Genetica (2008) 134:147–158
DOI 10.1007/s10709-007-9219-5

Female choice for genetic complementarity in birds: a review

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Received: 25 April 2007 / Accepted: 11 October 2007 / Published online: 2 November 2007

Abstract Data from avian species have played a prominent role in developing and testing theories of female mate choice. One of the most prominent models of sexual selection, the "good genes" model, emphasizes the indirect benefits of female preferences for male ornaments as indicators of a potential sire's additive genetic quality. However, there is growing interest in non-additive sources of genetic quality and mate choice models for self-referential disassortative mating based on optimal levels of genetic dissimilarity. We reviewed the empirical evidence for genetic-complementarity-based female mate choice among birds. We found the evidence for such choice is mixed but in general against the genetic complementarity hypothesis. The lack of evidence for genetic complementarity in many birds may be due to an inability to make the fine distinctions among potential mates based on genes, possibly due to the comparative anosmatic nature of avian sensory system. For some species however there is compelling evidence for genetic complementarity as a criterion used in female mate choice. Understanding the ubiquity of female mate choice based on genetic complementarity and the variation in this source of female preference among and within species remains a challenge.

Keywords Aves · Female mate choice · Genetic compatibility · Genetic complementarity · Heterosis · Heterozygosity · Sexual selection

Introduction

Many species exhibit conspicuous and elaborate characters that appear to convey no survival benefit. Darwin was the first to explain these elaborate traits as arising through competition for mates, a process he called sexual selection (Darwin 1871). Biased mating due to female preferences for males with particular traits is a major mechanism of sexual selection and female mate choice has been the focus of considerable research. The last two decades in particular have seen an explosion of studies on female mate choice (Andersson 1994; Andersson and Simmons 2006). Most of this research has focused on mate preferences in the classical sense where females bias mating towards those males with comparatively more elaborate ornaments. Such preferences spread in the population through a Fisherian runaway process (Fisher 1930; Mead and Arnold 2004), because of the benefits, either direct or indirect, preferences have on female fitness and offspring genetic quality (Zahavi 1975; Hunt et al. 2004) or through a combination of both Fisherian and "good genes" processes (Kokko et al. 2002; Mead and Arnold 2004). Models of sexual selection in which females gain genetic benefits from their choice are called genetic indicator or "good genes" models because male ornamentation indicates some heritable

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aspect of male quality (Andersson 1994; Andersson and Simmons 2006). In "good genes" models females that mate with the most ornamented males in the population gain additive genetic benefits for offspring. Trivers (1972) was the first to suggest that females may accrue fitness benefits not from choosing the most ornamented males but rather from choosing genetically dissimilar sires for their offspring.

> "Where the male invests little or nothing beyond his sex cells, the female has only to decide which male offers the ideal genetic material for her offspring, assuming that the male is willing and capable of offering it. The question can be broken down to that of which genes will promote the survival of her offspring and which will lead to reproductive success, assuming the offspring survive to adulthood. Implicit in these questions may be the relation between her genes and those of her mate: do they complement each other?" (Trivers 1972)

A number of theoretical and empirical studies have examined the idea that females may be biasing fertilizations, either pre- or post-copulation (i.e., cryptic choice), in favor of sires who differ genetically from themselves by some optimal degree (Zeh and Zeh 1996; Tregenza and Wedell 2000; Zeh and Zeh 2003; Mays and Hill 2004; Neff and Pitcher 2005). These genetic dissassortative mating preferences have been referred to as genetic compatibility or genetic complementarity based preferences. We prefer the latter term for it's fit with Trivers' (1972) original use of the term "complement" and to distinguish what is a model of intraspecific mate choice from the interspecific Dobzhansky–Müller compatibility model from the speciation literature (Pialek and Albrecht 2005).

Genetic indicator models of mate choice and those based on genetic complementarity are fundamentally different. Both represent "good genes" models in a broad sense (Puurtinen et al. 2005), but in indicator models, genetic quality is an additive character wherein variation in offspring fitness varies as a function of the sire females choose for their offspring. In sexually reproducing diploid organisms, however, parents can only pass genes to offspring not genotypes. When fitness benefits are associated with heterozygous genotypes, offspring fitness is a function of both the contributions of males and females and thus variation in fitness is non-additive. Because they involve non-additive genetic variation genetic complementarity models differ from the classic indicator models of mate choice (Neff and Pitcher 2005).

Under a "good genes" indicator model of mate choice, females within a particular environment will benefit equally from choice of a particular male. Female preferences under "good genes" sexual selection therefore converge on particular male phenotypes, typically the most exaggerated and elaborate phenotypes. The result is variation in male reproductive success relative to ornament display and directional selection on male ornamentation. In contrast, under a genetic complementarity model offspring fitness is a function of combinations of genes contributed by both sires and from dams. Female preferences in this model are therefore contingent upon their own genotype and there should be no mate choice bias towards one male phenotype over another (Colegrave et al. 2002; Mays and Hill 2004).

