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Extrapair Fertilization and Genetic Similarity of Social Mates in the Mexican Jay

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ABSTRACT: Inbreeding depression should favor the ability of females to avoid inbreeding or minimize its effects. We tested for a relationship between genetic similarity of social pairs and the occurrence of extrapair fertilization (EPF) in the Mexican jay (*Aphelocoma ultramarina*). Multilocus minisatellite and microsatellite DNA fingerprinting was used to detect extrapair young and measure genetic similarity between social parents. We found that 12 of 31 (39%) nests had at least one EPF and 15 of 93 (16%) young were the result of EPF. The mean DNA fingerprinting band sharing score between social mates who had at least one EPF was significantly higher than the mean band sharing score between mates who did not (0.35 versus 0.25). The mean band sharing score for non-EPF dyads (0.25) was similar to the background band sharing among nonrelatives (0.23). The mean band sharing score for mates that had an EPF was significantly higher than that of nonrelatives (background) and was significantly lower than that of half-siblings (0.52). Our results showed a highly significant relationship between genetic similarity of social mates and incidence of EPF.

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Mating behavior mediates the transmission of genes from one generation to the next, but the role of selection on mating behavior is still poorly understood. It has long been felt that females favor male sexual partners that exhibit attributes that act as quality indicators (Darwin, 1871; Williams, 1975). These attributes have been interpreted as being “condition sensitive” (Andersson, 1986; Emlen, 1973), thus indicating the presence of a male’s “good genes” (Arnold, 1983; Hamilton, 1990; O’Donald, 1983; Williams, 1966). In contrast, the increasingly frequent observation that females in many species, even those thought previously to be monogamous, mate with more than one male (Birkhead, 2000; Griffith et al., 2002; Jennions, 1997; Stockley et al., 1993; Tregenza and Wedell, 2000; Zeh JA and Zeh DW, 1996, 1997) suggests that more may be involved in a female’s choice than picking the one male with the most extreme condition indicators, especially in those species that do not have extreme sexual dimorphism. Females may choose males for reasons other than good genes revealed by male condition indicators. One possibility is that females choose males based on less obvious indicators of genotype, such as some attribute associated with genetic similarity between themselves and the potential mate and thus prefer males that are genetically dissimilar to themselves, resulting in greater heterozygosity among their offspring. Thus, in the offspring-heterozygosity hypothesis females “are predicted to value heterozygosity in their offspring” (Brown, 1997), thus minimizing the dangers of homozygosity of deleterious alleles and increasing heterozygosity at other loci that might be important for condition.

The negative fitness consequences associated with inbreeding are well documented (Crnokrak and Roff, 1999; Keller and Waller, 2002; Keller et al., 1996; Slate et al., 2000), but heterozygosity might also be valued for other reasons, possibly involving disease resistance and the major histocompatibility complex (Brown and Eklund, 1994; Potts and Wakeland, 1994; Tregenza and Wedell, 2000). In this perspective, developmental problems caused by homozygosity in the offspring create selection pressures for female tactics, such as pursuit of extrapair fertilization (EPF), that favor heterozygosity in some offspring. Following this reasoning, Blomqvist et al. (2002) showed a positive relationship between genetic similarity of social mates and incidence of EPF in three species of shorebirds. It is unclear, however, whether they had sufficient resolution to support this conclusion (Griffith and Montgomerie, 2003). Also, as Griffith and Montgomerie (2003) pointed out, the species of shorebirds studied by Blomqvist et al. (2002) have low natal philopatry, suggesting that the risk of inbreeding is minimal.

