



Asymmetrical incest avoidance in the choice of social and genetic mates

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Mating with close relatives generally results in reduced reproductive success (inbreeding depression) because it increases the risk that rare deleterious recessive alleles will be expressed in offspring. None the less, incest may occur when animals have incomplete knowledge about relatedness or when the costs of avoiding inbreeding are high. Over a 17-year period, Savannah sparrows, *Passerculus sandwichensis*, in an island population rarely paired incestuously (9 of 1110 pairs, 15 of 1609 nesting attempts). All but one case of close inbreeding (coefficient of inbreeding, $F \geq 0.25$) involved 1-year-old males breeding for the first time, whereas more than half of the cases involved females that were 3 years old or older. Father–daughter matings were avoided completely. Incest avoidance was apparent in the choice of genetic as well as social mates. Paternity analysis using microsatellites revealed that birds nearly always refrained from choosing close relatives as genetic mates. These results support a model of asymmetrical incest avoidance, which predicts differences in the likelihood of incestuous matings as a function of sex, age and relationship, even when coefficients of inbreeding are identical. The model and results also emphasize the importance of distinguishing types of inbreeding and considering the social and historical context of animals' mating choices. The model may help to explain such patterns as female-biased natal dispersal in birds.

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Mating with close relatives generally results in reduced reproductive success (inbreeding depression) because it increases the risk that rare deleterious recessive alleles will be expressed in offspring (Keller et al. 1994; Landry et al. 2001; Kruuk et al. 2002). As a consequence, natural selection should favour mechanisms to avoid inbreeding. Among animals, the major inbreeding-avoidance adaptations are natal dispersal and kin recognition (Greenwood 1980; Pusey & Wolf 1996; Gardner et al. 2001). In mammals, for example, young males tend to disperse further from their natal site than do females, which reduces the probability of accidental matings between siblings and between mothers and sons (Greenwood 1980). Where dispersal is not an option and chance encounters with close relatives are unavoidable, as in saturated or isolated habitats such as islands, inbreeding avoidance requires the ability to recognize kin and to refrain from mating

with them. Two mechanisms of kin recognition are possible. Individuals could learn to identify close relatives through early experience, such as interactions with parents, littermates or nestmates (Bateson 1978; ten Cate 1999; Russell & Hatchwell 2001; Komdeur et al. 2004). Alternatively, individuals could use cues that reflect genetic similarity independent of experience and familiarity (Penn & Potts 1999; Petrie et al. 1999; Hauber & Sherman 2001; Freeman-Gallant et al. 2003). The likelihood of asymmetrical incest avoidance will be influenced by which mechanism animals use.

Model of Asymmetrical Incest Avoidance

In theory, matings that have the same coefficient of inbreeding (F) should result in equivalent levels of inbreeding depression (Falconer & Mackay 1996). Consequently, selection to refrain from such matings should be similar, and they should be avoided to the same degree under natural conditions. Thus, the frequency of matings between fathers and daughters, mothers and sons, and full siblings ($F = 0.25$ for each) should be equally rare. However, asymmetries in the probability of inbreeding can

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arise in two ways (Table 1). First, if animals rely primarily on learning and prior association to identify close relatives (Bateson 1978; Komdeur & Hatchwell 1999; Komdeur et al. 2004), the reliability of information about kinship may vary depending upon the ages at which previous interactions occurred ('incomplete knowledge hypothesis': Slagsvold & Lifjeld 1997; Slagsvold et al. 2001). Second, males may have less incentive than females to avoid inbreeding even if they can recognize kin, because males typically invest less in reproduction than females and pay correspondingly lower costs of inbreeding ('cost of inbreeding hypothesis': Pärt 1996; Haig 1999; Perrin & Mazalov 1999; Kruuk et al. 2002; Lehmann & Perrin 2003). At the same time, the costs of inbreeding avoidance may be higher for males, particularly young males, as well as for older females. The incomplete knowledge hypothesis provides a proximate explanation for asymmetries in incest avoidance and emphasizes constraints on mate choice, whereas the cost of inbreeding hypothesis provides an ultimate explanation and emphasizes the selective advantages of sex- and age-specific mating strategies.

