of maternal and paternal genotype on offspring immunocompetence (Johnsen et al. 2000; see also Fossøy et al. 2008). Strong support in favour of the genetic benefit hypothesis of extra-pair mating also comes from a study in the Blue Tit *Cyanistes caeruleus*. Here, EPO sired by non-local extra-pair males showed higher average heterozygosity compared to their maternal half-siblings and individual heterozygosity was positively correlated with a number of fitness-related traits in both sexes (Foerster et al.

2003). In contrast to these findings, other studies failed to reveal any systematic differences in maternal half-sibling performance, sometimes in the same or in closely related species (e.g. Strohbach et al. 1998; Lubjuhn et al. 1999; Whittingham and Dunn 2001; Schmoll et al. 2003; Edly-Wright et al. 2007; Rosivall et al. 2009; Dunn et al. 2009). Furthermore, application of identical experimental protocols (e.g. the phytohemagglutinin test of cellular immunocompetence) in different species with similar extra-pair mating systems produced mixed results (Johnsen et al. 2000; Kleven and Lifjeld 2004; Kleven et al. 2006; Fossøy et al. 2008; Wilk et al. 2008; Forsman et al. 2008; Butler et al. 2009). The inconsistencies of results across EPP studies may be caused by methodological challenges and/or reflect true and meaningful differences in the respective study systems. In either case, it is important to address this heterogeneity in order to evaluate how reproducible and how generalisable these results may or may not be.

Effect sizes of genetic benefits likely to be small

The inconsistency of results across EPP studies may be related to the fact that additive genetic fitness benefits from mate choice are likely to be small in general (e.g. Kirkpatrick and Barton 1997; Møller and Alatalo 1999; Arnqvist and Kirkpatrick 2005). Thus, even studies with comparatively large sample sizes may fail to detect any effects of differential paternity on offspring fitness due to a type II statistical error (accepting the null hypothesis when it is wrong), which may contribute to the observed heterogeneity in results across EPP studies. Given small expected effect sizes, the other side of the same coin is that studies actually demonstrating differences in maternal half-sibling performance based on comparatively small samples sizes may be prone to a type I statistical error (rejecting the null hypothesis when it is true), potentially seconded by differential maternal investment in relation to paternity (see below).

Recent conceptual contributions emphasize the potential of non-additive genetic benefits from extra-pair mating (e.g. Kempenaers 2007; Griffith and Immler 2009). For example, a number of studies have reported that EPO were more heterozygous than their WPO maternal half-siblings (e.g. Foerster et al. 2003; Stapleton et al. 2007; Suter et al. 2007; Fossøy et al. 2008; but see Wetzel and Westneat 2009) or that EPO not only outperformed their maternal, but also their paternal half-siblings (Johnsen et al. 2000; Garvin et al. 2006), suggesting non-additive rather than additive genetic benefits of extra-pair matings. However, a recent meta-analytical approach revealed that effect sizes of heterozygosity-fitness correlations are generally positive in sign, but not large either (Chapman et al. 2009). Accordingly, the

magnitude of non-additive fitness benefits to be potentially obtained through extra-pair mating may be expected to be rather small, too. This may not be the case for all types of non-additive genetic effects, however, for example if extra-pair mating helps preventing fertilisations which would lead to a substantial fitness loss due to pronounced inbreeding (e.g. Keller 1998; Kruuk et al. 2002) or outbreeding (Veen et al. 2001) depression.

Differential maternal investment may confound paternal genetic effects

Selection may favour females with the ability to bias resource allocation in favour of offspring descending from preferred sires (Burley 1986; Møller and Thornhill 1998). If females selectively favour their extra-pair offspring because their sires were of superior genetic quality, superior EPO performance may at least partly be due to maternal rather than paternal genetic effects. Thus, differential maternal investment with respect to paternity may have the potential to confound paternal genetic effects on offspring fitness (Mousseau and Fox 1998; Møller and Thornhill 1998). On the other hand, it can be argued that a biased investment in favour of EPO may make a case for rather than against the genetic benefit hypothesis, since differential investment solely depends on differential paternity (Sheldon 2000). This argumentation seems less straightforward in light of recent studies suggesting that EPO occur earlier in the laying order and, accordingly, in the hatching sequence than their WPO maternal half-siblings, giving them a head start in sibling competition (e.g. Magrath et al. 2009; Ferree et al. 2010). For example, Magrath et al. (2009) not only demonstrated that EPO hatch slightly earlier than WPO, but also that statistically significant differences between maternal half-siblings in morphology and survival until fledging tend to diminish once hatching sequence is statistically controlled for. At present, it is unclear whether females time EPCs to occur early in their laying phase, whether these sequence effects reflect mating effort patterns of social or extra-pair sires, or whether they simply represent a by-product of social or ecological constraints on EPC behaviour (discussed in Magrath et al. 2009). In any case, such effects have the potential to confound paternal genetic effects on offspring fitness for both, additive as well as non-additive genetic benefits, possibly leading to an overestimation of the effects of differential paternity.

