Genetic similarity, extrapair paternity, and offspring quality in Savannah sparrows (*Passerculus sandwichensis*)

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The occurrence of extrapair paternity (EPP) in birds is often attributed to the action of good-genes sexual selection whereby females "trade up" on male genetic quality by allocating fertilizations to males with better genes than those possessed by their social mate. To date, most studies of EPP in birds focus on absolute measures of male quality as a criterion for female choice, although multiple mating by females in other taxa is more commonly ascribed to benefits associated with the individual optimization of offspring genotypes. Here, we examine whether the genetic similarity of social mates predicts female mating patterns in a population of Savannah sparrows (*Passerculus sandwichensis*) where as many as 70% of adults produce extrapair young (EPY). We consider the influence of genetic similarity across all stages of a female's decision-making process, from pair formation through the decision to produce EPY, to the allocation of fertilizations to specific extrapair sires. In a 4-year study of 175 males, 206 females, and 506 offspring, females were more likely to produce EPY when paired to genetically similar males, but they did not appear to be influenced by the size, age, mass, individual heterozygosity, and genetic diversity of their social mates. In paired comparisons, females were almost twice as likely to decrease their genetic similarity to males when producing EPY as they were to increase it. Nonetheless, females did not select especially dissimilar males when mating outside the pair-bond nor did they pair disassortatively with respect to genetic similarity. Relative measures of male quality may influence mating patterns in birds, but only at some points in a female's decision-making process. *Key words:* EPP, genetic compatibility, microsatellites, relatedness, sexual selection. *[Behav Ecol 17:952–958 (2006)]*

Multiple mating by females occurs in numerous taxa, including species in which females socially pair with males (Birkhead and Møller 1998; Simmons 2001; Zeh and Zeh 2001). In birds, multiple mating by females is a widespread but potentially costly strategy whereby females allocate fertilizations to males other than their social mate (Griffith et al. 2002; Westneat and Stewart 2003). Because females appear to obtain little direct benefit by mating outside the pair-bond, early efforts to explain this extrapair paternity (EPP) focused on indirect genetic benefits associated with the choice of high quality males as extrapair sires (Birkhead and Møller 1998). In some species, females do appear to increase the genetic quality of young by allocating fertilizations to older, larger, brighter, or more elaborate males (Hasselquist et al. 1996; Sheldon et al. 1997; but see Schmoll et al. 2003; Arnqvist and Kirkpatrick 2005).

Interestingly, the adaptive significance of multiple mating by females in other taxa has focused largely on indirect genetic benefits associated with the choice of complementary males rather than the choice of high quality males per se (Jennions and Petrie 2000; Tregenza and Wedell 2000). For example, females might mate with multiple males to avoid inbreeding or to generate particularly adaptive combinations of alleles (genotypes) at one or several key loci (Potts et al. 1991; Landry et al. 2001). This form of good-genes sexual selection is distinct from more traditional formulations of the good-genes hypothesis because it predicts the presence of individual- or genotype-dependent mating preferences and optima (Brown 1997). Only females with similar genotypes should agree on male quality.

Although increasing genetic similarity of mates has long been known to reduce female fitness in birds via decreased hatching success (Bensch et al. 1994; Kempenaers et al. 1996; Amos et al. 2001) and recruitment (Keller et al. 1994; Hansson et al. 2001), researchers have only recently considered the role of inbreeding avoidance in the context of EPP. Preliminary results are mixed. In some species, disassortative mating is evident in the choice of extrapair sires (Foerster et al. 2003; Masters et al. 2003; but see Bartos Smith et al. 2005; Schmoll et al. 2005). Other studies have shown that EPP is more likely to occur when females are socially paired to genetically similar males (Blomqvist et al. 2002; Freeman-Gallant et al. 2003; Eimes et al. 2005; but see Barber et al. 2005). For few species, do we know how genetic similarity influences female mating patterns across all stages of a female's decision-making process, from pair formation through the decision to be "faithful" or "unfaithful," to the allocation of fertilizations to specific extrapair sires (Oh and Badyaev 2006).