Birds are conspicuous examples of the power of sexual selection to generate morphological and behavioral diversity. Indeed in what has become the standard reference on sexual selection Andersson (1994) begins with an example from the avian world (i.e., sexual dimorphism in mallards). However, many of the most important studies addressing female mate choice based on genetic complementarity have been conducted on non-avian taxa including insects, fish and mammals. Studies of mate choice for genetic complementarity in birds have lagged behind, but, there has been a recent surge in such studies. In this paper we will review the current literature on avian mate choice for genetic complementarity and assess the strength of the available evidence that such mate choice does occur in the aves.

Heterosis and inbreeding depression

Implicit in models of mate choice based on genetic complementarity is the underlying assumption that offspring fitness is related to heterozygosity. A positive relationship between fitness and heterozygosity (heterosis or heterozygte advantage) adds a complication for models of female choice. Offspring cannot inherit parental genotypes; they inherit genes. Consequently, offspring heterozygosity is a non-additive source of variation in fitness (Neff and Pitcher 2005; Puurtinen et al. 2005; Lehmann et al. 2007). Inbreeding depression is the inverse of heterosis. Inbreeding depression results from the accumulation of deleterious mutations in homozygous genotypes. A fitness disadvantage of homozygotes implies either a fitness advantage to heterozygosity per se (i.e., overdominance and heterosis) or the masking of deleterious alleles when paired with a dominant allele (Charlesworth and Charlesworth 1987; Charlesworth and Charlesworth 1999).

There is considerable evidence for inbreeding depression and heterosis in wild avian populations. Perhaps the most studied fitness correlate of inbreeding is hatching success. Using data from paternity studies based on minisatellite band-sharing coefficients Spottiswoode and Møller (2004) found ample evidence for inbreeding depression across 99 species of wild birds. Hatching success in this study showed a significant negative correlation with band sharing. Inbreeding depression is likely to be more evident in isolated island populations and other small, genetically bottlenecked avian populations confined to a restricted area (Jamieson et al. 2003; Swinnerton et al. 2004), but, this effect was statistically independent of any variation in sociality, breeding system or population size (Spottiswoode and Møller 2004).

Numerous other studies have uncovered evidence for inbreeding depression in wild avian populations. Various components of fitness have been shown to correlate either with pedigree based measures of inbreeding or individual genetic diversity as measured by molecular markers. Genetic diversity within individual birds has been shown to be positively associated with resistance to pathogens and immunocompetence (Hawley et al. 2005; MacDougall-Shackleton et al. 2005), song characteristics (Marshall et al. 2003; Seddon et al. 2004), territory size (Seddon et al. 2004), and local recruitment and survival (Hansson et al. 2001; Foerster et al. 2003).

Much of the data on inbreeding depression in wild populations employs molecular markers as proxy measures of inbreeding for individuals. The value of estimates of relatedness based around genetic markers has been questioned especially when the number of loci used is small (Slate and Pemberton 2002; Pemberton 2004; Slate et al. 2004). For example, in the medium ground finch (*Geospiza fortis*) and the cactus finch (*Geospiza scandens*) the degree to which inbreeding depression affected fitness varied not only across species but varied according to whether inbreeding was measured using molecular markers or pedigree data (Grant et al. 2003; Markert et al. 2004). Pedigree-based estimates of inbreeding depression are typically only possible for relatively small, isolated populations. Among the best pedigree-based studies of inbreeding depression in a wild bird are the various studies on song sparrows (*Melospiza melodia*) on Mandarte Island in British Columbia, Canada. In this population Reid et al. (2003; 2005) uncovered significant effects of inbreeding on both male song repertoire size and cell-mediated immunity. Also, lifetime reproductive success of immigrants and resident song sparrows in the Mandarte Island population was similar, but immigrants (who are presumably more outbred) had higher survival (Marr et al. 2002).

Complementary-based mate choice

The genetic architecture underlying heterozygote advantage is fundamentally different than that responsible for the additive genetic influence on fitness in the classic "good genes" model. In those cases where overdominance or epistasic effects determine fitness selection should favor some self-referential mate choice for sires exhibiting some optimal level of genetic dissimilarity. In this way, females selecting mates based on genetic complementarity will tend to produce more heterozygous offspring compared to females without a preference for genetically dissimilar sires. Given the ample evidence that inbred, homozygous offspring have lower fitness compared to outbred, heterozygous offspring selection should favor complementary-based choice for some optimal level of genetic dissimilarity.

In this review we will focus on the female response to selection favoring heterozygous offspring. Choosiness on the part of males should be less likely in species where there is little male parental investment. With their comparatively low per offspring investment and their capacity for increasing offspring number according to the number of mates, forgoing a mating opportunity should be relatively more costly for males compared to females. Therefore, even though offspring quality will improve in matings between a male and a genetically complementary female these benefits are unlikely to outweigh the costs of rejecting mating opportunities with less complementary females (Andersson 1994; but see also Bonduriansky et al. 2001; Tang-Martinez and Ryder 2005). Also, it is important to note that much of the literature on mating strategies in birds has assumed an active if not dominant role of female behavior in determining mating patterns, however, this may or may not be true in all cases. More realistic is to view mating strategies as dynamic games between male and female players (Westneat and Stewart 2003). Our approach in this review is to acknowledge the potential influence of selection for heterozygous offspring on female mating preferences and examine the available empirical literature for evidence consistent with a female response to selection for complementary-based mate choice. However, we readily admit that data that on the surface may suggest active female choice for genetic complementarity may later be found to result from other forces (male choice, coercion, etc.). This is especially true given that most of the studies we examined were correlative in nature showing the outcomes of mating behavior and not the mating behavior itself. As such it cannot be overemphasized that these results should be the impetus for future, preferably experimental, studies of behavioral mechanisms (or potential physiological mechanisms in the case of post-copulatory cryptic sperm choice).