Context-dependent genetic benefits of mating preferences and their implications

Another explanation for inconsistent results from maternal half-sibling comparisons may be that the genetic benefits of extra-pair matings vary in magnitude in relation to the prevailing environmental conditions (please note that, while in the compatible alleles model the genetic background of a female may well be seen as an "environment" or a "context" within which

paternal alleles are expressed and with which they may interact, I reserve the use of these terms for extra-genomic components of the environment). Benefits may be large enough to be detectable in some ecological circumstances, but too small or non-existent in others. Such context-dependent genetic effects presuppose temporal and/or spatial variation in the environment - a ubiquitous feature in most natural bird populations. They also presuppose genotypes to differ in how their fitness is affected by variation in the environment, i.e. genotype-by-environment interactions for fitness must be present. If this is *not* the case, the relative genetic benefit a female may obtain from choosing among different sires is identical across environments (Fig. 1 a, b). However, whenever such genotype-by-environment interactions exist, there is a potential for context-dependent genetic effects to occur (Fig. 1 c, d). This refers to sire as well as offspring genotypes in the case of additive genetic effects, but only to offspring genotypes in the case of non-additive genetic effects for which offspring fitness is not normally a function of sire genotype but determined by the interaction of maternal and sire genotype.

Two principal cases of genotype-by-environment interactions can be distinguished. First, if fitness reaction norms do not cross and the fitness rank order of genotypes is preserved across the environments that are experienced, context-dependent genetic effects will affect the magnitude of the genetic benefit a female can potentially obtain, although not its sign (Fig. 1 c). Single best male genotypes on the level of the population (in case of additive genetic effects) or most compatible male genotypes on the level of the individual female (in case of non-additive genetic effects) may exist and they are transient across these environments. Second, if fitness reaction norms cross and the fitness rank order of genotypes is not preserved across the environments that are experienced, context-dependent genetic effects will not only affect the magnitude of the genetic benefit a female may obtain, but also its sign, rendering preferences for particular sire genotypes adaptive in some of these environments, but not in others (Fig. 1 d, also termed ecological cross-over). Here, no single best male genotypes on either the level of the population or the level of the individual female do exist. Indeed, the terms "good alleles" or "compatible alleles" in reference to any particular male genotype do not make sense under this scenario. In both cases, however, context-dependent genetic effects suggest selection on female mating preferences to vary across environments, which has interesting implications for the evolution of mating preferences and the maintenance of genetic variation in traits that are under sexual selection.

If relevant gradients of the environment that offspring will experience are fairly well predictable, we may expect females to show phenotypically plastic instead of static mating

preferences (discussed in Qvarnström 2001). In the case of non-crossing fitness reaction norms, they may be selected to balancing direct costs of choice against expected genetic rewards and hence express any given preference more or less strongly depending on environmental variation. In the case of additive genetic effects, the strength of sexual selection on preferred male traits (secondary sexual characters and genetically correlated traits) will then vary accordingly and episodes of relaxed selection could slow down the depletion of genetic variance in these traits or even contribute to its maintenance by allowing more time for deleterious mutations to occur. In the case of ecological cross-over, plastic preferences would need to be reversed to be adaptive and would hence directly support maintenance of genetic variation in male traits. If the environmental conditions that offspring will experience are largely unpredictable, however, females may not benefit at all from expressing mating preferences for any particular sire genotype. For example, in the case of ecological cross-over in fitness, females have no means to evaluate the relative genetic quality of potential mates and they may rather opt for genetic bet-hedging, mate multiply and thereby sample a number of different sires in order to increase the within-cohort genetic diversity of their offspring (see Yasui 1998 for more background on this argument and Schmoll et al. 2007 for an application to extra-pair mating behaviour in birds).