We suggest that the Mexican jay (*Aphelocoma ultramarina*) is a more appropriate avian species with which to test the increased heterozygosity hypothesis. Mexican jays are nonmigratory, have extremely conservative dispersal (Brown JL and Brown ER, 1984), live in groups of 5 to 25 that are known to contain close relatives (Brown JL and Brown ER, 1981), and have moderate levels of inbreeding and inbreeding depression (Brown JL and Brown ER, 1998). Reproduction is delayed until 3 years of age or later, and all social group members may help in the feeding of nestlings at different nests within the group (cooperative or communal breeding). Unlike most species that have helpers, in this species there are typically two to four breeding adults of each sex within a single group, a situation that increases opportunities for females to pursue EPF with males within the social group. Multiple paternity within broods of single females has already been reported in Mexican jays (Bowen et al.,

1995), and it has been shown that most (at least 93%) EPFs involve intragroup males (Li and Brown, 2000). In this study we tested for a positive relationship between genetic similarity of social mates and incidence of EPF in the Mexican jay.

METHODS

Study population

Behavioral data were collected from a population of Mexican jays near Portal, Arizona, USA, at the Southwestern Research Station of the American Museum of Natural History and the surrounding Coronado National Forest. Geographical coordinates were 318839 N, 1092039 W. This population has been studied annually since 1969. We used ground and pole traps baited with peanuts and sunflower seeds to trap birds. Most birds are color banded for individual identification, and blood samples have been collected for all banded birds since 1990. For this study, we used behavioral and genetic data collected over 10 years (1993–1995, 1997–2003) for nests for which we had identification and preserved blood samples of both parents as well as chicks that were alive at banding age (usually 14 days after hatching). Data from 10 different social groups (flocks) were used in this study (Table 1).

Adults were identified as nest owners (mated pairs) if they were seen bringing nest material to the nest site, building the nest, or incubating eggs (only females incubate eggs). Males were usually identified during the nest-building phase. Males were also assigned to a female if they were observed closely following the female when returning to or leaving a completed nest, chasing other males away from the female, and/or perching at the nest while the female was in the nest. Males were only assigned to a nest if the preceding behaviors were observed before egg laying was complete. No males were assigned to nests that were found after the female was in the incubating phase.

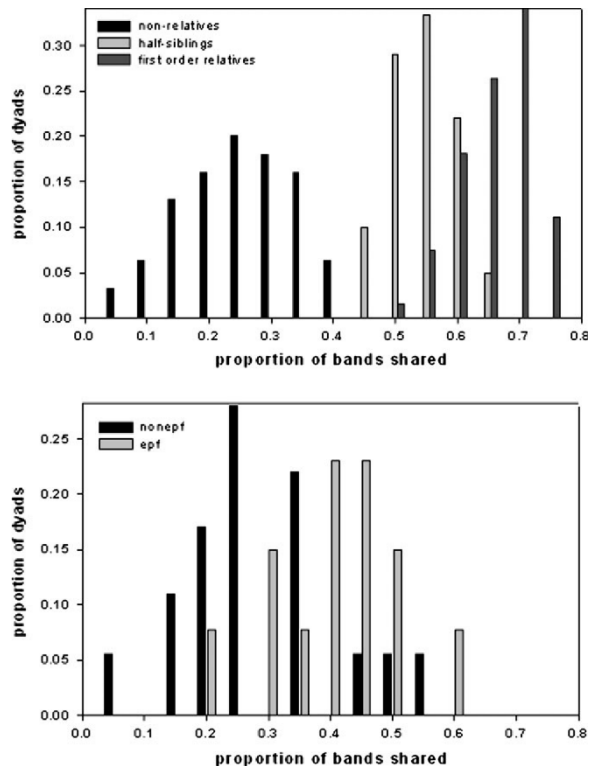


Figure 1

(A) Distributions of band sharing values for three types of relationships: parent to offspring, $n = 242$; half-siblings, $n = 31$; unrelated, $n = 46$. (B) Distributions of band sharing values for social pairs with at least one EPF in the nest ($n = 12$) and pairs with no EPF ($n = 19$).