Here, we describe the importance of absolute and relative measures of male quality to social and genetic mating patterns in a population of Savannah sparrows (*Passerculus sandwichensis*) showing high rates of EPP. Forty-five percent of young derive from extrapair fertilizations in this population (Freeman-Gallant et al. 2005). We were able to identify the parentage of most young, allowing us to compare the attributes of within- and extrapair males and consider the importance of parental genetic similarity to offspring quality and success. Savannah sparrows appear to avoid social kin in the

choice of mates, although certain types of close inbreeding are especially avoided (Wheelwright and Mauck 1998; Wheelwright et al. 2006). The importance of subtle (nonincestuous) levels of inbreeding to female mating patterns has not been thoroughly explored (Freeman-Gallant et al. 2003).

MATERIALS AND METHODS

We studied mate choice in a population of Savannah sparrows breeding at the Bowdoin Scientific Station on Kent Island, New Brunswick, Canada from 1994–1995 and from 2002–2003 as part of a longer term (1987–2004) study. Savannah sparrows are migratory passerines found in grassland habitats across North America (Wheelwright and Rising 1993). On Kent Island, they show high natal and breeding philopatry (Wheelwright and Mauck 1998). In any 1 year, as many as 53–79% of adults are of known age and social pedigrees extend an average of 3 generations. All adults in our study area were individually marked with a random combination of 3 colored leg bands and a United States Fish and Wildlife Service aluminum band. At the time of banding, we measured the wing length (to nearest 0.5mm) and mass (to nearest 0.1g) of each adult and obtained a small sample of blood (50–75 µl) from the brachial vein. We identified social pairs based on observations of mate guarding, territory defense, and parental care (Wheelwright and Mauck 1998). Nests were found by following females during the incubation stage and censused every other day to determine date of hatching. On Kent Island, all eggs within a clutch typically hatch within 24–36 h (Wheelwright and Rising 1993). Young were banded, measured (mass, wing length), and sampled on day 8, where the first occurrence of hatching is day 1. We stored blood in a lysis buffer (Seutin et al. 1991) until DNA could be isolated after a series of phenol and phenol–chloroform extractions. Offspring were sexed by amplifying a diagnostic region of the *CHD* gene via the polymerase chain reaction (see Kahn et al. 1998 and Freeman-Gallant et al. 2001 for full details).

We used residuals of a regression of offspring mass on wing length as a measure of the condition of young. Savannah sparrow nestlings typically fledge after 10–12 days in the nest (Wheelwright and Rising 1993). Both the mass and size-adjusted mass (condition) of young are positively correlated with survivorship to independence and recruitment in Savannah sparrows (NT Wheelwright and CR Freeman-Gallant, unpublished data), as they are in other birds (Hochachka and Smith 1991).

Female mating fidelity was determined by screening broods for the presence of extrapair young (EPY). In 1994 and 1995, paternity analysis was conducted with multilocus DNA fingerprinting profiles generated by a $(GGAT)_4$ oligonucleotide probe or, in the case of 7 nests, by segregation analysis of restriction fragment length polymorphism bands generated by class II β gene fragment cloned from the sparrows' major histocompatibility complex (*MHC*; see Freeman-Gallant et al. 2003 for details of oligonucleotide and *MHC* fingerprinting). Extrapair sires were not identified in 1994 and 1995. In 2002 and 2003, we used a suite of 4–6 microsatellite loci to identify EPY and their sires. Except in a single instance of apparent mutation, offspring always matched their mothers at all loci, allowing us to rule out the possibility of intraspecific brood parasitism and identify unambiguously the set of paternal alleles inherited from each offspring's sire. Paternal alleles found in offspring but not in their social fathers were taken as evidence of EPP. Extrapair sires were identified by comparing the EPY's paternal haplotype with the genotypes of all males breeding in the study site each year. Over the 2 years combined (2002–2003), we were able to assign parentage to 396 of 411 nestlings (96.4%) including sires for 179 of 194 EPY (92.3%; Freeman-Gallant et al. 2005).