Context-dependent genetic benefits from mate choice in general have been shown in a range of taxa including insects (Jia and Greenfield 1997), anurans (Welch 2003; Sheldon et al. 2003), and mammals (Mills et al. 2007). Furthermore, context-dependent genetic benefits from mate choice may be inferred from studies demonstrating genotype-by-environment interactions on the expression of male sexual signal traits under directional intersexual selection (e.g. Qvarnström 1999; Jia et al. 2000; David et al. 2000; Danielson-François et al. 2006; see also Greenfield and Rodriguez 2004). In the following paragraph, I will apply the idea of context-dependent genetic effects to extra-pair mating behaviour in birds and briefly review the few studies that have suggested such effects up to date.

Context-dependent genetic effects of extra-pair mating

In order to demonstrate context-dependent additive genetic effects of extra-pair matings, it is necessary to test for a two-way interaction effect of differential paternity and the focal environmental variable on offspring traits, i.e. EPO and WPO "genotypes" are predicted to react in a different manner to different environmental conditions. In a purely operational view, the same is true for non-additive genetic effects, although conceptually, a three-way interaction effect of maternal genotype, paternal genotype and the environment is predicted. Here, the

magnitude of the fitness effects of the interaction between maternal and paternal genotypes depends on the environmental context.

As far as I am aware, only five studies – relating to five different species – have demonstrated context-dependent genetic effects when testing for maternal half-sibling performance. In the socially monogamous Coal Tit *Periparus ater* EPO had a higher probability of local recruitment into the breeding population compared to their WPO maternal half-siblings only when they originated from late (i.e. second) broods, but not when they originated from early (i.e. first) broods (Schmoll et al. 2005). Recruitment probability in general was significantly reduced in late broods, such that the superior performance of EPO coincides with environmental conditions that are stressful compared to those in early broods (Schmoll et al. 2005). First-year reproductive performance was affected in a similar way, reflecting the differential recruitment patterns (Schmoll et al. 2005). No context-dependent effects were apparent in the same study population in an analysis of fitness-related traits that are expressed beyond recruitment (Schmoll et al. 2009).

In the socially monogamous Common Yellowthroat *Geothlypis trichas*, EPO mounted a stronger cellular immune response than their WPO maternal half-siblings only in the colder of two study years, but not in the warmer one (Garvin et al. 2006). Low ambient temperatures negatively affect offspring immunocompetence (directly and/or indirectly e.g. via food abundance) such that superior performance of EPO coincides with environmental conditions that are relatively stressful (Garvin et al. 2006).

In the socially polygynous Red Bishop *Euplectes orix*, WPO were found to be more immunocompetent than their EPO maternal half-siblings only in the hotter of two study years, but not in the cooler one (Edler and Friedl 2008). Compared to the yellowthroat study (Garvin et al. 2006), the pattern thus appears reversed with respect to both, the relative genetic quality of maternal half-siblings and the effect of ambient temperature as a key environmental variable. Hotter seasons, however, are likely to provide *less* favourable breeding conditions in this African species due to a lack of nestling food and increased heat stress (Edler and Friedl 2008). The fact that WPO instead of EPO perform better under such stressful conditions may be explained by the polygynous mating system of this species. Females paired to highly attractive and therefore more strongly polygynous males face an increased risk that their social mate runs out of sperm and seem to use EPC as a means to insure themselves against their high-quality social mates being temporarily infertile. Consequently, mainly less attractive males of presumably lower genetic quality may be successful in siring EPO (Friedl and Klump 2005; Edler and Friedl 2008). In this mating system, it thus seem to be WPO, not EPO, which are of

higher genetic quality, so that the superior performance of offspring of relatively better genetic quality coincides with relatively stressful environmental conditions (Edler and Friedl 2008).