DNA fingerprinting

For this study we used multilocus minisatellite DNA fingerprinting (Jeffreys et al., 1985; Rabenold et al., 1990, 1991) and data from a previous study using microsatellites (Li and Brown, 2000). Blood samples of approximately 100 μ l were taken from birds either when they were chicks or when trapped as juveniles or adults, by venipuncture of the major wing vein. Genomic DNA was extracted from blood using a standard proteinase K and phenol/chloroform/isoamylalcohol procedure followed by ethanol precipitation (Sambrook et al., 1989). Five micrograms of DNA was cut using the restriction enzyme HaeIII. After digestion, the fragments were separated on 0.8% agarose gels for 65 h at 20 V. After Southern blotting, the DNA was hybridized using Jeffreys' probe 33.15 (Jeffreys et al., 1985; Rabenold et al., 1990). The probe was radiolabeled with [32 P]dCTP and visualized using phosphor-imaging.

Extrapair young for nests from 1990 to 1996 were identified in a previous study using microsatellites (Li and Brown, 2000). All other genetic data for this study were generated using minisatellites. We tested whether results using minisatellites were consistent with those using microsatellites by comparing results using both molecular markers for parental exclusions from 17 nests from the years 1993 through 1995. We found one additional paternal exclusion using minisatellites.

Results from the two methods were highly correlated: 14 of 15 (93%) paternal exclusions matched and 44 of 45 (98%) nonexclusions matched. Together, 59 of 60 (98.3%) chick assignments of EPF or non-EPF matched between the two molecular markers. Confidence limits were generated for this proportion based on the binomial distribution and the F distribution (Zar, 1999). The 95% confidence interval was 0.9108–0.9996.

Fingerprints of social mate pairs were scored by J.A.E. blind with respect to whether a dyad had an EPF in the nest. Scores were confirmed by an independent scorer also scoring dyads blind with respect to the tested hypothesis. Individuals were not scored across gels, and dyad lanes were never more than three lanes apart. Band sharing values (Dice's index, D) were calculated using the formula $D = 2S/(A + B + 2S)$, where S equals the number of bands shared between a dyad, A equals the number of bands unique to the first individual, and B equals the number of bands unique to the second individual (Lynch, 1988, 1991; Rabenold et al., 1990).

Using minisatellite markers we generated distributions of genetic similarity for three classes of kin (Figure 1A), nonrelatives (background genetic similarity), half-siblings, and parent-offspring, and we derived inferences of other levels of genetic similarity from them. The distribution of band sharing values for parent-offspring was calculated from dyads of parents and offspring in which there were no unattributable bands. The distribution of band sharing scores for nonrelatives was generated by scoring dyads of individuals from different flocks that were not adjacent to each other. The distribution of band sharing scores for half-siblings was calculated from dyads of chicks from the same nest that shared the putative mother but had different fathers.

Extrapair young were detected by identifying bands in offspring lanes that are unattributable to either parent. In this study, putative fathers were excluded from parentage using two criteria: if a chick had more than one band that was unattributable to either parent and if the putative father and chick had a band sharing value less than the lower 95% confidence interval of the distribution of band sharing values for parent-offspring (0.52). In generating the reference distributions, some adults were used in the nonrelative analysis and in the social pair analysis. In no cases were chicks that were used in the parent-to-offspring or half-sibling kin distributions used again (as adults) as a part of the social mate EPF/non-EPF analysis.

Because Mexican jays are not socially monogamous over their lifetime (Brown, 1994), we used some individuals more than once in the data set; however, we used only one nesting attempt from each pair, regardless of how many times they nested together. Nests from these five repeat pairs were chosen randomly. To make sure we were not choosing the nests that best fit our prediction, a counterbias sampling method was employed. From the two repeat nesting pairs that never had an EPF, we randomly selected a single nest. For the three pairs that had multiple nests and had EPF in one nest but not in any other nests, we chose the nesting event that contradicted the major prediction of the inbreeding avoidance hypothesis. There were three cases where there were three nests for a mate pair (each with band-sharing values of 0.31, 0.35, and 0.42) and two non-EPF nests. We used a nonEPF case each time, thus skewing our data toward the null hypothesis. We report results of both random sampling and counterbias sampling.

To test for independent segregation of DNA fragments (linkage) we used seven families of five offspring with no EPFs and checked for band combinations that always transferred from parent to offspring as a pair or not at all. We found no such linked band combinations.