Birds provide a good illustration of the model of asymmetrical incest avoidance (Table 1). An adult female bird can be certain of her close genetic relationship with her own nestlings (assuming intraspecific brood parasitism does not occur) and learn to recognize them from an early age. However, once juvenile birds reach independence and cease interacting with their mother, they have yet to adopt a distinctive adult breeding plumage, body size or song, features that play a critical role in individual recognition and mate choice among adult birds (Grant & Grant 1989; Kempnaers et al. 1992; Hasselquist et al. 1996; Sheldon et al. 1997). A mother's recollection of the phenotypes of her immature sons may be of little use to her in recognizing and avoiding mating with them a year or more later when they return as adults to breed. Likewise, even though sibling birds have weeks or months to become acquainted with each other as nestlings and fledglings, they may not have sufficient information to assess their relatedness when they encounter each other again as adults, unless juvenile phenotypes are strongly correlated with adult phenotypes. Moreover, because most young male birds disperse from their natal site (Greenwood & Harvey

1982; Wheelwright & Mauck 1998), mothers and sisters lack information about where their sons and brothers will establish a territory. In short, mothers have incomplete knowledge about their sons, and sisters have incomplete knowledge about their brothers, which makes accidental incest in such relationships more likely.

Father–daughter relationships are fundamentally different. Once males of most bird species reach reproductive maturity, they sing individually distinctive and relatively constant songs (Marler 1987; Payne et al. 1987; Grant & Grant 1996). Body size and shape of adult birds also change little with age (Searcy et al. 2004). From the perspective of mate choice by females, father–daughter matings should be more easily avoided than mother–son or sister–brother matings. Adult birds tend to show strong breeding philopatry (Greenwood 1980), so a female can predict the location of her father's territory. If juvenile females are capable of retaining an accurate memory of their father (Bolhuis & Eda-Fujiwara 2003), the consistency of his song, phenotype and territory should enable daughters to recognize and avoid mating with him (Grant & Grant 1989). High levels of extrapair paternity in birds (Westneat & Stewart 2003; Freeman-Gallant et al. 2005) mean that females can never be certain about the identity of their true genetic father. As a result, females may have little option other than to assume that their father is the male who was socially paired with their mother and who provided them paternal care. We refer to these males as 'social fathers' or, for simplicity, 'fathers', as opposed to 'genetic fathers', or males whose genetic paternity has been confirmed.

From the perspective of mate choice by males, incest avoidance should also be asymmetrical (Table 1). By the time that males are reproductively mature, they may not be able to recognize their mothers as easily as females can their fathers, because females of most bird species do not produce individually recognizable songs. Perhaps more importantly, the costs of mating with a close relative are less for males than for females because males generally invest less in reproduction and typically mate socially (in polygynous species) or genetically (in species where extrapair paternity is common) with more than one female (Birkhead & Møller 1998; Lehmann & Perrin 2003). Reduced reproductive success in any given breeding

Table 1. Model of asymmetrical incest avoidance

Social relationship of male to female	Actual coefficient of inbreeding with male (F)	Information about relatedness based on male's breeding phenotype	Relative probability of encounter with male	Cost of incest avoidance for male	Cost of incest avoidance for female	Predicted frequency of close inbreeding
Son	0.25	None	Low	High	High	Uncommon
Brother	<0.25	None	Low	High	Low	Uncommon
Father	<0.25	Song, plumage, body size, shape	High	Low	Low	Very rare

Model of asymmetrical incest avoidance predicting differences in the frequency of incest despite similar social inbreeding coefficients. The actual coefficient of inbreeding (F) for brother–sister and father–daughter matings is lower than 0.25 because of extrapair paternity. Unless juvenile phenotypes are correlated with adult phenotypes, females have little information about their relatedness with males whom they last knew as nestmates or fledglings. Because of natal dispersal and adult breeding philopatry, the probability of a female encountering her brother is lower than that of encountering her son or father. Males breeding for the first time may be constrained in their ability to acquire a territory, leading to higher costs of inbreeding avoidance. The costs of inbreeding avoidance for young females should be lower than that for older females (see text for details).

attempt is less disadvantageous for males. Additionally, dispersing away from female relatives to avoid inbreeding has its own costs, such as having to find an undisputed territory and forfeiting the benefits of philopatry (e.g. familiarity with foraging sites and refuges from predators). Such costs may be particularly high for young males attempting to establish and defend territories for the first time (Wheelwright & Mauck 1998; Lehmann & Perrin 2003). Both the incomplete knowledge hypothesis and the cost of inbreeding hypothesis predict that there should be asymmetries between different types of close inbreeding in the choice of social and genetic mates. Specifically, father–daughter matings should be rarer than mother–son or sister–brother matings, despite identical coefficients of inbreeding. The model of asymmetrical incest avoidance assumes female mate choice; aspects of the model may not apply to mating systems involving male mate choice, forced copulation or (as in the case of human societies) cultural factors (Haig 1999).