The effect of inbreeding depression on selection for complementary-based mate choice will depend on the genetic architecture underlying the effect of inbreeding on fitness (Charlesworth and Charlesworth 1987; Charlesworth and Charlesworth 1999). Inbreeding depression that is counteracted by pairing a deleterious allele with a dominant allele favors choice for sires with dominant alleles and therefore the influence of sire choice on offspring fitness constitutes an additive effect. However, if inbreeding depression is tied to heterozygote advantage then selection should favor choice for sires with some optimal level of genetic dissimilarity. In this case, females should be judging potential sires on the basis of a self-referential criterion of genetic disassortative mating to maximize offspring heterozygosity. Choice for genetically dissimilar sires should be balanced with choice against interspecific hybridization and the maintenance of locally adaptive gene complexes such that females should favor some optimal level of dissimilarity among potential mates.

Heterozygote advantage should favor self-referential mate preferences based on genes but not preferences for the most heterozygous males as some authors have assumed (Brown 1997; Weatherhead et al. 1999). Female choice for the most heterozygous males will produce a greater variety of genotypes including homozygous genotypes not favored at those loci exhibiting overdominance. Given the non-additive nature of heterozygote advantage preference for the most heterozygous males is therefore an inaccurate criterion for maximizing offspring heterozygosity compared to a self-referential criterion (Lehmann et al. 2007).

Evidence for mate choice for genetic complementarity can be found in invertebrates (Bretman et al. 2004) and a number of vertebrate species including fish (Aeschlimann et al. 2003), amphibians (Garner and Schmidt 2003), lizards (Olsson et al. 2003), and mammals (Wedekind et al. 1995; Penn and Potts 1999; Roberts and Gosling 2003). Some evidence indicates that female preferences in birds are consistent within but not across females (Forstmeier and Birkhead 2004; Whittingham et al. 2006). These observations are consistent with choice based on a self-referential criterion, like genetic complementarity, but more direct evidence for genetic complementarity-based choice in birds remains mixed.

Most studies of genetic complementarity in birds have focused on complementarity as an explanation for multiple mating by females. This begs the question: why shouldn't females choose the most genetically complementary male as a social partner rather than only using complementarity as a strategy for choosing extra-pair sires? One confounding factor is that social mate choice in most birds is tied to choice of a breeding territory. The cost of passing up a good territory may outweigh the benefits, in terms of offspring fitness, of choosing the most genetically complementary social mates. However, if genetic complementarity is a major source of variation in offspring survival then females should consider complementarity in choice of pair and extra-pair males. Studies of genetic complementarity should start with the first mating decision made by a female that of a pair male, as the complementarity of a pair mate may influence future mating decisions. To our knowledge, only a few studies have examined genetic complementarity as a basis for female choice for social partners in birds (see Table 1). The results of these studies vary considerably. Given the degree of variability in the importance of genetic complementarity among species, and in some cases even among populations, the ubiquity of this model of female choice remains unresolved.

Genetic complementarity-based choice of a social mate should result in females paired to more genetically dissimilar males compared to the genetic similarity of randomly chosen male-female dyads. Freeman-Gallant et al. (2003) found that first-year female savannah sparrows (*Passerculus sandwichensis*) do not pair at random with respect to RFLP-based major histocompatibility complex (MHC) genotypes. Rather females pair with genetically dissimilar males at these loci. Richardson et al. (2005), however, found no evidence for disassortative pairing by MHC genotypes in the Seychelles warbler (*Acrocephalus sechellensis*). Other studies employed microsatellite measures of genetic similarity. Employing 9 microsatellite loci Marshall et al. (2003) found that repertoire size predicted individual genetic diversity in the sedge warbler (*Acrocephalus schoenobaenus*) and that females paired significantly more often with genetically dissimilar males. Oh and Badyaev (2006) found that female house finches (*Carpodacus mexicanus*) pair with genetically dissimilar males later in the breeding season. Using minisatellite multilocus DNA fingerprinting Edly-Wright et al. (2007) found no evidence that house sparrows (*Passer domesticus*) choose their social mates on the basis of genetic similarity. For some species the results vary across populations. For populations of blue tits (*Parus caeruleus*) in Austria and on the mainland of Norway there is no evidence that pairing decisions are made on the basis of genetic relatedness (Krokene and Lifjeld 2000; Foerster et al. 2006). For a blue tit population on Jomfruland Island off the coast of Norway, however, mated pairs were more genetically similar than were randomly chosen dyads (Krokene and Lifjeld 2000). A similar result was found for great frigatebirds (*Fregata minor*). Female great frigatebirds choose to pair with mates with whom they have higher multilocus DNA fingerprinting band sharing coefficients compared to random males in the population (Cohen and Dearborn 2004). This finding suggests that for frigatebirds pairing decisions are the opposite of what one would predict based on a genetic complementarity model.

