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Genetic similarity between mates and extra-pair parentage in three species of shorebirds

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Matings between close relatives often reduce the fitness of offspring, probably because homozygosity leads to the expression of recessive deleterious alleles[1–5]. Studies of several animals have shown that reproductive success is lower when genetic similarity between parents is high[4–7], and that survival and other measures of fitness increase with individual levels of genetic diversity[8–11]. These studies indicate that natural selection may favour the avoidance of matings with genetically similar individuals. But constraints on social mate choice, such as a lack of alternatives, can lead to pairing with genetically similar mates. In such cases, it has been suggested that females may seek extra-pair copulations with less related males[4], but the evidence is weak or lacking[4,5]. Here we report a strong positive relationship between the genetic similarity of social pair members and the occurrence of extra-pair paternity and maternity ('quasi-parasitism') in three species of shorebirds. We propose that extra-pair parentage may represent adaptive behavioural strategies to avoid the negative effects of pairing with a genetically similar mate.

Molecular studies of socially monogamous birds have shown that broods often contain offspring that are not related to one of the parents tending the nest[12]. Extra-pair fertilizations can result from females engaging in copulations with extra-pair males (extra-pair paternity; EPP), or from males copulating with extra-pair females that lay their eggs in the male's nest (quasi-parasitism; QP). Generally, EPP is common in passerines (songbirds) and, although other hypotheses cannot be discarded, it may be explained by females seeking 'good genes' for their offspring[12,13]. In contrast, EPP is less common in non-passerine birds[14], in which its adaptive significance remains unexplained. QP is rare among birds and poorly understood[15]. Here we propose an adaptive explanation for the occurrence of EPP and QP in non-passerine birds and show that it is over-represented in pairs with genetically similar mates.

We examined genetic parentage in western sandpipers *Calidris mauri*, common sandpipers *Actitis hypoleuca* and Kentish plovers *Charadrius alexandrinus*. Multilocus DNA fingerprinting identified low rates of EPP in these birds (Table 1), comparable to those found in most other shorebirds (ref. 16, and references therein). In contrast to previous studies, however, we also found evidence for QP in two of the species examined (Table 1). Thus, our study species are predominantly genetically monogamous, with alternative reproductive behaviours occurring at low frequencies.

The females laying the quasi-parasitic eggs may have been either mated (and thus were having extra-pair copulations) or unmated (floaters). Because we did not identify extra-pair parents in our study, we do not have evidence that can directly separate these two possibilities. If quasi-parasites were mated, however, we would expect their parasitic eggs to be fathered by their social mate (unless those females have extreme control over paternity). Given the low rate of EPP and the lack of intraspecific brood parasitism (only two cases documented in the Kentish plover; C.K., unpublished data), it seems more likely that the quasi-parasites were floaters. Observations suggest that female floaters are present in the common sandpiper (M.A., unpublished data), but information for the other species is lacking. In all cases of QP the clutch sizes were not increased, suggesting that the parasitic female (or the receiving

Table 1 **Frequency of extra-pair fertilizations in three species of shorebirds determined by DNA fingerprinting**

Species	Number of broods (number of chicks)	EPFs % (*n*)	EPP % (*n*)	QP % (*n*)
Kentish plover	65	4.6 (3)	1.5 (1)	3.1 (2)
	(170)	2.9 (5)*	0.6 (1)	1.2 (2)
Western sandpiper	25	8.0 (2)	8.0 (2)	0 (0)
	(61)	6.6 (4)	6.6 (4)	0 (0)
Common sandpiper	15	20.0 (3)	6.7 (1)	13.3 (2)
	(53)	7.5 (4)	1.8 (1)	5.7 (3)

Only broods where both putative parents were fingerprinted are included. EPF, extra-pair fertilization; EPP, extra-pair paternity; QP, quasi-parasitism.
*Two EPF chicks could not be classified as EPP or QP owing to high band-sharing between pair members.

male) removed one or two eggs from the host female's nest. Alternatively, the parasitic female may have laid her eggs early in the laying sequence of the host female and the latter stopped laying when the nest contained the normal number of eggs.