To test whether animals avoid inbreeding in nature, most researchers have taken one of two approaches. Traditionally, researchers have observed marked populations across generations, examining mating patterns in the context of social genealogies (pedigrees). Genealogical studies can be problematic in species with extrapair paternity, however, because social pairing may not reflect actual genetic mating (Rowley et al. 1993; Westneat & Stewart 2003). More recently, molecular techniques have been applied to calculate genetic similarity between mates (Blomqvist et al. 2002; Duarte et al. 2003; Foerster et al. 2003). The advantage of molecular studies is that they do not require marked individuals or long-term observations, and they can be used to estimate coefficients of inbreeding (but see Pemberton 2004). However, a shortcoming of most molecular studies is that they do not distinguish between different types of inbreeding with the same F values or consider the behavioural context of mating decisions (e.g. sex, age or experience: Gardner et al. 2001; Duarte et al. 2003; Westneat & Stewart 2003; Pemberton 2004).

We tested the model of asymmetrical incest avoidance in a long-term study of an island population of Savannah sparrows, *Passerculus sandwichensis*, combining 17 years of data on social mate choice with 3 years of data on genetic mate choice. Our results suggest that birds tended to avoid close social kin (parents, offspring, siblings) in choosing both social and genetic mates. However, father–daughter matings were totally avoided, presumably because of differences in the reliability of information about relatedness and in the costs of inbreeding.

METHODS

Species and Study Area

Since 1987 we have studied a marked population of Savannah sparrows on Kent Island, an isolated 80-ha island in the Bay of Fundy, New Brunswick, Canada (44°35'N, 66°46'W; Wheelwright & Rising 1993; Wheelwright & Mauck 1998). Savannah sparrows are migratory, wintering

mainly in the central and southern U.S.A. On their return, females typically spend 1–3 weeks on the breeding grounds before beginning to nest, which presumably gives them an opportunity to assess the relatedness of potential mates (Slagsvold & Lifjeld 1997). Within the study area, all adults are uniquely colour-banded, all nests located and all nestlings banded. Social mate choice is determined by detailed behavioural observations (mate guarding, copulations, territoriality, nest location, care of nestlings and fledglings) daily over a 2-month period.

Natal and breeding philopatry is high (about 11% of nestlings and 50% of adults return the following year to breed on the island: Wheelwright & Mauck 1998), which enabled us to construct social pedigrees going back as many as 10 generations. Although it is commonplace among birds for young females to disperse further than young males from their natal site (Greenwood & Harvey 1982), sex-biased natal dispersal does not occur in this isolated population (Wheelwright & Mauck 1998).

The sex ratio of Savannah sparrows breeding on Kent Island is routinely female biased (Table 2), and 15–40% of males in the population are simultaneously polygynous, depending upon the year (Wheelwright et al. 1992; Freeman-Gallant 1997). Females invest more heavily in reproduction than males: only females incubate the eggs, and although both sexes feed nestlings, females provide approximately 70% of all feeding trips (Wheelwright & Rising 1993; Freeman-Gallant 1998). After the young leave the nest, care of the fledglings is divided equally between the parents and continues for an additional 15 days (Wheelwright et al. 2003). As a result, social parents, offspring and siblings have ample time to become familiar with each other. Extrapair paternity is high: in 2002–2004, 45.1% of all offspring ($N = 700$) were sired by males other than their social father, and 67.3% of all broods ($N = 202$) contained at least one extrapair offspring. Females are more likely to seek extrapair copulations when socially paired with genetically similar males (Freeman-Gallant 1997; Freeman-Gallant et al. 2003, 2005).

Paternity Analysis and Offspring Sex Determination

In 2002, 2003 and 2004, we collected 20–100- μ l blood samples from the brachial vein of all adults ($N = 220$) and nestlings ($N = 700$) in the study area. DNA was isolated following standard protocols (Freeman-Gallant et al. 2003, 2005). We used four microsatellite loci (*Escu6*, *Psa12*, *Mme1*, *Mme8*) to assign paternity (combined probability of false inclusion $< 5.5 \times 10^{-4}$). In 29 ambiguous cases, we used two additional loci (*Psa29*, *Psap61*) to confirm paternity (Freeman-Gallant et al. 2003, 2005). Offspring were sexed by amplifying a diagnostic region of the CHD gene via the polymerase chain reaction (PCR; Kahn et al. 1998; Freeman-Gallant et al. 2001).