For each year of the study, we used 5 microsatellite loci to quantify the genetic similarity between females and all males breeding in the study site at the same time. Following Li et al. (1993), we calculated a single-locus estimator of relatedness (r_{xy}) based on the similarity index (S_{xy}) between individuals x and y, where $S_{xy} = 1$ when genotype $x = $ aa and genotype $y = $ aa; $S_{xy} = 0.75$ when genotype $x = $ aa and genotype $y = $ ab; $S_{xy} = 0.50$ when genotype $x = $ ab and genotype $y = $ bc; and $S_{xy} = 0$ when genotype $x = $ ab and genotype $y = $ cd. Li et al. (1993) show that if the expected similarity among unrelated individuals (S_0) is

$$S_o = 2 \sum p_i^2 - \sum p_i^3,$$

then

$$r_{xy} = \frac{S_{xy} - S_o}{1 - S_o},$$

where p_i is the population allele frequency of allele i.

We combined r_{xy} estimates across loci by weighting the contribution of each locus by its inverse sampling variance (found empirically by assuming individuals x and y were unrelated and examining the distribution of r_{xy} values around the mean of 0; Lynch and Ritland 1999). Van de Casteele et al. (2001) show that Li's relatedness estimator is robust in comparison with other relatedness estimators, particularly when a sizeable fraction of individuals are related and/or when there exists variation among loci in the degree of polymorphism. Both situations hold in Savannah sparrows (Wheelwright and Mauck 1998; Freeman-Gallant et al. 2005; Wheelwright et al. 2006). We tested Li's estimator on a set of 56 offspring from 15 nests known from micosatellite paternity analysis to be full siblings. Here, mean r_{xy} was 0.51 ± 0.03 (standard error [SE]) and the interquartile range 0.37–0.63. In comparison, mean r_{xy} for 14 pairs of maternal half-sibs was $0.32 \pm .05$ (SE), significantly lower than the similarity observed among full sibs (*t*-test, df = 68, $t = 3.44$, $P = 0.001$). Assuming a homoscedastic distribution of r_{xy} values around true means of 0.50 and 0.25, and using the empirically derived distribution of r_{xy} values from the full-sib analysis, a critical value of $r_{xy} > 0.27$ captures 90% of all first-order kin (coefficient of relatedness = 0.5; full siblings, father–daughter, mother–son) and at least 50% of all second-order kin (coefficient of relatedness = 0.25; half-siblings, uncle–niece, aunt–nephew) among pairs of adults with unknown genetic relatedness. We thus categorized pairings between adults showing $r_{xy} > 0.27$ as "genetically incestuous." Apart from this one distinction, we use r_{xy} values as estimates of overall genetic similarity between individuals, not as indices of true r_{xy} (which are better estimated with social pedigrees confirmed by molecular paternity analysis).

We used our full complement of 6 microsatellite loci (the 5 autosomal loci used to calculate r_{xy} described above and an additional Z-linked locus, *Psa*29) to calculate a male's individual heterozygosity (H) and genetic diversity. Heterozygosity is the proportion of loci for which an individual was heterozygous. Genetic diversity (mean d^2) is the squared difference in number of repeated units between the 2 alleles at a given microsatellite locus averaged across loci (Coltman et al. 1998; Coulson et al. 1998). Assuming a stepwise mutation model, mean d^2 is sensitive to both inbreeding (generating low mean d^2 values) and outbreeding (generating high mean d^2 values) and may be interpreted as a measure of the genetic distance between the gametes that formed an individual (Coulson et al. 1998). Prior to analysis, heterozygosity was square root arcsine transformed and mean d^2 was $\log_{10}$ transformed to improve normality.

Over the 4 years of the study, we observed 175 males and 206 females. Mating fidelity was known for 144 of these females (69.9%). In total, 60 of these observations derive from 30 females who were present in consecutive years (1994 and 1995 or 2002 and 2003). In all but 3 cases, returning females paired with different males. Nonetheless, we tested whether this pseudoreplication affected the results by randomly choosing only a single set of observations for each of the 30 repeated females. Because analyses with and without these exclusions were qualitatively and quantitatively similar, only the results from the full data set are presented below.

Analyses were performed using StatView version 4.5.1 or JMP version 5.12 for the Macintosh. Residuals were normal and approximately homoscedastic throughout, justifying the use of parametric statistics. All P values are 2 tailed.