In all three species, the occurrence of extra-pair fertilizations (EPP and QP combined) was related to genetic similarity between social pair members, which was estimated as band-sharing from multilocus DNA fingerprints (Fig. 1; logistic regression; Kentish plover: $\chi^2(1) = 7.99$, $P = 0.0047$; western sandpiper: $\chi^2(1) = 13.9$, $P = 0.00019$; common sandpiper: $\chi^2(1) = 5.98$, $P = 0.014$). Because regression analysis is sensitive to outliers, we also tested the relationship using ranked data. This confirmed that band-sharing between the mates was significantly higher in pairs tending broods with extra-pair offspring than in pairs with only within-pair young (Fig. 1; Mann–Whitney *U*-test; Kentish plover: $U = 29.5$, $P = 0.046$; western sandpiper: $U = 0$, $P = 0.021$; common sandpiper: $U = 3$, $P = 0.027$). The combined probability, based on the results of the Mann–Whitney *U*-tests, was $P < 0.01$ ($\chi^2(6) = 21.1$). An independent scoring of band-sharing between mates, carried out by a colleague who did not know whether broods contained extra-pair young or not (Methods), yielded a qualitatively similar result (combined Mann–Whitney tests; $\chi^2(6) = 15.3$, $P < 0.02$). Thus, genetic similarity between mates significantly predicted the occurrence of extra-pair fertilizations.

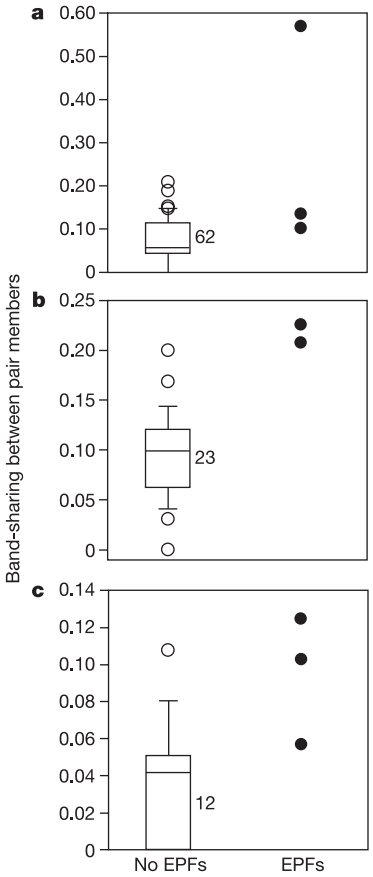

Figure 1 Band-sharing between mates and occurrence of extra-pair fertilizations (EPFs) in three species of shorebirds: **a**, Kentish plover; **b**, western sandpiper; and **c**, common sandpiper. EPFs include EPP and QP. For broods without extra-pair young, data are presented as box plots showing the 25th and 75th percentiles (box), median (line within the box), 10th and 90th percentiles (bars), and data points outside the latter percentiles. The number of broods is given beside the box. For broods with EPFs, the individual data points are shown. In all species, the difference in band-sharing between broods with or without extra-pair young was statistically significant (combined probability: $P < 0.01$, see text). The mean ± s.e.m. number of scored bands per adult was 18.8 ± 0.4 (Kentish plover, $n = 130$), 35.8 ± 1.0 (western sandpiper, $n = 50$) and 20.8 ± 1.0 (common sandpiper, $n = 30$).

Our data are insufficient to examine EPP and QP separately for each species. But because the genetic analyses were carried out in the same laboratory and by the same protocols (Methods), we can pool the data after standardizing the band-sharing values for each species (by subtracting the species-specific mean and dividing by the species-specific standard deviation). The pooled data show that the genetic similarity between mates explains the occurrence of EPP and QP, independently (logistic regression, $n = 105$ broods in total; EPP (4 broods): $\chi^2(1) = 5.47$, $P = 0.019$; QP (4 broods): $\chi^2(1) = 11.2$, $P = 0.0016$). We obtained similar results using Mann–Whitney *U*-tests on ranked data (data not shown). Note that we conservatively included the broods with QP in the group 'no EPP' in the first logistic regression, and the broods with EPP in the group 'no QP' in the second test (excluding these broods gives $\chi^2(1) = 17.0$, $P = 0.00004$ for EPP and $\chi^2(1) = 11.2$, $P = 0.00081$ for QP).