Statistical Analysis

We used Monte Carlo simulations and different null models to estimate the probability that observed levels of

Table 2. Frequency of close social inbreeding (pairing between a female and her social father, son, or brother) in an isolated population of Savannah sparrows

Year	Breeding birds			Number of close inbreeding possibilities*					Observed inbreeding	
	Density (individuals/ha)	Sex ratio (males/ female)	Nesting attempts	Father- daughter pairs	Mother- son pairs	Full siblings pairs	Half-siblings pairs	Total possible pairs	Pairs	Nesting attempts
1988	13.5	0.74	108	6	7	1	1	15	0	0
1989	15.5	0.68	117	3	3	3	0	9	0	0
1990	13.5	0.77	106	5	7	5	1	18	0	0
1991	14.7	0.86	113	13	19	8	6	46	0	0
1992	12.7	0.76	103	14	10	4	6	34	0	0
1993	11.7	0.66	109	6	6	6	3	21	0	0
1994	11.7	0.76	92	11	8	5	9	33	1†	1
1995	13.1	0.81	92	15	13	5	11	44	0	0
1996	9.7	0.97	63	4	8	4	6	22	1‡	1
1997	10.7	0.82	94	6	7	2	1	16	0	0
1998	10.5	0.88	82	10	9	3	6	28	2‡§	5
1999	14.3	0.95	85	13	16	15	6	50	2‡	3
2000	10.3	0.67	77	5	4	3	4	16	0	0
2001	12.9	0.76	82	6	11	10	11	38	1†	1
2002	14.4	0.80	115	7	14	14	11	46	0	0
2003	7.5	0.56	86	3	5	5	6	19	0	0
2004	8.7	0.75	85	11	6	4	11	29	2§	4
Total			1609	138	153	97	99	484	9	15

*Inbreeding possibilities refer to cases where a female and a closely related male returned the same year to the study site.

†Sister-half-brother.

‡Sister-full brother.

§Mother-son.

inbreeding could have occurred by chance (Manley 1991; Pärt 1996; Keller & Arcese 1998). In the simulations, individuals were paired at random with birds of the opposite sex known to be alive at the same time, and the number of incestuous matings was tallied in each of 1000 iterations (Manley 1991; Wheelwright & Mauck 1998). Table 2 lists the number of opposite-sex close relatives (inbreeding possibilities) alive in each year of the study, broken down by type of relationship. We distinguished between social inbreeding (Table 2) and genetic inbreeding (Table 3). Close social inbreeding was pairing between parents and offspring or between full siblings ($F = 0.25$) or half-siblings ($F = 0.125$). Close genetic inbreeding was producing offspring with a parent or sibling (as confirmed by paternity analysis using microsatellites). We did not have genetic data on paternity for the first 14 years of this study, and the model we tested was based on the avoidance of mating with kin as determined by social familiarity; therefore, we use the terms social and genetic inbreeding to refer to pairing (social inbreeding) or producing offspring (genetic inbreeding) with individuals that were known from pedigrees to be social relatives. These are not necessarily genetic relatives, although in the case of mothers, the two are equivalent (brood parasitism does not occur in this population, so a female's social offspring are also her genetic offspring). Thus, we use the shorthand term 'genetic inbreeding' to refer to genetic mating between individuals with a close social pedigree that may or may not reflect their exact genetic pedigree. An example would be a case where microsatellites showed that a male sired the offspring of a female with whom he

had shared the same social parents (e.g. the male and female had been nestmates), even if the true genetic parents of the male and female had not been established.

To test whether birds avoided close social inbreeding, the data were analysed at the level of nesting attempts (each nesting attempt was considered an independent event) and, more conservatively, at the level of breeding pairs (each unique social male-female combination was counted only once per season, regardless of how many nesting attempts they made). To test whether birds avoided close genetic inbreeding, the data were analysed at the level of individual offspring (each nestling was considered an independent sample) and, more conservatively, at the level of breeding pairs (each unique genetic father-mother combination was counted only once per season, regardless of how many offspring they produced together). Because males nesting within 88 m of a focal nest were responsible for more than 95% of extrapair paternity in the study (median distance between nests in which extrapair paternity occurred and nests of extrapair sires = 39.5 m; $N = 104$), simulations testing for genetic inbreeding avoidance were restricted to the subset of potential sires nesting within that distance. No female nested within 88 m of her social father in 2002 or 2003, and only four females nested within 88 m of their social fathers in 2004, so our simulations (limited to neighbouring males) did not allow us to distinguish whether the observed absence of father-daughter genetic inbreeding was statistically significant. Relaxing the distance restriction and including in the simulations all males within the population produced similar results. *P* values refer to

Table 3. Frequency of close genetic inbreeding (genetic mating between a female and her father, son, or brother) in an isolated population of Savannah sparrows