In the socially monogamous Tree Swallow *Tachycineta bicolor*, EPO had longer ninth primary feathers at nestling day 16 than their maternal half-siblings only when natural parasite abundance was low *and* when they had hatched early relative to their WPO maternal half-siblings (O'Brien and Dawson 2007). The difference in ninth primary length at a particular developmental stage (i.e. near fledging) is seen as reflecting a genetic benefit of extra-pair mating, because nestling wing length predicts time of fledging and wing length at fledging is positively related to recruitment probability in the study species (discussed in O'Brien and Dawson 2007). This study differs from the previous ones not only in that it considers, conceptually, a three-way interaction (the effects of differential paternity were dependent on the interaction of *two* environmental dimensions, parasite abundance and relative hatch order). In contrast to the former studies, it was also in relatively favourable, not stressful, conditions that EPO have differed from their WPO half-siblings (O'Brien and Dawson 2007).

Finally, in the predominantly socially monogamous House Wren *Troglodytes aedon* WPO were more immunocompetent than their EPO maternal-half-siblings in two out of three study years, but the publication did not give reference as to whether these differences were related to relevant variation in (the quality of) the environment (Forsman et al. 2008).

Poor environmental quality – revealing or concealing paternal genetic effects?

The studies summarised above differ in how they see the role of environmental quality in determining the extent of genetic variation that is expressed in offspring phenotypes. Three out of the five studies that have demonstrated context-dependent genetic effects show a pattern where only comparatively poor environments seem to reveal genetic variation. An explanation for this could be that under beneficial environmental conditions all offspring may perform relatively well irrespective, to some degree, of their genetic quality (i.e. of being sired within-pair or extra-pair). Beneficial environments may thus have the potential to mask genetic variation in fitness-related traits, and, as a consequence, it would be difficult to demonstrate the differences in maternal half-sibling performance predicted by the genetic benefit hypothesis. This is particularly relevant when taking into account that the magnitude of genetic benefits of mate choice must be expected to be small in general (see above). In contrast, comparatively stressful conditions where essential resources are limited may reveal this genetic variation and it is only then that the small genetic differences between maternal half-siblings are reflected in their phenotypic performance and become detectable with limited sample sizes. Along similar

lines, inbreeding depression is generally (although not universally) more pronounced under stressful conditions across a wide range of taxa according to a recent meta-analysis (Fox and Reed 2011). As an example in birds, Keller et al. (2002) report a case of inbreeding-by-environment interaction in the Cactus Finch *Geospiza scandens*. For example, inbreeding depression for adult survival was most severe under unfavourable conditions (i.e. dry climate and high population densities), but substantially less pronounced under a range of other conditions (Keller et al. 2002). Similarly, nestling survival in great tits *Parus major* was negatively affected by parental genetic similarity only late in the season when food resources are likely to be more restricted (Van de Castele et al. 2003). Thus in both examples inbred versus outbred genotypes differed in their response to varying conditions with only stressful environments reflecting the existing genetic variation in the phenotype (see also Marr et al. 2006; Szulkin and Sheldon 2007).

In contrast to the former work, the Tree Swallow study by O'Brien et al. (2007) found that it is in relatively favourable conditions when half-siblings differ in performance. The difference between this study and the previous ones may be the type of focal trait considered or the type of genetic effect supposed to create the observed differential half-sibling performance. In the case of a morphological character such as feather length, the underlying type of effect is likely to be additive genetic and the full range of existing genetic variation may only be expressed in the phenotype under favourable conditions, when individual genotypes can maximize their genetic potential (Hoffmann and Merilä 1999; see also Qvarnström 1999 reporting higher heritability of a sexually selected feather ornament under beneficial conditions). The other studies did not address differences in morphological characters but traits that seem more closely related to fitness. In contrast to morphometric traits, the phenotypic expression of genetic variation for such traits does not seem to be promoted by favourable conditions (Charmantier and Garant 2005). Neither do differences in these traits necessarily reflect *additive* genetic benefits of extra-pair matings. For example, a significantly better performance of EPO not only in maternal, but also in paternal half-sibling comparisons reported in Garvin et al. (2006) indicates a non-additive type of benefit in this case.

Conclusions

In conclusion, only five empirical studies have suggested context-dependent genetic effects of extra-pair mating in birds up to date. None of these studies, however, has experimentally manipulated the focal environmental dimensions and hence results are open for alternative explanations. Furthermore, four of the studies have not controlled for maternal effects in

general and hatching sequence in particular. This is problematic because differential maternal investment in favour of EPO may not only confound effects of differential paternity in general, but lead to effects similar to those predicted from the context-dependence hypothesis. Finally, it is also mostly not clear, how variation in offspring quality traits relates to variation in fitness and how variation in the environmental variables highlighted in these studies affects offspring quality traits (with year effects being a case in point). Thus evidence for context-dependent genetic benefits from extra-pair matings in birds is suggestive rather than conclusive at present and it is unclear how important and how widespread context-dependent genetic effects of extra-pair mating may actually be and how consistently specific (e. g. high-stress versus low-stress) environments may affect the context-dependent expression of genetic variation.