Among those species lacking pair bonds, there is almost nothing known about female mate choice relative to genetic complementarity. Male ruffs (*Philomachus pugnax*) display on leks and have no pair bonds (Van Rhijn 1991). Thuman and Griffith (2005) looked at female choice for genetic complementarity in a population of ruffs on Gotland Island off the coast of Sweden. Female ruffs are

Table 1 Summary of recent empirical studies on mate choice based on genetic complementarity in wild birds

Common name	Scientific name	Social mate choice	Extra-pair mate choice	Marker(s) used	References (sample size for relevant tests)
Barn Swallow	*Hirundo rustica*	–	–	Microsatellites (9)	Kleven et al. 2005 ($n = 90$)
Black-throated Blue Warbler	*Dendroica caerulescens*	na	–	Microsatellites (4)	Smith et al. 2005 ($n = 92$)
Blue Tit	*Parus caeruleus*	–	–	DNA fingerprinting; Microsatellites (4–7)	Charmantier et al. 2004 ($n = 177$); Foerster et al. 2003 ($n = 96$); Foerster et al. 2006 ($n = 202$, $n = 99$)*; Krokene and Lifjeld 2000 ($n = 28$, $n = 42$)
Coal Tit	*Parus ater*	na	–	DNA Fingerprinting	Schmoll et al. 2005 ($n = 63$)
Great Frigatebirds	*Fregata minor*	–	na	DNA Fingerprinting	Cohen and Dearborn 2004 ($n = 91$)
Great reed Warbler	*Acrocephalus arundinaceus*	na	–	Microsatellites (21)	Hansson et al. 2004 ($n = 18$)
Great Tit	*Parus major*	na	–	Microsatellites (5)	Otter et al. 2001 ($n = 17$)
House Finch	*Carpodacus mexicanus*	+	+	Microsatellites (16)	Oh and Badyaev 2006 ($n = 30$)
House Sparrow	*Passer domesticus*	–	–	DNA Fingerprinting; MHC; Microsatellites (10)	Edly-Wright et al. 2007 ($n = 98$); Stewart et al. 2006 ($n = 126$); Bonneaud et al. 2006 ($n = 30$)
House Wren	*Troglodytes aedon*	na	–	Microsatellites (5–7)	Masters et al. 2003 ($n = 17$)**
Mexican Jay	*Aphelocoma ultramarina*	na	+	DNA Fingerprinting	Eimes et al. 2005 ($n = 31$)
Pied Flycatcher	*Ficedula hypoleuca*	na	–	DNA Fingerprinting	Rätti et al. 1995 ($n = 36$)
Reed Bunting	*Emberiza schoeniclus*	na	–	Microsatellites (6–9)	Bouwman et al. 2006 ($n = 61$); Kleven and Lifjeld 2005 ($n = 68$, $n = 53$)
Savannah Sparrow	*Passerculus sandwichensis*	±	±	DNA fingerprinting; MHC; Microsatellites (5)	Freeman-Gallant et al. 2003 ($n = 43$); Freeman-Gallant et al. 2006 ($n = 144$)
Sedge Warbler	*Acrocephalus schoenobaenus*	+	na	Microsatellites (6)	Marshall et al. 2003 ($n = 12$)
Seychelles Warbler	*Acrocephalus sechellensis*	–	–	MHC; Microsatellites (14)	Richardson et al. 2004 ($n = 43$); Richardson et al. 2005 ($n = 144$)
Shorebirds (three species) Western Sandpipers, Common Sandpipers and Kentish Plovers	*Calidris mauri; Actitis hypoleuca; Charadrius alexandrinus*	na	+	DNA Fingerprinting	Blomqvist et al. 2002 ($n = 25$, $n = 15$, $n = 65$)

Table 1 continued

Common name	Scientific name	Social mate choice	Extra-pair mate choice	Marker(s) used	References (sample size for relevant tests)
Splendid Fairy Wren	*Malurus splendens*	na	+	Microsatellites (6)	Tarvin et al. 2005 ($n = 114$)
Tree Swallow	*Tachycineta bicolor*	na	±	DNA Fingerprinting; Microsatellites (11)	Barber et al 2005 ($n = 72$); Stapleton et al. 2007 ($n = 40$, $n = 24$)***
Wandering Albatross	*Diomedea exulans*	na	−	Microsatellites (10)	Jouventin et al. 2007 ($n = 74$)