Years	Sample	Sample size	Relationship	Number of cases of inbreeding	<i>P</i>
2002–2004	Individual nestlings	700 nestlings	Father–daughter	0	0.28
			Mother–son	9	0.94
			Full siblings (from same nest)	0	0.04
			Full siblings (from different nests)	0	0.49
			Half-siblings (different nests)	5	0.13
			Overall	14	0.088
2002–2004	Unique pairs	284 nesting attempts	Father–daughter	0	0.57
			Mother–son	2	0.56
			Full siblings (from same nest)	0	0.37
			Full siblings (from different nests)	0	0.77
			Half-siblings (different nests)	1	0.25
			Overall	3	0.074

P values refer to the probability of observing a particular number of (or fewer) cases of genetic mating with close kin, assuming genetic mating was independent of an individual's relatedness (based on social pedigrees in which genetic relatedness was not necessarily established).

the probability of observing a particular number of (or fewer) cases of close inbreeding, assuming that mate choice was independent of an individual's relatedness based on pedigree analysis.

Testing the Assumptions of the Model

The model of asymmetrical incest avoidance makes several assumptions. The most critical assumption is that there is a cost of inbreeding. In the population of Savannah sparrows that we studied, the number of eggs, hatchlings and recruits per clutch were similar between socially incestuous and nonincestuous pairs over a 17-year period (eggs: $t_{1634} = 0.49$, $P = 0.63$; hatchlings, for nests in which at least one egg hatched: $t_{1326} = 1.54$; recruits, for nests in which at least one nestling fledged: $t_{1190} = 1.18$, $P = 0.24$). However, nests of socially incestuous pairs produced significantly fewer fledglings than did nests of nonincestuous pairs (2.9 ± 0.25 fledglings versus 3.7 ± 0.03 fledglings; $t_{1190} = 2.72$, $P = 0.007$). The date of hatching or of nest failure did not differ as a function of relatedness of the parents (hatching: $t_{1326} = 0.29$, $P = 0.77$; failure: $t_{432} = 0.08$, $P = 0.94$), and nests of incestuous and nonincestuous pairs were equally likely to be successful, abandoned or preyed upon (chi-square test: $\chi^2_2 = 0.73$, $N = 1609$, $P = 0.70$). Starting in 2002, we were able to establish not only whether females paired socially with close relatives (social inbreeding) but also whether close relatives sired their young (genetic inbreeding; see *Statistical Analysis*). Paternity analysis in 2002–2004 using microsatellites identified a small sample of nestlings whose genetic parents were either a mother and her son, or opposite-sex nestlings raised by the same parent or parents. Controlling for sex and year, offspring of genetic inbreeding ($N = 14$) averaged slightly smaller than offspring of parents that were unrelated ($N = 676$), but differences were not significant (mean \pm SE wing length: 28.4 ± 1.0 mm versus 29.2 ± 0.2 mm; ANOVA: $F_{1,686} = 0.57$, $P = 0.45$; mean \pm SE mass: 13.3 ± 1.7 g versus 13.9 ± 0.1 g; $F_{1,679} = 1.16$, $P = 0.28$).

One indication of inbreeding depression is that in 2003 we found that the mass and immunocompetence of sons (although not daughters) declined significantly with increasing genetic similarity of parents (using six microsatellite loci to estimate genetic similarity; C. Freeman-Gallant, N. Wheelwright & S. Sollecito, unpublished data). Close inbreeding occurred so infrequently that we may have lacked sufficient statistical power to document a stronger effect of inbreeding. Our evidence for inbreeding depression may also be relatively weak because, for most years of the study, we did not know the true genetic relationship of social or extrapair mates. While it is possible that the genetic load has been largely purged in this island population (Crnokrak & Barrett 2002), some reduction in fitness from close inbreeding is likely even if it is difficult to detect (Rowley et al. 1993). Close inbreeding reduces immune function in another species of sparrow (song sparrow, *Melospiza melodia*: Reid et al. 2003), and inbreeding depression is likely to be widespread in birds (Kruuk et al. 2002).

A second assumption of the model is that there is a cost of avoiding inbreeding. Inbreeding avoidance can take many forms including natal dispersal, breeding dispersal or kin avoidance without dispersal, so it is difficult to know whether a particular behaviour is a response to the risk of inbreeding, and even harder under natural conditions to quantify its costs (including opportunity costs). We do know, however, that the median natal dispersal for Savannah sparrows on Kent Island is only 228 m, and the median distance between successive nests within and between seasons is only 17 and 30 m, respectively, regardless of whether females have opposite-sex relatives nearby or change mates (Wheelwright & Mauck 1998). Such strong natal and breeding philopatry suggests that there may be costs to dispersal as an incest-avoidance strategy.