RESULTS

Social mates

There is no evidence to suggest that females avoided pairing with genetically similar males. Mean similarity between social mates reflected the overall distribution of similarity values obtained by pairing each female to all males present in the population each year (one-sample t-tests, $P > 0.46$; Table 1). Although pairings between especially similar birds ($r_{xy} > 0.27$) were rare (see also Wheelwright et al. 2006), few such pairings were expected given the overall distribution of similarity values between females and potential mates (Table 1). Of the 7 genetically incestuous pairings we observed, 3 were between birds with known social pedigrees and 3 more were between birds where social parentage was known for 1 of the 2 adults. In no case did the birds appear to share recent common ancestry (i.e., mother–son, father–daughter, etc.).

Female mating fidelity

Rates of EPP were high in all years. Forty-seven of 64 females (73.4%) produced EPY in 2002, whereas 32 of 52 females (61.5%) produced EPY in 2003 (Freeman-Gallant et al. 2005). The lowest incidence of EPP occurred in 1995 when 10 of 18 females (55.6%) produced EPY. In 1994, 7 of 10 females (70.0%) produced EPY. Differences among years in the percentage of females producing EPY were not significant ($\chi^2 = 2.99$, df = 3, $P = 0.39$), and over all years combined, 96 of 144 females (66.7%) produced at least one extrapair offspring.

On average, females that produced young outside the pairbond showed higher genetic similarity to their social mates than females who produced only within-pair young (WPY; 2-way ANOVA controlling for year, $F_{1,136} = 7.06$, $P = 0.009$;

Figure 1). Males paired to faithful females, however, were no different in size, mass, age, genetic diversity, or heterozygosity than males paired to unfaithful females (2-way ANOVAs controlling for year, $P > 0.20$; Table 2). In a series of logistic regressions with year as a covariate, only genetic similarity between social mates tended to be correlated with the occurrence of EPY in a female's brood (Wald $\chi^2 = 3.62$, df = 1, $P = 0.057$; all other $P > 0.43$).

Extrapair mates

In 2002 and 2003, we identified sires for 179 of 194 EPY (92.3%), which allowed us to compare the genetic and phenotypic characteristics of social and extrapair mates. In paired comparisons pooling over the 2 years, extrapair males were not older, heavier, longer winged, or more genetically diverse than the males they cuckolded (paired t-tests, $P > 0.17$) but unexpectedly they tended to be less heterozygous ($t = -1.80$, df = 55, $P = 0.077$). When the 2 years were considered separately, only in 2003 were extrapair sires significantly less heterozygous than the males they cuckolded ($t = -2.03$, df = 32, $P = 0.05$). These paired comparisons exclude 11 broods in 2002 and 6 broods in 2003 where the female produced EPY with more than one male.

EPP often resulted in fertilizations from less genetically similar males. In paired comparisons involving 47 females where extrapair copulations could have resulted in fertilizations by males more or less similar to the female than the female's social mate (i.e., where choice was possible), females were almost twice as likely to decrease their similarity to males when producing EPY ($n = 29$) as they were to increase it ($n = 15$; paired sign test, $P = 0.049$). In 3 cases, females already paired to relatively dissimilar males chose extrapair sires to whom they were equally dissimilar (mean genetic similarity between these 3 females and their social mates = -0.06 ± 0.05 [SE]).

There is no evidence to suggest that females targeted especially dissimilar males when producing EPY. Among the 47 females identified above, mean genetic similarity between females and extrapair sires did not differ significantly from the overall distribution of similarity values obtained by comparing females with all males that nested within 87 m of the focal nest (one-sample t-test, $t = 0.063$, df = 46, $P = 0.95$), the distance within which sires for 95% of all EPY were found (Freeman-Gallant et al. 2005).