Positive evidence for genetic complementarity in social mate choice would be greater genetic dissimilarity between mated pairs compared to random male-female dyads. Positive evidence for genetic complementarity in extra-pair mate choice would include cases where EPP is positively correlated to genetic similarity between social mates or where extra-pair sires are more genetically dissimilar to females than compared to pair-bonded males or the available extra-pair males in the population. Other suggestive or indirect evidence is indicated by asterisks

na—not applicable or not studied

Number of loci for microsatellite markers shown in parentheses

+ Evidence consistent with predictions of genetic complementarity hypothesis

− Evidence inconsistent with genetic complementarity hypothesis

± Evidence mixed

* Evidence suggests cryptic, post-copulatory choice for genetically dissimilar males

** Evidence suggests females do not prefer dissimilar males but do prefer males with rare alleles

*** Extra-pair offspring from unknown sires were more heterozygous compared to those sired by known males and within-pair offspring

more likely to have their eggs fertilized by sperm obtained from genetically dissimilar males (Thuman and Griffith 2005). This suggests that choice for genetic complementarity in this species is post-copulatory and cryptic, occurring within the female reproductive tract.

For most avian species mating systems take the form of social monogamy with genetic promiscuity with females having a single pair bonded mate but engaging in extra-pair matings with additional males. These extra-pair matings often result in offspring (Bennett and Owens 2002; Westneat and Stewart 2003). Females in these species may therefore choose social mates, extra-pair mates or both on the basis of genetic complementarity. With the exception of the studies mentioned above, research on genetic complementarity in birds has focused on testing mate choice for genetic complementarity as an explanation for multiple mating outside of established pair bonds. Again, the results have been mixed (see Table 1) and often the evidence for choice of extra-pair mates is indirect. If females are choosing extra-pair sires on the basis of genetic complementarity then the expectation is that extra-pair offspring should be more heterozygous or simply more fit than their within-pair half sibs. Bluethroats (*Luscinia svecica*) sired by extra-pair males have higher scores of T-cell mediated immunity compared to both maternal and paternal half-sibs (Johnsen et al. 2000). This pattern has been found in some birds (i.e., common yellowthroat *Geothlypis trichas*, Garvin et al. 2006) but not others (i.e., reed bunting *Emberiza schoeniclus*, Kleven and Lifjeld 2004; barn swallow *Hirundo rustica*, Kleven et al. 2006a). If variation in immune performance is related to variation in sire-dam genetic interactions, as is the case for species like bluethroats and common yellowthroats, then extra-pair mate choice should favor genetically dissimilar sires. Most of these analyses examine the relationship between the prevalence of extra-pair paternity and the degree of genetic similarity between members of pair-bonded male-female dyads. A few of these studies have uncovered a significant positive relationship between genetic similarity and the prevalence of extra-pair offspring. In a comparative study of three species of shorebirds Blomqvist et al. (2002) found just this result with genetic similarity of pairs predicting extra-pair paternity. Studies examining within-population variation in extra-pair paternity have found a similar result with genetic similarity within pairs positively correlated with extra-pair paternity in Mexican jays (*Aphelocoma ultramarina*, Eimes et al. 2005), splendid fairy-wren (*Malurus splendens*, Tarvin et al. 2005), savannah sparrows (*Passerculus sandwichensis*, Freeman-Gallant et al. 2006), and house finches (*Carpodacus mexicanus*, Oh and Badyaev 2006).

Contrary to these findings Kleven et al. (2005) found that female barn swallows (*Hirundo rustica*) choose extra-pair sires that are more genetically similar compared to their pair mates. Pied flycatchers (*Ficedula hypoleuca*) also do not seem to match the traditional expectations of the genetic complementarity hypothesis when it comes to extra-pair paternity. Rätti et al. (1995) found that females paired with genetically dissimilar mates had more, not fewer, extra-pair offspring in their nests and a similar result was found for tree swallows (*Tachycineta bicolor*, Barber et al. 2005). Several other studies have found no effect of genetic similarity between females and their pair mates on the probability of extra-pair paternity (Krokene and Lifjeld 2000; Otter et al. 2001; Masters et al. 2003; Charmantier et al. 2004; Richardson et al. 2004; Kleven and Lifjeld 2005; Richardson et al. 2005; Schmoll et al. 2005; Smith et al. 2005; Stewart et al. 2006; Edly-Wright et al. 2007; Stapleton et al. 2007).

The absence of evidence for genetic complementarity in female mate choice may be an artifact of statistical sampling in those studies with too few replicates to detect what could be a small, but significant, effect. Statistical power is certainly a concern in any study, particularly field studies of birds where logistics can limit the number of independent replicates available for analysis. However, for many of the studies with negative results the sample size and number of genetic marker loci used were greater than those with positive results. Using 16 microsatellite loci across 45 episodes of female mate choice Oh and Badyaev (2006) found positive effects of genetic dissimilarity on pairing and extra-pair decisions in house finches while, for other species, studies with nearly as many microsatellite markers and approximately 2–4 times the sample size found no evidence consistent with genetic complementarity-based choice (Charmantier et al. 2004; Richardson et al. 2004; Kleven et al. 2005; Foerster et al. 2006; Stewart et al. 2006; Edly-Wright et al. 2007; Table 1). Clearly number of loci, loci variability and sample size all will affect the ability of a particular study to detect an effect of genetic complementarity on mate choice decisions, but, given that many studies with large sample sizes and many highly variable loci have failed to detect such effects, statistical limitations are not the only contributing factor to the variation across studies (Table 1).