Finally, the model assumes that various aspects of a father's phenotype are predictable to his daughter. Male Savannah sparrows sing one song (or, in rare cases, two songs), and each song is individually recognizable and remains relatively invariant throughout a male's lifetime (Wheelwright & Rising 1993). In adult males,

morphological measurements such as bill length and depth, wing and tarsus length, and mass vary little between years and show high repeatability (0.52–0.96; unpublished data). The location of a male's territory is also highly predictable from year to year (Wheelwright & Mauck 1998). (Adult females also show relatively constant morphology and breeding philopatry, but they do not sing.) Thus, the major assumptions of the model are likely to be reasonable in this population.

RESULTS

Avoidance of Close Social Inbreeding

Between 1988 and 2004, there were 484 cases in which a female could have paired with her social father or one of her sons or brothers (i.e. both were alive and nested within the 7.5-ha study area; Table 2). Despite abundant opportunities for incestuous pairings, females formed pair bonds with close relatives in only nine instances: three with sons, three with full brothers and three with half-brothers. None of the relatives paired incestuously again in subsequent years. Although the infrequency of pairing with close relatives collectively (not distinguishing between types of relationships) was statistically significant from 1988 to 1995 (Wheelwright & Mauck 1998) and suggested active incest avoidance from 1996 through 2004, when all years were combined, the pattern could not be distinguished from random mating (Monte Carlo simulations: $P = 0.63$).

When we differentiated between specific types of incestuous relationships (pairings between parents and offspring, between full siblings and between half-siblings), only pairings between daughters and the males who had raised them (their social fathers) were significantly less frequent than expected by chance. Of 1609 nesting attempts, none involved father–daughter pairs, even though there were 138 cases where both a daughter and her social father simultaneously bred nearby, sometimes within 10 m of each other (Monte Carlo simulations: $P < 0.005$; Table 2). Although mate switching within and between seasons commonly occurs in birds (Cockburn et al. 2003), the choices of mates in successive nesting attempts within a season may not be statistically independent events. Therefore, we took a more conservative approach by limiting the sample to unique social pairs within a year, regardless of how many clutches they produced (Pärt 1996). As with the larger sample, the absence of father–daughter pairs was unlikely to have occurred by chance (Monte Carlo simulations: $P = 0.047$, $N = 1110$ unique pairs). To test whether father–daughter pairs were significantly less common than other types of close incest, we looked at those Monte Carlo simulations that produced either nine cases of close inbreeding pairs or 15 cases of close inbreeding nesting attempts (the numbers observed in this study; Table 2). In the simulations, the mean proportion of cases of close inbreeding that involved fathers and daughters was 2.7% and 8.0%, respectively. In only 0.8% of the pair simulations and 1.4% of the nesting attempt simulations was the proportion of father–daughter pairs 0%, as observed in this study. Father–daughter pairs were therefore significantly under-represented compared to mother–son

and sibling–sibling pairs ($P = 0.008$) and nesting attempts ($P = 0.014$).

The incidence of pairing with close social kin varied between years (Table 2). In 11 of the 17 years, there were no cases of close inbreeding of any kind (Wheelwright & Mauck 1998). Factors such as population density and sex ratio of breeding birds could conceivably explain annual variation in the occurrence of inbreeding by changing the magnitude of inbreeding depression or the costs of inbreeding avoidance in different years (Rowley et al. 1993; Keller et al. 2002). In fact, population density, the adult sex ratio within the population, opportunities for close inbreeding and the total number of nesting attempts did vary annually (Table 2). Collectively, however, they were poor predictors of the number of cases of inbreeding observed in different years (multiple regression: $F_{4,12} = 2.13$, $P = 0.14$). Unaccountably, during years in which close social inbreeding occurred, the sex ratio of breeding birds tended to be less female biased (i.e. females appeared to have had more rather than fewer choices of potential mates; Student's t test: $t_{15} = 2.25$, $P = 0.04$) and there were fewer nesting attempts than in years in which there was no inbreeding ($t_{15} = 3.75$, $P = 0.002$). The density of breeding birds and the number of opportunities for close inbreeding were unrelated to the occurrence of inbreeding ($t_{15} < 1.17$, $P > 0.26$; Table 2).