Perspectives

Studies addressing the genetic benefits of extra-pair matings by comparing maternal half-siblings have generally used a range of different offspring quality traits and the few studies that have demonstrated context-dependent effects have likewise picked a number of different environmental variables to test for interactions with differential paternity (see above). The availability of many such potential response variables and, in particular, the availability of many potentially important predictor variables (i.e. environmental dimensions) harbours the risk of revealing spurious associations when testing for two-way (or even higher-order) interactions with differential paternity. Obviously, focal offspring quality traits must exhibit a verifiably close relationship with fitness, preferably as demonstrated in the very study population, to allow meaningful inference regarding the fitness consequences of extra-pair mating behaviour (frequently this relationship is assumed rather than established). Furthermore, to qualify as a "relevant" dimension of environmental quality, any candidate variable should predictably affect the focal offspring quality trait, preferably in a manner that is also understood mechanistically in some detail. Which offspring quality traits may be regarded and which particular dimension of the environment may be considered "relevant" will ultimately depend on the particular study system, but response and predictor variable(s) should be carefully chosen and well defined *a priori* for both, the observational as well as the experimental approaches outlined below.

A number of high-quality data sets on maternal half-sibling performance is meanwhile available (or being collected) and may frequently have been sampled across different environmental contexts. These data could be (re-) analysed while explicitly considering relevant environmental variation. Studies that have failed to establish the predicted differences

in maternal half-sibling performance may then find that under some circumstances these effects are detectable (note that there was no support for an "overall" (i.e. main) effect of differential paternity in some of the studies that demonstrated context-dependence, cf. Fig.1 in Schmolle et al. 2005). However, also studies that *have* shown differences in maternal half-sibling performance may benefit by allowing a deeper understanding when taking ecology into account, for example if an overall effect of differential paternity largely relates to particular sub-samples in the data sets (but see discussion on the risk of spurious findings above). At this stage, reporting a lack of evidence for context-dependence is also of considerable interest (given sample sizes are reasonably large), to avoid publication bias and obtain a balanced view on how common such effects may or may not be in natural populations.

As an example, in many bird populations in temperate regions, environmental conditions deteriorate predictably and substantially over the breeding season while laying and/or hatching date are recorded routinely in many studies. They could thus serve retrospectively as a proxy for ecological contexts of varying quality to compare the relative performance of maternal half-siblings against, even if more meaningful data like quantitative estimates of food abundance are not available. Similarly, available weather data combined with longterm data sets could identify key meteorological variables affecting fitness-related traits and these gradients of environmental variation could be used to test for interactions with differential paternity.

Instead of considering laying or hatching order primarily a potentially confounding factor when analysing maternal half-sibling performance (see above), it could also be seen as reflecting yet another relevant dimension of the natural environment. There is evidence that hatching order directly affects early survival prospects in many altricial bird species through asymmetrical sibling competition, particularly when hatching asynchrony is pronounced (Magrath 1990; see also Magrath et al. 2009). Thus, once hatching sequence has been recorded in order to control its effects, testing for differential paternity-by-hatching sequence interactions may also represent a valuable option for testing the context-dependence hypothesis.

Different from the truly ecological variables discussed above, offspring sex may also be regarded a relevant dimension of environmental context. Fitness effects of particular alleles may be sex-dependent, for example due to sexually antagonistic selection resulting from intralocus sexual conflict (Bonduriansky and Chenoweth 2009). Such sexually antagonistic fitness variation could render effects of paternal genetic contribution sex-dependent, too. Thus it may be worthwhile considering offspring sex as an (intra-genomic) dimension of the environment within which paternal alleles are expressed, and test for differential paternity-by-