To test for a significant difference between EPF and nonEPF social pairs we used a Mann-Whitney U test. We also tested for a positive correlation between EPF occurrence and genetic similarity by dividing all nests into three categories of genetic similarity using minisatellite band sharing values, A, 0–0.2; B, 0.21–0.34; and C, 0.35–1.0, and performed a chi-square test with a 2 (EPF and non-EPF dyads) 3×3 (the genetic similarity categories) contingency table. We employed the same chisquare contingency table to test if the proportion of EPF young was positively correlated to genetic similarity of social mates. All means are reported as mean \pm standard error (SE).

RESULTS

In 31 nests sampled we found that 12 of 31 (39%) nests had at least one EPF and 15 of 93 (16%) young were the result of EPF. Comparing the band sharing values of mated pairs with EPF to those with no EPF, we found that most of the band sharing values for EPF dyads fall between and overlap the distributions of nonrelatives and those of half-siblings (Figure 1A,B). The band sharing score for non-EPF social pairs (mean = 0.25 ± 0.003) was not significantly different from that of nonrelatives (mean = 0.23 ± 0.011) (normal approximation to Mann-Whitney U test, sample size > 40, U (23) (46) = 495, Z = 0.163, $p > .5$, Zar, 1999). Band sharing scores for social pairs with EPF (mean = 0.35 ± 0.004) were significantly lower than those of half-siblings (mean = 0.52 ± 0.010 , U (15) (31) = 228, $.005 < p < .01$) and significantly higher than those of nonrelatives (mean = 0.23 ± 0.011 , normal approximation to Mann-Whitney U test: U (15) (46) = 597, Z = 4.81, $p < .001$). The mean band sharing value for parent to offspring of 0.65 ± 0.004 was nearly identical to the predicted value of 0.63 calculated from the mean background band sharing value of 0.23 ± 0.011 (Georges et al., 1988).

Table 1
Breakdown of families sampled over 10 years

	1993	1994	1995	1997	1998	1999	2000	2001	2002	2003
A			11 (4)							
B	5 (2)	7 (5), 9 (2)	12 (2)	18 (3)				26 (3)		
C				19 (3)	2 (1)			4 (1)		31 (4)
D		10 (2)		23 (3)		1 (5)				
E	6 (3)	8 (3)	13 (5)							
F					24 (3), 25 (4)					
G			14 (3), 15 (2)	20 (2), 22 (1)			3 (5)	27 (3)	30 (4)	
H			16 (3)							
I			17 (4)	21 (3)						
J								28 (3), 29 (2)		

Rows A–J correspond to social groups, and grouped numbers refer to social pairs (families). Numbers in parentheses are the number of offspring of the family. There was a total of 31 families.

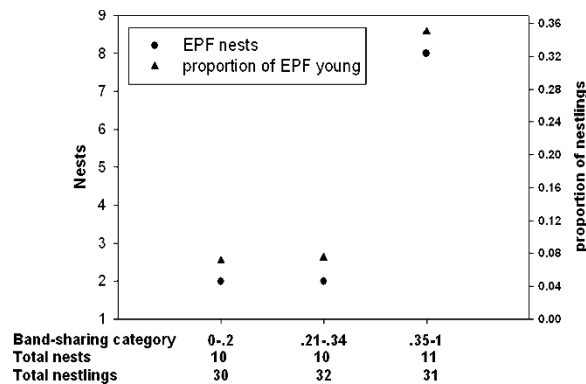


Figure 2

Correlation of EPF occurrence and band sharing values of social pairs, and proportion of nestlings that were EPF in each band sharing category. Band sharing categories were generated by dividing the distribution of all social pairs in the data set into three categories of band sharing: 0.05–0.20, 0.22–0.34, and 0.35–1.0.

There was a positive relationship between genetic similarity of social mates and the occurrence of EPF: Mann-Whitney calculated $U(12)(19) = 188$, $.005 > p > .001$. The mean band sharing value of 0.23 ± 0.011 for unrelated individuals was similar to that for non-EPF pairs (mean = 0.25 ± 0.003).