Age and Social Inbreeding

The ages of birds involved in incestuous social pairings were nonrandom. Although in any given year only about 50% of males in the breeding population were 1 year old ($N = 783$ breeding males), eight of the nine incestuous males (89%) were yearlings and first-time breeders (binomial test_(0.5/9): $P = 0.02$). Life expectancy of Savannah sparrows is about 1.5 years (Wheelwright & Rising 1993) and typically only about 20% of females in the breeding population were 3 years old or older in any given year, yet five of the nine incestuous females (56%) were 3 years old or older (binomial test_(0.2/9): $P = 0.017$). The average age of females was significantly greater than that of the male relatives with whom they were mated (paired t test: $t_8 = 2.58$, $P = 0.03$). In no cases were incestuous females younger than their mates (binomial test_(0.74/9): $P = 0.067$).

Avoidance of Close Genetic Inbreeding

In three different breeding seasons (2002–2004), we used microsatellites to determine the genetic parents of more than 96% of all offspring produced within the study area ($N = 700$ nestlings; 316 (45.1%) were extrapair offspring). Fourteen of the nestlings (2.0%) were the result of close genetic inbreeding. Five of them were extrapair offspring from two broods produced within the same season by a yearling male and his 4-year-old mother, four were within-pair offspring from two broods produced within the same season by a yearling male and his 3-year-old mother, and five were extrapair offspring from a single brood produced by a yearling male and his 2-year-old half-sister (Table 3). Thus, genetically incestuous pairs, like socially incestuous pairs, tended to be

made up of yearling males and older females. Combining the nine cases of social inbreeding and the three cases of genetic inbreeding, the probability was 0.003 that as many as 11 of the 12 cases would involve yearling males (binomial test_(0.5/12)) and that as many as seven cases would involve females 3 years old or older (binomial test_(0.2/12)).

As with social inbreeding, there were no cases of genetic inbreeding between fathers and daughters. In accordance with earlier findings that Savannah sparrows are more likely to disperse if their opposite-sexed parent is still alive (Wheelwright & Mauck 1998), no female nested within 88 m of her social father in 2002 or 2003 and only four females did in 2004, so Monte Carlo simulations (restricted to neighbouring males; see Methods) lacked power to evaluate whether the absence of genetic mating between fathers and daughters could have occurred randomly (individual nestlings: $P = 0.28$; unique pairs: $P = 0.57$). Combining all relationships, the birds showed an overall tendency to avoid close inbreeding (individual nestlings: $P = 0.088$; unique pairs: $P = 0.074$; Table 3).

Forty-three per cent of all broods contained nestlings sired by two males, and 5.5% contained nestlings sired by three males ($N = 202$ broods). Although these results suggest that females may be able to select the genetic father of each offspring independently, we also analysed our data by considering each unique pair of genetic mates only once, regardless of how many offspring they produced. Using this more conservative approach, there were only three cases of close inbreeding in the choice of a genetic mate. However, the smaller sample size ($N = 183$ unique genetic pairs, 284 nesting attempts) and reduced power of the test did not allow us to distinguish between overall inbreeding avoidance and random genetic mating ($P = 0.086$).

DISCUSSION

In an isolated population of Savannah sparrows studied over a 17-year period, females rarely paired socially with their sons and brothers. However, they never paired with the males that had reared them (their social fathers). Three years of microsatellite data showed that birds' choices of genetic mates were also nonrandom with respect to close inbreeding; of 700 nestlings from 284 nesting attempts, there were no instances of genetic mating between fathers and daughters. All but one of the cases of close social inbreeding involved 1-year-old males mating for the first time, and more than half of the cases involved old females, in their penultimate or final breeding season. Similarly, two of the three cases of close genetic inbreeding involved older females and their yearling sons (the third case involved a 2-year-old female and her 1-year-old half-brother). These results are consistent with a model of asymmetrical incest avoidance, which predicts that sex- and age-specific differences in the reliability of information about relatedness and in the costs of inbreeding and inbreeding avoidance lead to differences in the frequency of incestuous matings, even when coefficients of inbreeding are identical and would seem to be equally disadvantageous.

The model of asymmetrical incest avoidance may also explain why the observed frequency of different types of inbreeding in this population did not reflect the true risks

of inbreeding, specifically why father–daughter matings did not occur but mother–son and brother–sister matings did. These three types of social relationships do not in fact have the same F . Intraspecific brood parasitism does not occur in Savannah sparrows (Freeman-Gallant 1997), so a male's social mother is in actuality his genetic mother. In contrast, because of high rates of extrapair paternity in this population, there is only about a 50% probability that a female's social father is her genetic father (Freeman-Gallant 1997; Freeman-Gallant et al. 2003). As a consequence, the coefficient of inbreeding for a mating between a female and her son is always 0.25, but that expected for a mating between a female and her social father, discounted by uncertainty of paternity, would be about 0.125. Any two nestmates in this study had different genetic fathers about one-third of the time ($N = 148$ broods), so the average F of matings between (social) full siblings (i.e. individuals sharing the same mother and social father) would be less than that of mother–son matings but more than that of social father–daughter matings (expected value for F of a mating between nestmates = 0.167).