We have shown that in three species of shorebirds, breeding in North America, Europe and Asia, respectively, parents tending broods with extra-pair young are genetically more similar than those rearing exclusively within-pair chicks. This suggests that, in these species, males and females are more likely to engage in extra-pair matings when they are closely related to their social mate. This behaviour should be adaptive if high genetic similarity between parents has negative fitness consequences for their genetic offspring, and if genetic similarity with the extra-pair mate is lower. We do not have sufficient data to test this in our species, but the first assumption has been verified repeatedly[1–11] and several studies have suggested that EPP may function to avoid the negative effects of inbreeding[4,17–19].

We know of only two other studies that have directly examined the relationship between genetic similarity of social mates and the occurrence of extra-pair fertilizations. In great reed warblers *Acrocephalus arundinaceus*, four of five females shared fewer bands with their extra-pair mate than with their social mate[4]. By contrast, in blue tits *Parus caeruleus*, band-sharing between the social parents did not differ for broods with or without extra-pair young, and the genetic similarity between the female and her social mate did not differ from that between the female and her extra-pair mate ($n = 18$ comparisons)[5]. In both species, there is evidence that females seek extra-pair copulations with high-quality males to increase the genetic quality of their offspring (the 'good genes' hypothesis)[20,21].

With respect to QP, our data suggest that a male may copulate with a female other than his social mate and allow her to lay one or more eggs in his nest. This is in agreement with the hypothesis that QP is male driven[15] and may be adaptive, increasing the genetic quality of his offspring (but see ref. 15 for other explanations for the occurrence of QP). Note that, from a male perspective, QP differs from extra-pair copulations in that, first, males involved in QP do not gain extra offspring and, second, they do provide care for the QP offspring.

If males or females adjust their choice of genetic mate as suggested by our results, then an intriguing implication is that they can assess the genetic similarity with their social mate. The band-sharing between parents that raised extra-pair offspring varied between 5.7% (common sandpiper) and 57.1% (Kentish plover), suggesting that their ability to recognize kin is not restricted to first-order relatives. In support of this possibility, a study of lekking peacocks *Pavo cristatus* suggests that males can assess their genetic similarity with other males independently of social learning and environmental cues[22], and such ability may be more widespread[23,24]. Alternatively, a bias against genetically similar mates may

arise through sperm competition if fertilization success is reduced for sperm that are genetically similar to the egg[13], but this mechanism cannot explain the occurrence of QP. The cues used by birds to assess genetic similarity are unknown, presenting a challenging problem for future research.

In conclusion, we propose that EPP and QP in shorebirds and other non-passerine birds may be adaptive responses to avoid inbreeding depression or other negative effects of genetic similarity between social mates. □

Methods

Species and study sites

We studied western sandpipers at Nome, Alaska (64° 20′ N, 164° 56′ W), Kentish plovers at Tuzla, Turkey (36° 43′ N, 35° 03′ E) and common sandpipers at Säveån, Sweden (57° 47′ N, 12° 19′ E). All three species are waders or shorebirds (suborder Charadrii), have small clutches (3–4 eggs) and precocial young[25]. Both sexes incubate the eggs, but males usually provide most care for the young. Western and common sandpipers are socially monogamous, whereas sequential polyandry is frequent in Kentish plovers[25]. Breeding habitats consisted of tundra ponds and low ridges along the coast (western sandpiper), inland salt marshes (Kentish plover) and forested riverbanks (common sandpiper). We collected blood and tissue samples for fingerprinting from these populations in 1996 (western sandpiper), 1998–1999 (Kentish plover) and 1998–2000 (common sandpiper), respectively. Parents were caught while incubating or tending newly hatched chicks, whereas chicks usually were caught in or near the nest soon after hatching. For most pairs, observations from the pre-laying period are lacking. Thus, rapid mate replacement cannot be completely excluded as an alternative explanation for the occurrence of EPP.

Genetic analyses

We determined genetic parentage by multilocus DNA fingerprinting[26]. Nuclear DNA was extracted from blood or tissue samples (dead chicks) using proteinase K and phenol/chloroform/isoamylalcohol. We separated 3–7 μg of *Hae*III-digested DNA on 0.8% agarose gels (20 × 40 cm) by electrophoresis at 1.2 V cm^{-1} for 40 h. The DNA was transferred to nylon membranes using Southern blotting and hybridized with the multilocus probe *per*[27]. The probe was radioactively labelled with [^{32}P]dCTP by random priming using the Prime-a-Gene labelling system (Promega).