The results from the chi-square contingency table comparing EPF to non-EPF nests showed a positive correlation between genetic similarity of social mates and occurrence of EPF: $.0025 > p > .001$ (Figure 2). The same test also showed a positive correlation between the proportion of EPF young and the genetic similarity of social mates (Figure 2): $p < .001$.

The results from the counterbias sampling method described above showed that mated pairs with EPF were more genetically similar than non-EPF mate pairs, $p = .025$, which was consistent with the results from the random sampling method ($.005 > p > .001$).

DISCUSSION

Our finding that EPF was positively correlated to genetic similarity of social mates is consistent with theories of EPF based on increasing heterozygosity of offspring (Brown, 1997, 1999) as well as those based on genetic compatibility (Griffith et al., 2002; Kempenaers et al., 1999; Tregenza and Wedell, 2000). More specifically, our results agreed with the inbreeding avoidance hypothesis proposed for Mexican jays (Brown, 2001). Inbreeding is more likely when dispersal is reduced, and in the Mexican jay dispersal is more conservative than that of any other known continental bird species in North America (Brown, 1994). Many individuals of both sexes breed on their natal territory, and individuals that do disperse usually emigrate to a neighboring flock (Brown JL and Brown ER, 1984). Approximately 5% of broods are inbred on our pedigrees, and the costs of inbreeding are severe; inbred pairs have smaller broods, and their young have lower rates of survival through their first year (Brown JL and Brown ER, 1998).

Although our results were consistent with inbreeding avoidance and increased offspring heterozygosity by preinsemination mechanisms, kin recognition and female choice are not necessary to explain them. Postinsemination mechanisms could also explain our findings. If all females in the study population were equally promiscuous, our results could be explained by female cryptic choice (Birkhead and Pizzari, 2002; Pilastro et al., 2004; Pizzari and Birkhead, 2000; Sakaluk and Eggert, 1996; Ward, 2000; Wedell, 1996) or sperm competition (Birkhead et al., 1988; Pizzari et al., 2003; Shimmin et al., 2000; Stockley and Preston, 2004). Sperm from males more genetically similar to the female might be less successful than sperm from less similar males. In this scenario, females need not assess genetic similarity of potential mates prior to insemination.

Although offspring heterozygosity and/or genetic compatibility appeared to be possible factors contributing to EPF occurrence in Mexican jays, they are probably not the only ones; EPFs were identified in broods of some genetically dissimilar mated pairs (band sharing scores near the background of 0.23). It is possible that in some situations female Mexican jays pursued good genes for their offspring (Frederick, 1987; Westneat et al., 1990) by using unknown phenotypic cues correlated to overall fitness. The Mexican jay, however, lacks significant sexual dimorphism (Brown and Bhagabati, 1998; Pitelka, 1945) and has no advertising song (Brown, 1994). Thus, song repertoire (Hasselquist et al., 1996) and plumage brightness (Moller and Birkhead, 1994) are unlikely cues to good genes in this species. Age (Richardson and Burke, 1999) and dominance might be possible cues, but the EPF fathers tended to be unmated (Li and Brown, 2000). Unmated males tended to be subordinate and younger (Brown et al., 1997), and there is no known phenotypic correlate of age in this species after the age of first breeding.

Our results are similar to those reported by Blomqvist et al. (2002) in that both studies showed a positive correlation between minisatellite band sharing and occurrence of EPF. Our study differs from theirs by providing empirically generated band sharing distributions for different classes of kin (Figure 1A) and comparing them to the band sharing distributions of mated pairs (Figure 1B). These distributions allowed us to infer levels of relatedness of individuals of unknown pedigree, such as social mates. Figure 2 illustrates that EPFs occurred more often when genetic similarity of social mates is substantially high (.0.35) and, indeed, five of the eight EPF nests in the third category of genetic similarity (0.35–1.0) had band sharing values at or above 0.40.

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