Many studies have assumed mate choice for genetic complementarity on the basis of indirect evidence (Johnsen et al. 2000; Forstmeier and Birkhead 2004; Kupper et al. 2004; Blomqvist et al. 2005; Garvin et al. 2006; Whittingham et al. 2006; Stapleton et al. 2007). However, this indirect evidence may not stand up to direct tests. Previous results for an Austrian population of blue tits (*Parus caeruleus*) showed that extra-pair offspring were more heterozygous than their within-pair maternal half-sibs suggesting a role for genetic complementarity in female choice for extra-pair sires (Foerster et al. 2003). However in a later study on the same population Foerster et al. (2006) found no evidence that females had more extra-pair offspring when paired to genetically similar males, and a similar result was found in a Mediterranean population of blue tits (Charmantier et al. 2004). The Foerster et al. (2003, 2006) studies of blue tits in Vienna provide a cautionary tale for studies seeming to find indirect evidence of genetic complementarity-based mate choice.

These disparate results from studies of female choice for genetic complementarity in birds are reminiscent of the empirical literature on the evolutionary and ecological causes of diversity in extra-pair paternity (Petrie and Kempenaers 1998; Westneat and Stewart 2003). Despite nearly 20 years of research few ecological factors have been shown to be reliable predictors of extra-pair paternity (Westneat and Stewart 2003). Currently studies in which there is little or no evidence of female choice for more dissimilar extra-pair sires outnumber those studies finding a relationship between the genetic similarity of a pair and the prevalence of extra-pair paternity (Table 1). The evidence for pairing decisions based on genetic complementarity is also mixed and ranges from choice for genetically dissimilar males (i.e., Freeman-Gallant et al. 2003) to no genetic basis for choice of a pair male (i.e., Richardson et al. 2005) to choice favoring genetically similar males (i.e., Cohen and Dearborn 2004) to variable strategies with choice for either similar or dissimilar males varying with time of season (i.e., Oh and Badyaev 2006) or among populations (i.e., Krokene and Lifjeld 2000). Just as diversity in extra-pair mating systems within and among species has presented a major challenge to evolutionary ecologists explaining the diversity in genetic complementarity-based mate choice will also likely be a significant hurdle.

The diversity of findings among studies in regards to the importance of genetic complementarity in female mate choice may be a function of behavioral plasticity in female mating decisions. Females cannot simultaneously choose the most ornamented males and the most genetically complementary males (Colegrave et al. 2002; Mays and Hill 2004; Neff and Pitcher 2005). For both criteria to be incorporated into a female's mate choice strategy she should switch between the two mate preferences in accordance with male availability. The context-specific nature of genetic complementarity-based choice versus choice favoring exaggerated male ornaments as a signal of their genetic quality could explain the diversity of results regarding genetic complementarity-based choice in the empirical literature. Roberts and Gosling (2003) found that female mice switched strategies between preferences based on genetic complementarity versus choice based on an absolute criterion such as urinary scent marking behavior in accordance with the diversity presented to them among potential mates. A plastic strategy based on the available diversity of males likely explains how both mate choice criteria may exist in the same population (Mays and Hill 2004).

A good example of flexible criteria may be the choice strategies of female house finches. In all house finch populations studied to date colorful plumage is favored by female choice (Hill 1991; Badyaev and Hill 2002). When Oh and Badyaev (2006) looked at patterns of female mating preferences across a breeding season, they found that bright male plumage is preferred early in the breeding season, but, later in the breeding season, when the available variation in male plumage is exhausted, females prefer genetically dissimilar sires as mates. Changes in the relative frequency of highly ornamented males versus genetically dissimilar males across time and space is likely to affect the prevalence of one female mate choice criterion over another. It is easy to see how such shifts in mating strategy among females within a population could generate apparently contradictory observations among studies of choice for genetic complementarity.

Also, in certain situations it might be better to choose mates so that the number of alleles in offspring is optimized rather than maximized, and there is a possibility that females having many alleles would prefer males with few (or similar) alleles. This could be particularly true for MHC based choice, where an optimal number of MHC alleles per individual are expected due to the trade off between number of MHC alleles and number of T-cell clones (Milinski 2006). In sticklebacks (*Gasterosteus aculeatus*) females prefer dissimilar males in inbred populations, but prefer similar males in outbred ones (Aeschlimann et al. 2003; Milinski 2003). The same might be true with birds, but level of inbreeding is often unknown for many bird populations where complementary mate choice has been studied.