Fitness consequences of EPP and parental similarity

Pooling over 2002 and 2003, extrapair offspring were heavier (paired t-test, $t = -2.10$, df = 48, $P = 0.041$) and tended to be

Table 1

Genetic similarity (r_{xy}) between females and their social mates compared with r_{xy} between females and all males present in the population each year. Data are presented as mean $\pm$ SE (n)

| Year | Genetic similarity of females to | | | Incestuous pairings[a] | | | |
	Social mate	All males	P[b]	% expected	No. expected[c]	% observed	No. observed
1994	-0.03 ± 0.03 (26)	-0.02 ± 0.01 (780)	0.70	4.4	1.1	0.0	0
1995	0.00 ± 0.02 (50)	-0.02 ± 0.00 (2250)	0.46	3.4	1.7	6.0	3
2002	-0.01 ± 0.02 (64)	-0.01 ± 0.00 (3840)	0.73	4.1	2.6	4.7	3
2003	-0.02 ± 0.02 (52)	-0.01 ± 0.00 (2160)	0.80	4.1	2.2	1.9	1

[a] A pairing is considered genetically incestuous if $r_{xy} > 0.27$ (see Methods).

[b] One-sample t-test comparing mean r_{xy} of social mates to mean r_{xy} between females and all males present in the population.

[c] Null expectation assumes that the potential for incestuous pairing is distributed uniformly across females.
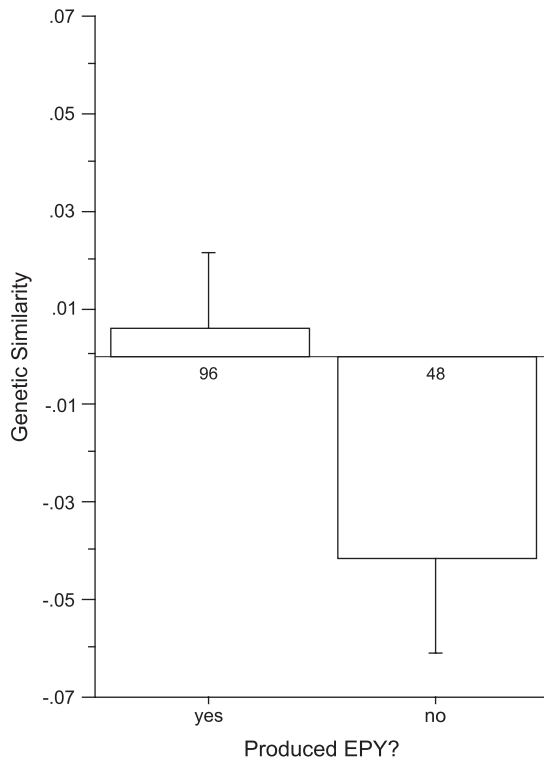
Figure 1
Females that produced at least one extrapair offspring were more genetically similar to their social mates than females that produced only within-pair offspring. The estimator of Li et al. (1993) was used to calculate genetic similarity (relatedness; r_{xy}) based on 5 microsatellite loci. Figure shows mean $\pm$ SE.

in better condition on day 8 (paired t-test, $t = -1.87$, df = 48, $P = 0.068$) than within-pair offspring from the same nest, although nestling wing length was unaffected by parentage ($P > 0.25$). Because male nestlings were heavier and in better condition by day 8 than female nestlings (2-way ANOVA controlling for year, $F_{1,383} > 30.5$, $P < 0.002$), it is possible that EPP effects were mediated by offspring gender. Although EPY showed a greater (though nonsignificant) tendency to be male in 2003 (56.9% of 65 EPY were male compared with 43.4% of 122 WPY; $\chi^2 = 3.09$, $P = 0.08$), EPY were not disproportionately male in 2002 (42.1% of 121 EPY were male compared with 40.0% of 95 WPY; $\chi^2 = 0.10$, $P = 0.75$). Moreover,

Table 2
Genetic and phenotypic characteristics of males according to within-pair mating success. Data are pooled over years and presented as mean $\pm$ SE (n). P values derive from a 2-way ANOVA controlling for year

	Full paternity	Lost paternity	P
Wing length (mm)	60.1 $\pm$ 0.2 (94)	69.0 $\pm$ 0.2 (47)	0.43
Mass (g)	20.3 $\pm$ 0.1 (95)	20.5 $\pm$ 0.2 (46)	0.21
Age[a]	1.8 $\pm$ 0.1 (79)	1.8 $\pm$ 0.1 (37)	0.70
Heterozygosity (H)[b]	0.9 $\pm$ 0.01 (96)	0.9 $\pm$ 0.02 (48)	0.60
Genetic diversity (mean d^2)[b]	96.0 $\pm$ 6.9 (96)	108.0 $\pm$ 10.8 (48)	0.20

[a] Males from 2002 and 2003 only.