offspring sex effects on fitness traits in both, observational and experimental approaches (see below). Of course, the magnitude of such effects may again depend on external dimensions of the environment, which may require testing for three-way interactions of differential paternity, offspring sex and quality of the environment. If the effects of differential paternity were indeed sex-dependent or even sexually antagonistic, it would be adaptive for females to adjust sex allocation in relation to paternity, because only then would they be able to obtain a (maximum) net genetic benefit from extra-pair mating. For example, male extra-pair offspring may inherit alleles from their attractive (i.e. extra-pair) fathers that will make themselves more attractive as extra-pair sires while the same alleles may negatively affect the fitness prospects and thus the reproductive value of female offspring. In general, there is good evidence for the ability of female birds to facultatively bias offspring sex ratio, for example in relation to the sexual attractiveness (e.g. Ellegren et al. 1996) or the genetic compatibility (e.g. Pryke and Griffith 2009) of their social mates. However, in the context of extra-pair mating behaviour, evidence for facultative sex allocation in relation to paternity is rather weak. Only a single study has unequivocally demonstrated the predicted sex ratio bias towards males in extra-pair offspring (Johnson et al. 2009), while many others tried, but failed (e.g. Sheldon and Ellegren 1996; Leech et al. 2001; Dietrich-Bischoff et al. 2006). Thus, if differential paternity was indeed sexually antagonistic in its effects, fitness gains realised via the advantaged sex would possibly have to exceed the fitness costs incurred by the disadvantaged sex to render extra-pair matings adaptive.

Most importantly, however, experimental approaches are needed that systematically manipulate relevant environmental contexts and subsequently test for differential paternity-by-treatment effects. If genetic benefits are assumed to be apparent more clearly under relatively poor conditions, the goal is provoking genetic effects by deteriorating environmental contexts to a degree that provides stressful conditions that could be encountered by the study population (at least from time to time), but that is still acceptable from an ethical point of view (and does also not lead to an overwhelmingly detrimental environmental effect which would also blur differences between genotypes). We may then predict a significant interaction between paternity and experimental treatment with differences between half-siblings being more pronounced under relatively poor conditions. Ideally, any treatment would create more than just two experimental environments to better understand the predicted differential reaction norm trajectories of offspring quality traits (which may not necessarily be linear as assumed in Fig. 1 for the sake of clarity). As expected effect sizes are small, such experiments need to be carried out on a larger scale that maximises the number replicates (i.e. broods with multiple paternity).

Given that differential maternal investment with respect to paternity may lead to the same type of context-dependent effects as predicted by the genetic benefit hypothesis, future studies need to control such effects in general and hatching order in particular.

In the field, brood size manipulation experiments are one straightforward option to manipulate the degree of sibling competition and thus resource availability. Cross-fostering designs may then easily be tailored to create a range of experimental environments of different quality. Furthermore, by separating offspring from their natural parents at an early stage through cross-fostering of entire (half-) sibships, potential post-hatching effects of maternal or paternal differential allocation in relation to paternity could be controlled. Manipulation of parasite prevalence and/or abundance or nest temperature regimes or enforcing replacement clutches while taking advantage of naturally deteriorating conditions in seasonal environments offer further opportunities depending on the biology of the focal species.

In order to unequivocally demonstrate genetic benefits of female mating preferences, it is necessary to allocate paternity randomly to a focal female's offspring, raise her progeny under identical environmental conditions and then test for differences in fitness between maternal half-sibships descending from preferred versus less preferred sires. This is comparatively easily achieved in laboratory studies of externally fertilising species by means of split-clutch in-vitro fertilisations (e.g. Barber et al. 2001; Welch 2003) and feasible to some degree within captive (semi-natural) populations of certain internally fertilising species (e.g. Petrie 1994). However, the use of artificial insemination techniques in laboratory populations would offer interesting perspectives here, too. Such systems would not only exclude differential maternal investment, but also allow for a much better control and resolution of the experimental environments. One drawback here is that in the few established model species such as the zebra finch, EPP may play only a minor role in natural populations (Griffith et al. 2010).