Fingerprints were scored by standard methods[28] by C.K. (Kentish plover) and D.B. (common and western sandpiper). Scoring was done blind with respect to the tested hypothesis. We also obtained an independent analysis by asking a colleague (J. T. Lifjeld, Zoological Museum, University of Oslo, Norway) to score band-sharing[26] between mates, which he did without knowing whether their broods contained extra-pair young or not. We excluded a tending parent as a genetic parent when chick fingerprints showed several unattributable DNA fragments (novel bands) and low band-sharing with the parent in question. Pooling the three species in our study, extra-pair chicks showed 4–17 novel bands (6.9 ± 1.0 (mean ± s.e.m), $n = 11$) and shared 14.0–27.8% of the bands with the excluded parent (23.3 ± 1.2, $n = 11$). Band-sharing between non-excluded parents and their offspring varied between 32.0 and 78.8% (mother-offspring, 51.5 ± 0.6, $n = 271$) and between 31.3 and 74.5% (father-offspring, 52.0 ± 0.6, $n = 271$), respectively, with 0–2 novel bands owing to mutation or other random causes.

Measures of genetic similarity based on DNA fingerprinting are more reliable if it can be shown that bands segregate independently from parents to young following mendelian inheritance[26]. We checked this by carrying out a segregation analysis on 15 randomly selected families (five in each species) without extra-pair young. In each family, we scored unique parental bands (males: 21.6 ± 2.0 bands, range 11–38; females: 21.7 ± 1.5, range 12–33) as either present (1) or absent (0) in their chicks. Mean transmission frequencies of single parental fragments were close to the expected value (0.50) for unlinked loci; they varied between 0.45 and 0.57 for paternal pedigrees (pooled mean = 0.51) and between 0.45 and 0.56 for maternal pedigrees (pooled mean = 0.50). In addition, only 10% of the parental bands ($n = 649$) were transmitted to all offspring in a brood, suggesting that most fragments were from heterozygous loci.

We examined linkage and allelism by calculating correlation coefficients (r) for all pairwise combinations of parental bands. Mean r varied between −0.03 and +0.14 in the paternal pedigrees (pooled mean 0.04) and between −0.04 and +0.14 in the maternal pedigrees (pooled mean 0.02), suggesting that most bands segregated independently. Indications of consistent co-segregation ($r = 1.0$) or allelism ($r = -1.0$) occurred infrequently in all families; on average, 6–9% (paternal pedigrees) and 7–8% (maternal pedigrees) of the pairwise combinations showed either of these patterns. Given the small brood sizes in our study species, however, several (if not all) of these cases may be coincidental. Consistently, the proportion of band combinations showing either co-segregation or allelism was significantly higher in families with three chicks than in those with four chicks (Mann–Whitney U-test combining both sexes: co-segregation, $U = 63$, $P = 0.04$, $n = 16$; allelism, $U = 52$, $P = 0.01$, $n = 14$). We therefore conclude that most bands stem from alleles at unlinked heterozygous loci, as found in many other studies using DNA fingerprinting (for example, see refs 5, 15).

In the field, adults were sexed by behaviour (such as courtship displays), size (especially bill length) or plumage characteristics (Kentish plovers)[25]. To confirm cases of EPP and QP, we determined the sex of all parents with extra-pair offspring by polymerase chain reaction (PCR) amplification of the *CHD-W* and *CHD-Z* genes using two sets of primers for each individual: P2 and P8 (ref. 29), and 3007 and 3112 (ref. 30), respectively. In brief, amplification was done in 10-μl reactions using a touchdown profile (Perkin Elmer 9600): 94 °C for 5 min; 60 °C, 72 °C, 94 °C, 58 °C, 72 °C, 94 °C, 52 °C and 72 °C for 30 s; 25 cycles at 94 °C, 50 °C and 72 °C for 30 s; and finally 4 °C for 10 min. We analysed the PCR products with an automatic sequencer (ABI 310 Genetic Analyzers, PE Biosystems), which in all cases confirmed the previously assigned sex.

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