[b] Untransformed values are given for heterozygosity (H) and genetic diversity (mean d^2).

pooling over nests, EPY were in better condition at fledging than WPY regardless of gender, at least in 2002 (2-way ANOVA controlling for gender; $F_{1,196} = 5.59$, $P = 0.019$, Figure 2). In 2003, these differences in condition were not statistically significant (2-way ANOVA controlling for gender; $F_{1,176} = 2.57$, $P = 0.11$, Figure 2).

Parental similarity did not predict the condition, mass, or size of daughters in either year (Table 3). However, in 2003, the mass of sons declined significantly with increasing parental similarity. Sons produced by the most genetically similar adults fledged 2.2 g lighter on average than sons produced by the least similar adults. Wing length on day 8 also appeared to decline with the increasing genetic similarity of parents in 2003 (Table 3). There was no effect of parental similarity on offspring quality or success in 2002.

DISCUSSION

Based on traditional models of good-genes sexual selection, female birds are predicted to cuckold poor quality social mates in preference for males that are of intrinsically higher genetic quality (Birkhead and Møller 1998). Good-genes sexual selection by females can also take the form of complementary choice where the ultimate goal is to produce offspring with a more advantageous (or less incompatible) combination of maternal and paternal haplotypes (Brown 1997; Tregenza and Wedell 2000; Neff and Pitcher 2005). We found that female Savannah sparrows are more likely to produce EPY when paired to genetically similar males but that females' decisions about mating fidelity are largely insensitive to absolute measures of male quality, including the size, mass, and age of their social mates. Observations of increased heterozygosity among EPY have suggested the presence of disassortative mating in some songbirds (Foerster et al. 2003), but this study provides direct evidence that genome-wide levels of similarity can predict female mating fidelity. Similar results have been previously described in shorebirds (Blomqvist et al. 2002; Thuman and Griffith 2005), where EPP is less widespread, and in other passerines where females risk fertilizations from close kin (Eimes et al. 2005; Tarvin et al. 2005).

Our earlier work with Savannah sparrows revealed disassortative mating with respect to genetic similarity at the *MHC* (Freeman-Gallant et al. 2003), but it was unclear whether females cuckolded males according to relatedness, similar *MHC* haplotypes, or both. The present results confirm that overall genetic similarity is informative and indicate that females can evaluate subtle levels of similarity among males to avoid even nonincestuous levels of inbreeding. Only 6 of 144 females with known mating fidelity in our study were apparently paired to close kin based on genetic similarity values, and when these 6 birds were excluded, genetic similarity continued to predict the occurrence of EPP. Avoidance of close genetic relatives was not responsible for generating the overall patterns described here.