As the magnitude of the genetic benefits a female may obtain from extra-pair mating is expected to be small (see above), comparatively large sample sizes will normally be required to demonstrate them. When analysing the fitness consequences of extra-pair mating, a replicate typically consists of a brood with multiple paternity and it may thus be challenging to achieve substantial samples, especially in species with relatively low frequencies of EPP. Properly controlling potentially confounding effects of differential maternal investment (see above) makes this an even more difficult enterprise. However, in species where EPO have been unequivocally shown to be more heterozygous than their WPO maternal half-siblings (see above), a shortcut may be testing for the context-dependence of the predicted heterozygosity-fitness correlations in the study population/study species instead of testing the context-

dependence of the fitness effects of differential paternity directly. Similar to context-dependent effects of (close) inbreeding discussed above, heterozygosity-fitness correlations may vary in their strength across environments of different quality, giving rise to heterozygosity-by-environment interactions (for an interesting example in anurans see Lesbarrères et al. 2005). This approach would not only allow making use of (much) larger samples by also including offspring from broods without multiple paternity (in observational as well as experimental studies). As we can expect substantial random variation in the degree of individual heterozygosity also within each of the two groups of maternal half-siblings (i.e. WPO and EPO), it might also provide a means to efficiently control differential maternal investment, because significant heterozygosity-fitness correlations as well as heterozygosity-by-environment interactions *within* these groups cannot be confounded by differential maternal investment in relation to paternity.

Context-dependent genetic benefits imply that it would be adaptive to express costly mating preferences in a phenotypically plastic manner, depending on the expected net benefit within a given environment (Qvarnström 2001; Welch 2003) and there are remarkable examples of adaptive phenotypic plasticity in female mate choice in birds (e.g. Qvarnström et al. 2000; Chaine and Lyon 2008). This flexibility presupposes the ability of females to evaluate the specific quality of the environment that their offspring are likely to experience, which should not pose a major problem in seasonal environments that may vary predictably in quality (see above). Assuming extra-pair matings to be costly, we may thus predict adaptive phenotypic plasticity in female propensity to engage in extra-pair matings. For example, in the Coal Tit population referred to above, the frequency of EPP was substantially higher in second broods (relatively stressful environment) compared to first broods (relatively beneficial environment, Dietrich et al. 2004). This pattern is compatible with a plastic female response in relation to differential environmental conditions, although other explanations may seem more likely (for example a better availability of extra-pair mating opportunities with preferred sires, Dietrich et al. 2004). Nevertheless, comparing the frequency of EPP against the magnitude of genetic benefits (i.e. the difference in half-sibling performance) across different environments (within as well as across populations) may represent a first step to elucidate this idea further.

If context-dependent genetic effects could be demonstrated in a robust and repeatable manner, it may be of interest to determine how frequently environmental contexts arise that allow females to realise a net genetic fitness benefit by mating extra-pair and thus maintain selection for this behaviour in the long run. Analysis of long-term data sets – where available –

may help to evaluate this and could possibly be used to parameterise models that address the maintenance of mating preferences for extra-pair sires in heterogeneous environments.

This article has focused on how variation in environmental quality may affect the phenotypic expression of the predicted, genetically based differences between EPO and WPO maternal half-siblings, assuming that genotype fitness ranks are maintained across environments (i.e. non-crossing reaction norms as illustrated in Fig. 1c). However, different environments as opposed to environments of different quality (for example in terms of the prevalence of different *types* of parasites) may also reflect relevant environmental heterogeneity and ecological cross-over of reaction norms in fitness-related traits has been demonstrated in other taxa (e.g. Jia and Greenfield 1997; Welch 2003; Mills et al. 2007) and may also be considered.

The idea of a context-dependence of genetic benefits of extra-pair matings may offer one possible approach for reconciling mixed results from different EPP studies and may thus contribute to resolving the longstanding puzzle why female birds mate extra-pair so frequently. More generally, it may allow understanding under which environmental conditions selection will act to maintain a female mating bias towards extra-pair males. This has potentially far-reaching implications for the ecology and evolution of female mating preferences, the maintenance of genetic variation in (sexually) selected traits and possibly the co-evolution of male sexual signals and female mating preferences. Taking into consideration that evidence from other taxa also suggests that context-dependence of genetic benefits of mate choice may be of considerable importance, I conclude that context-dependent genetic effects of mate choice in birds deserve more attention in general and in the context of extra-pair mating in particular.

Acknowledgments

Thanks to Klaus Reinhold, Peter Korsten and Verena Dietrich-Bischoff who commented on earlier drafts of this manuscript. Thomas Friedl and an anonymous reviewer also provided helpful comments.