Consequently, if kin recognition and inbreeding avoidance were favoured in direct proportion to the probability of genetic inbreeding, one might expect mother–son matings to be rarer than matings between full siblings and matings between full siblings to be rarer than father–daughter matings. Yet, in accordance with the incomplete knowledge and cost of inbreeding hypotheses, we found the reverse: inbreeding occurred between mothers and sons as well as between siblings, but daughters never paired with their social fathers ($N = 1609$ nesting attempts over 17 years) or chose them as their genetic mates ($N = 284$ nesting attempts over a 3-year period). Even though there is a relatively high likelihood that a female's social father is not her genetic father, the best strategy may be to be conservative, to use the available information and to avoid mating with him none the less.

The model of asymmetrical inbreeding avoidance is also consistent with the results that 92% of incestuous social and genetic pairs involved 1-year-old males breeding for the first time, and 58% of incestuous pairs involved old females in one of their last breeding seasons. These results strongly suggest that the costs of inbreeding avoidance vary as a function of sex and age. Yearling males generally arrive on the breeding grounds later than experienced males do, and they commonly face challenges in finding a mate or uncontested territory. A yearling male's familiarity with his mother and his natal site may make it easier for him to insert himself into the breeding population. On the other hand, once a female nests in a particular territory, she rarely moves between seasons, presumably because of the advantages of philopatry (Wheelwright & Mauck 1998). If a female's mate from the previous year fails to return, it may be less disadvantageous for her to mate with a yearling male establishing himself for the first time (even if he may be a close relative) than to move late in life to a new location. For inexperienced, subordinate males and ageing, philopatric females, inbreeding may be less costly than inbreeding avoidance.

Few other long-term studies have combined information about pedigrees of natural populations with tests of

social and genetic inbreeding avoidance (Bensch et al. 1994). The possibility of asymmetrical incest avoidance appears to have been overlooked in previous studies. In three of the most detailed studies of inbreeding in birds (song sparrows, *Melospiza melodia*: Keller & Arcese 1998; great reed warblers, *Acrocephalus arundinaceus*: Bensch et al. 1994; great tits, *Parus major*: Greenwood et al. 1978), no cases of pairing between females and their (social) fathers were reported, although other types of incestuous matings did occur.

The general applicability of the model of asymmetrical incest avoidance will depend upon the biology of the species. For example, patterns may be different in species that have cooperative breeding (Rowley et al. 1993; Daniels & Walters 2000) or in populations provisioned with artificial nestboxes (Greenwood et al. 1978; van Noordwijk & Scharloo 1981; Foerster et al. 2003). Nevertheless, asymmetrical constraints on knowledge about kinship and costs of inbreeding are likely to occur even in those systems, so researchers should consider differentiating between social and genetic inbreeding, between types of close inbreeding and between age classes. Although our results emphasize the importance of social familiarity as a criterion to avoid inbreeding, and cross-fostering experiments and other studies of kin recognition in birds provide little evidence that birds can distinguish kin from nonkin in the nest using cues other than association (Russell & Hatchwell 2001; Komdeur et al. 2004), the possibility remains that birds may use phenotypic traits or other information to assess genetic relatedness (Komdeur & Hatchwell 1999; Petrie et al. 1999; Hauber & Sherman 2001; Freeman-Gallant et al. 2003).

The model of asymmetrical incest avoidance may help to explain patterns of natal dispersal in birds. Sex-specific natal dispersal has traditionally been interpreted as an adaptation to avoid close inbreeding (Greenwood 1980; Greenwood & Harvey 1982). For example, if young females routinely disperse further than males, two nest-mates of the opposite sex are unlikely to encounter each other and pair accidentally. The argument seems reasonable when applied to sibling-sibling matings, but sex-specific natal dispersal does not diminish the risk of incestuous matings between individuals of the nondispersing sex and their opposite-sexed philopatric parents (Piper et al. 2001). Moreover, it does not fully account for why, in birds, females rather than males tend to show greater natal dispersal (Greenwood & Harvey 1982). The model of asymmetrical incest avoidance may help to explain this pattern, because in birds, females are the sex with more reliable information about inbreeding risks and greater incentives to avoid inbreeding, which reduces the relative cost of dispersing for females.

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