Variation in complementarity-based choice within and among populations is a possible explanation for the variable results from avian field studies to date, but there remains the possibility that this form of mate choice is simply a rare occurrence in birds under any circumstances. There are proximate reasons to suspect that complementarity-based choice should be rare in birds. In other vertebrates olfactory sense is well-developed and olfactory cues enable females to distinguish between genetically similar versus genetically dissimilar males (Wedekind et al. 1995; Penn 2002; Aeschlimann et al. 2003; Garner and Schmidt 2003; Milinski 2003; Olsson et al. 2003; Roberts and Gosling 2003). In contrast to fishes, amphibians, squamates, and mammals, the olfactory acuity of birds appears to be poor, although, the dismissal of avian olfaction as a meaningful sensory mode in birds has been challenged by some authors (Zelano and Edwards 2002). A limited ability to distinguish genetically dissimilar from similar males could constrain an evolutionary response to selection favoring female choice for genetically complementary sires and could explain why mate choice for genetic complementarity is comparatively rare in birds. Despite these potential limitations, however, evidence suggests that some birds do seem to make distinctions between genetically dissimilar and similar males (i.e., savannah sparrows, Freeman-Gallant et al. 2003; Freeman-Gallant et al. 2006).

Not only may potential mates be recognized on the basis of their genetic similarity, but some birds also appear to be able to make distinctions among kin. Goldeneyes (*Bucephala clangula*) have been shown to discriminate between kin when making decisions regarding conspecific brood parasitism (Andersson and Ahlund 2000) and long-tailed tits (*Aegithalos caudatus*) can distinguish kin on the basis of call variation (Hatchwell et al. 2001). Associative learning has also shown to contribute in kin discrimination on Seychelles warblers (Komdeur et al. 2004). Kin discrimination in these cases is comparatively crude, only biasing behavior in relation to first or second order relatives, and does not invoke the sort of genetic distinctions implied by models of mate preferences based on genetic complementarity (but see Kleven et al. 2005).

Birds may also rely on proxies of relatedness in their mate choice decisions. Limited opportunities for dispersal may result in local males being genetically more similar compared to rare immigrants to the population. Female preferences for unfamiliar males may evolve because of the benefits such choice provides in terms of genetic complementarity. Some data support the idea that females prefer rare males. Extra-pair sires in house wrens (*Troglodytes aedon*) have more rare alleles compared to the within-pair males they cuckold (Masters et al. 2003). Choice for unfamiliar males therefore may result in sires contributing rare, and therefore dissimilar, alleles to offspring such that choice favoring unfamiliar males will also favor genetically dissimilar males. Such proxy measures of a potential sire's genetic dissimilarity would rely heavily on the genetic structure of the population.

Limitations on a female bird's ability to make precopulatory decisions based on self-referential genetic complementarity may be overcome by post-copulatory choice. The potential interactions between sperm, ova and the female reproductive tract may provide more opportunity for distinguishing genetically similar from dissimilar sperm. If birds as a group truly have a limited capacity to distinguish genetically complementary males prior to mating then selection may favor post-copulatory mechanisms to bias fertilization against genetically similar sperm. Perhaps the best avian example of this so-called "cryptic choice" comes from the red jungle fowl (*Gallus gallus*). Pizzari et al. (2004) found that females retained less sperm from inseminations originating from brothers compared to inseminations from unrelated males. Most of the studies of female mate choice in birds are focused on reproductive outcomes. Little data on female willingness to mate with one male as opposed to another exists. Studies of genetic complementarity as a post-copulatory decision are much more amenable to experimental manipulation as the researcher may uncouple behavior from reproductive outcomes. Distinguishing pre from post-copulatory female mate choice strategies remains a major challenge in assessing the relative importance of different models of sexual selection in birds.

Consequences of genetic complementarity-based choice

Female mate choice for genetically dissimilar and thus genetically complementary males has some important implications for sexual selection on male traits. Indicator models of mate choice and those based on based on genetic complementarity differ in the expected variation in male reproductive success as a result of different female mating preferences. If females seek good genes and use an absolute criterion of male attractiveness, such as sexual ornaments, bearers of these genes/ornaments should be disproportionably more successful in attracting females and realize higher reproductive compared to other males in a population. Such directional selection for traits leads to high variation in reproductive success among males and to increased opportunity for sexual selection (variance in reproductive success divided by its mean squared, Shuster and Wade 2003). On the other hand, mate choice based on genetic complementarity does not select for one best phenotype or genotype. Any given male might be the best match for any given female. In such a system, the variation among males in reproductive success and the opportunity for sexual selection might be comparatively low since no one male in a population is generally attractive to all females (Mays and Hill 2004; Neff and Pitcher 2005).

Extra-pair fertilizations in socially monogamous songbirds provide an opportunity to test the effects of 'genetic complementarity' and 'good genes' mate choice on variation in male reproductive success. Indirect (genetic) benefits to females should play a central role in choice of extra-pair mate, because females apparently obtain only sperm from these mates (Griffith et al. 2002). In most passerine species analyzed to date, extra-pair mating increases the opportunity for sexual selection (Whittingham and Dunn 2005; Albrecht et al. 2007). However, the importance of extra-pair mating to variance in male reproductive success varies considerably across species from no effect in great-reed warbler *Acrocephalus arundinaceus* (Hasselquist et al. 1995) to many-fold increase in barn swallow *Hirundo rustica* (Kleven et al. 2006b). Surprisingly, there seems to be no positive correlation between the levels of promiscuity and the contribution of extra-pair fertilizations to variance in male reproductive success in songbirds (Freeman-Gallant et al. 2005). One possible but often neglected explanation is that genetic complementarity plays a role in extra-pair mating decisions in at least some passerine species. When females are incongruent in extra-pair mating preferences, low contribution of extra-pair fertilizations to variance in male reproductive success should be expected even at relatively high rates of promiscuity. Low effects of extra-pair fertilizations on the opportunity for sexual selection accompanied with moderate or high levels of promiscuity might therefore indicate the choice of extra-pair mate based on genetic complementarity, such as in Savannah Sparrow *Passerculus sandwicensis* (Freeman-Gallant et al. 2003, 2006). This hypothesis requires further testing.