In cases where a female could choose among potential extrapair sires either more similar or less similar than her social mate, females were almost twice as likely to decrease their genetic similarity to males when producing EPY as they were to increase it. However, there is no evidence to suggest that females selected especially dissimilar males from the set of males breeding within 87 m of the focal nest, the "neighborhood" from which extrapair sires are typically recruited (Freeman-Gallant et al. 2005). For example, in 2002, only 7 of 46 females (15.2%) secured extrapair fertilizations from the least similar male in their neighborhood. Moreover, the average genetic similarity between females and extrapair sires was not significantly lower than the genetic similarity between females and all males available locally. Taken together, these
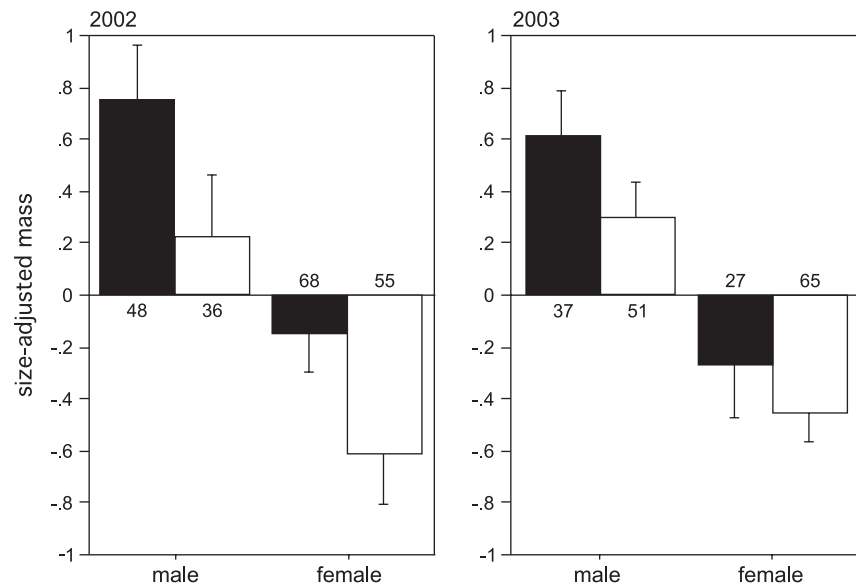
Figure 2
EPY (shaded boxes) showed greater mean size-adjusted mass on day 8 than WPY (open boxes), regardless of gender. Differences between WPY and EPY were only significant in 2002, however. Figures show mean ± SE. Sample sizes differ from total number of offspring with known parentage because several young in both years were not measured on day 8.

observations may indicate that females assess their genetic similarity to their social mates, choose to cuckold them if they are similar, but then mate at random with respect to their genetic similarity to local males. Because the relative abundance of less similar males depends strongly on the extent of genetic similarity between females and their social mates (Figure 3), such a strategy should result in fertilizations from more compatible (less similar) males as long as similar social mates are reliably identified and cuckolded.

EPP appears to be advantageous for females producing EPY. EPY fledged heavier and tended to be in better condition than WPY in the same brood, indicating that they probably also had higher survivorship (NT Wheelwright and CR Freeman-Gallant, unpublished data). In part, this result may be attributed to the underlying importance of parental similarity to offspring quality. The fledging mass of sons (but not daughters) declined substantially with increasing parental similarity, at least in 2003. Growth rates (reflected in wing length at fledgling) also appeared to be negatively correlated with parental similarity. In 2002, however, there was no relationship between parental similarity and any index of offspring quality. In this context, it is potentially revealing that we observed in 2002 the highest rates of nestling attrition ever recorded on Kent Island. Stochastic sources of mortality may have obscured the relationship between parental similarity and offspring quality that year.

If females are able to assess their genetic similarity to social mates when making decisions about their mating fidelity, and if the genetic background of offspring truly influences their quality, why do females not avoid genetically similar males as social mates or consistently select dissimilar males as extrapair sires? Females do appear to avoid choosing some classes of close social kin (Wheelwright et al. 2006), but they seem

Table 3
Effect of parental similarity (r_{xy}) on indices of offspring quality after controlling for hatching date and brood size with multiple regression; male and female nestlings are analyzed separately by year because of pervasive gender effects on condition and mass. The analyses consider 79 males and 115 females in 2002 and 95 males and 89 females in 2003

	Sons				Daughters			
	2002		2003		2002		2003	
Model	β[a]	P	β	P	β	P	β	P
Offspring condition								
Parental r_{xy}	−0.10	0.93	−0.81	0.25	−0.73	0.38	0.82	0.20
Hatching date	−0.06	0.01	−0.04	0.01	−0.07	0.01	−0.04	0.01
Brood size	−0.52	0.02	−0.28	0.16	−0.67	0.01	−0.19	0.20
Offspring mass								
Parental r_{xy}	0.05	0.98	−2.52	0.03	−0.76	0.58	1.33	0.21
Hatching date	−0.02	0.50	−0.06	0.01	−0.02	0.40	−0.04	0.01
Brood size	−1.05	0.01	−0.95	0.01	−0.60	0.07	−0.83	0.01
Offspring wing length								
Parental r_{xy}	0.39	0.91	−4.12	0.06	−0.07	0.98	1.47	0.51
Hatching date	0.10	0.10	−0.06	0.10	0.14	0.01	−0.04	0.32
Brood size	−1.36	0.04	−1.62	0.01	0.18	0.79	−1.56	0.01