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784

Figure captions

Fig. 1 Schematic representation of linear fitness reaction norms of two offspring genotypes (represented by lines) to illustrate potential effects of genotype-by-environment interactions on the genetic benefits of mate choice. **a** Genotypes show no phenotypically plastic response, the slopes of their reaction norms are identical and equal zero (parallel reaction norms, no genotype-by-environment interaction). **b** Genotypes show a phenotypically plastic response, the slopes of their reaction norms are identical, but different from zero (parallel reaction norms, no genotype-by-environment interaction). **c** Genotypes show a phenotypically plastic response, the slopes of their reaction norms are different, but reaction norms do not cross within the range of environmental conditions experienced (genotype-by-environment interaction with non-crossing reaction norms). **d** Genotypes show a phenotypically plastic response, the slopes of their reaction norms are different, and reaction norms cross within the range of environmental conditions experienced (genotype-by-environment interaction with crossing reaction norms, ecological cross-over). Relative genetic fitness benefits from preferring a male siring either one or the other offspring genotype are identical (a), (b), differ in magnitude (c), or may even be reversed (d) across environments.

802 **Figures**

803 Figure 1

804 (a)

805
806 (b)

809 (c)

810
811 (d)

Experienced environmental variation

812
813 German abstract for article 10336-683: A review and perspective on context-dependent genetic
814 effects of extra-pair mating in birds
815

Kontextabhängige genetische Effekte von Fremdkopulationen bei Vögeln: Review und Perspektive

Der evolutionäre Ursprung und die Aufrechterhaltung von außerpaarlichem Kopulationsverhalten bei Vögeln sind in den letzten Jahrzehnten intensiv untersucht worden. Allerdings konnte bisher kein Konsens bezüglich des adaptiven Nutzens dieses Verhaltens für Vogelweibchen erzielt werden. Die genetische Vorteile-Hypothese postuliert, dass Fremdkopulationspartner Genvarianten von höherer Qualität oder besserer Kompatibilität im Vergleich zum sozialen Paarpartner aufweisen, was zu Nachkommen von höherem Reproduktionswert führen würde. Ein häufig genutzter Ansatz zur Überprüfung dieser Hypothese besteht darin, mütterliche Halbgeschwister in Bruten mit multiplen Vaterschaften bezüglich fitness-relevanter Merkmale zu vergleichen. Die Ergebnisse solcher Vergleiche sind allerdings nicht konsistent. In diesem Beitrag diskutiere ich die Idee, dass das Ausmaß genetischer Fitnessvorteile aus Fremdkopulationen vom Umweltkontext abhängt. Kontextabhängige genetische Effekte wurden bisher nur bei fünf Singvogelarten nachgewiesen. In keiner der betreffenden Studien wurden jedoch die entscheidenden Umweltvariablen experimentell manipuliert. Auch wurden die potentiell konfundierenden Effekte von differentiellm mütterlichen Investment in Abhängigkeit der Vaterschaft zumeist nicht kontrolliert. Eine Reihe von hochqualitativen Datensätzen zu den Fitnesskonsequenzen von Fremdkopulationsverhalten ist verfügbar, die bezüglich ihrer Umweltabhängigkeit (re-) analysiert werden könnten. Dies gilt, sofern relevante Umweltgradienten erfasst wurden und ihre Berücksichtigung *a priori* plausibel gemacht werden kann. Relevante Variation könnte zum Beispiel den Zeitpunkt des Brütens in gemäßigten Breiten, die Reihenfolge des Schlupfes, aber auch das Geschlecht der Nachkommen umfassen. In erster Linie sind jedoch experimentelle Ansätze nötig, die fitnessrelevante Gradienten der Umwelt wie Futterverfügbarkeit oder Parasitenbelastung systematisch und graduell variieren. Die Kontextabhängigkeit genetischer Effekte von Fremdkopulationen könnte möglicherweise erlauben, widersprüchliche Resultate verschiedener Studien innerhalb und zwischen Arten zu integrieren. Eine solche Kontextabhängigkeit könnte aber auch ganz allgemein helfen zu verstehen, unter welchen Umweltbedingungen Selektion eine weibliche Paarungspräferenz für Fremdkopulationspartner aufrechterhält. Dies hätte potenziell weit reichende Folgen für die Ökologie und Evolution von Paarungspräferenzen und die Aufrechterhaltung genetischer Variation von (sexuell) selektierten Merkmalen.