Conclusions

There remain many questions regarding self-referential, complementarity-based mate choice in birds; first among these is the ubiquity of this variety of mating preference in birds. Simple correlative datasets are a logical start. Data on variation in male reproductive success, consistency of mating decisions across females, comparisons of genetic similarity among pairs compared to random male-female dyads, heterozygosity of pair versus extra-pair offspring, prevalence of extra-pair offspring in relation to pair genetic similarity and genetic similarity between females and extra-pair sires compared to that between females and their pair mates or random dyads can all provide clues to the existence of genetic complementary-based mate choice. However, these correlations may or may not be the direct result of an active female strategy evolved in response to selection for heterozygous offspring. More detailed behavioral data and experimental approaches would be needed to unequivocally test the genetic complementarity hypothesis. Field and aviary mate choice trials would be very useful in this regard and mate removal experiments involving females could be done as part of a field based mate choice experiment. If genetic complementarity is important then replacement females should settle with the most genetically complementary males as opposed to the most ornamented males or those males occupying the most productive territories. Of course such a design is best suited for cavity nesting species. For other birds direct experimental tests will prove more difficult and researchers may have to adopt other approaches such as detailed behavioral observations of female behavior during extra-pair encounters to better understand the relationship between extra-pair behavior and extra-pair fertilizations.

Large comparative datasets like those available for extra-pair paternity in birds (Bennett and Owens 2002) would be very useful not only in determining the ubiquity of this phenomenon among avian species but also in providing clues to the evolution of complementary based choice and understanding the consequences of such behavior. Simple metrics using the same genetic markers employed for determining paternity such as genetic similarity among pairs versus random male-female dyads could be reported alongside paternity data. These measures may have limited utility compared to pedigree data (Slate and Pemberton 2002; Pemberton 2004; Slate et al. 2004) but pedigree data are difficult to obtain outside of small, isolated populations. In most cases use of carefully chosen genetic markers will be a necessary alternative to pedigrees. Using the maximum number of markers practical is advised, however, given that significant correlation between microsatellite markers and various correlates of fitness have been found in studies with as few as 5 microsatellite loci (Hansson et al. 2001; Foerster et al. 2003) researchers should not ignore testing genetic complementary solely because they believe they have too few markers. Researchers may even examine the possibility of complementary based pairings and heterosis as an ancillary piece of data to accompany a paternity study.

Marker choice is likely to be important. Most often genetic markers chosen for studies of parentage are those loci that do not deviate from Hardy–Weinberg (H–W) equilibrium, but choice for genetic dissimilarity should produce deviations from H–W. An excess of heterozygotes for a microsatellite locus could be an indicator that these alleles are linked to genes involved in non-additive heterosis based fitness variation and therefore the targets of mate choice for genetic complementarity. Omitting these loci from a study may prevent the detection of complementary-based choice.

Attention should also be paid to genetic complementarity as a potential criterion for social mates as well as extra-pair mates. The continuing effort to explain extra-pair mating systems in birds has directed much of the research on complementary-based choice towards explaining variation in multiple mating in avian systems. Focusing on choices of pair mates may strip tests of much of the debate on control of extra-pair copulations (Westneat and Stewart 2003) and provide more direct support for those cases where females are choosing mates on the basis of genetic complementarity. In addition to comparing genetic similarity of actual mates against genetic similarity generated for random male-female dyads, direct tests of choice based on genetic complementarity consisting of mate choice trials either in the field or aviary could be used. These direct experimental approaches could examine social mate choice while controlling for other factors, like territory quality.

Genetic complementarity holds promise as an explanation for patterns of female mate choice in wild birds, but at present its true importance in avian mating systems remains unclear. Clearly there are some cases where genetic dissimilarity is used as a criterion for mate choice in birds, however these cases may be the exception rather than the rule. Explaining variation in the importance of genetic complementarity remains a major challenge on par with the related and ongoing debate on the ecological correlates of extra-pair mating systems in birds.

Acknowledgements Thanks to two anonymous referees who contributed very useful comments to this manuscript. HLM, ML and GEH were supported under National Science Foundation Grant #NSF-IBN0235778 and TA was supported through funding from Charles University in Prague and The Academy of Sciences of the Czech Republic, and the Grant Agency of the Czech Republic (MSMT 0021620828, AV0Z60930519 and 206/06/0851).

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