[a] β values are partial regression coefficients.
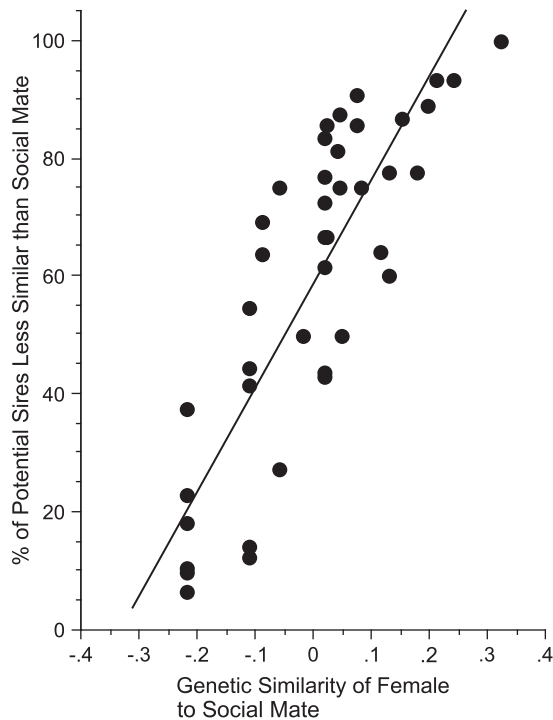
Figure 3
Relationship between the genetic similarity of a female to her social mate and the local availability of less similar males. Local neighborhoods become enriched with dissimilar males when the similarity between a female and her social mate increases (2002 data; simple linear regression, $n = 43$ females, $P < 0.001$).

unable to avoid genetically similar birds with whom they have no social experience (e.g., birds related via EPP) or even their own sons when choosing social mates and seeking extrapair copulations (Wheelwright et al. 2006). These results may suggest that the decision to produce EPY depends on a different set of cues not available to females at the time of pair formation or when extrapair mates are selected. For example, the proximity associated with repeated copulation after pairing may be required for females to evaluate their genetic similarity to males (via odor cues) or cryptic female choice of genetically dissimilar sperm may occur within the female's reproductive track (Thuman and Griffith 2005). Before copulating with a male, a female may have insufficient information about his genetic similarity, in which case females may have to base mating decisions on other male attributes.

Evidence that complementary mate choice occurs at some stages of reproduction in birds has important implications. If disassortative mating in the context of EPP proves to be widespread, there is little reason to equate the prevalence of EPP with the opportunity for selection in comparative studies because EPP may have only a moderate effect on variation in male fertilization success (contra Møller and Ninni 1998). This is because males that maintain full within-pair paternity should not be uniformly attractive as extrapair sires, only attractive to females with complementary genotypes. As a result, any statistical covariance between within- and extrapair mating success would be minimized, thereby constraining the influence of EPP on the overall variance in male fertilization success (Webster et al. 1995, Freeman-Gallant et al. 2005). Complementary mate choice could thus help explain a growing paradox: some of the most promiscuous passerines (with EPP accounting for more than 40% of all young) are also among the most dull or sexually monochromatic, showing

little evidence of the strong sexual selection for exaggerated traits that might be predicted based on their high rates of EPP. Tree swallows (*Tachycineta bicolor*, Kempenaers et al. 1999), Savannah sparrows, and red-eyed vireos (*Vireo olivaceus*; Morton et al. 1998) fall in this category.

All stages of a female's decision-making processes must be considered before conclusions regarding the importance of genetic compatibility mechanisms of female choice can be drawn. The limited information on complementary mate choice in birds gathered to date suggests that overall genetic similarity can be an important determinant of EPP but, apparently, not social mating patterns (Rätti et al.1995; Blomqvist et al. 2002, Foerster et al. 2003; Masters et al. 2003; but see Oh and Badyaev 2006). Whether this result is artifactual or arises from real behavioral, ecological, or selective constraints remains to be determined.

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