

Extra-group mating increases inbreeding risk in a cooperatively breeding bird

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Abstract

In many cooperatively breeding species, females mate extra-group, the adaptive value of which remains poorly understood. One hypothesis posits that females employ extra-group mating to access mates whose genotypes are more dissimilar to their own than their social mates, so as to increase offspring heterozygosity. We test this hypothesis using life history and genetic data from 36 cooperatively breeding white-browed sparrow weaver (*Plocepasser mahali*) groups. Contrary to prediction, a dominant female's relatedness to her social mate did not drive extra-group mating decisions and, moreover, extra-group mating females were significantly *more* related to their extra-group sires than their social mates. Instead, dominant females were substantially more likely to mate extra-group when paired to a dominant male of low heterozygosity, and their extra-group mates (typically dominants themselves) were significantly more heterozygous than the males they cuckolded. The combined effects of mating with extra-group males of closer relatedness, but higher heterozygosity resulted in extra-group-sired offspring that were no more heterozygous than their within-group-sired half-siblings. Our findings are consistent with a role for male–male competition in driving extra-group mating and suggest that the local kin structure typical of cooperative breeders could counter potential benefits to females of mating extra-group by exposing them to a risk of inbreeding.

Keywords: genetic dissimilarity, good genes, heterozygosity hypothesis, kin structure, *Plocepasser mahali*, reproductive skew

Received 29 April 2013; revision received 15 August 2013; accepted 24 August 2013

Introduction

In many species, females engage in copulations with males other than their social mate, but despite considerable research effort, the mechanisms driving such extra-pair mating (EPM) in wild populations remain poorly understood (reviewed in Griffith *et al.* 2002; Westneat & Stewart 2003; Akcay & Roughgarden 2007). A key focus of the adaptive explanations of EPM for females is that it may allow them to gain indirect, genetic benefits for their offspring that are unavailable from their social mates (Griffith *et al.* 2002; Reid *et al.* 2011; Gohli *et al.* 2013). Such genetic benefits could include superior genes to those available from the social mate, as envisaged

in the 'good genes' hypothesis (Neff & Pitcher 2005), which assumes that there is additive genetic variation among males in fitness-determining traits. However, an alternative possibility is that females use EPM to increase offspring viability by maximizing offspring heterozygosity, that is, the 'heterozygosity hypothesis' (Brown 1997; reviewed in Kempnaers 2007). Increased heterozygosity has been associated with several traits reflective of individual fitness in wild species, including reduced disease susceptibility (e.g. Acevedo-Whitehouse *et al.* 2003), increased survival (Cohas *et al.* 2009) and increased reproductive success (e.g. Harrison *et al.* 2011). Collectively these suggest there are adaptive advantages to maximizing offspring heterozygosity because of their potential positive effect on offspring fitness. For example, heterozygosity at the loci of the major histocompatibility complex (MHC), which form

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an important component of the acquired immune response in vertebrates, may be beneficial as it could allow an individual to recognize and defend against a wider range of pathogens (reviewed in Tregenza & Wedell 2000; Spurgin & Richardson 2010). Females can maximize offspring heterozygosity in two ways: (i) mating with a genetically dissimilar male (Tregenza & Wedell 2000); or (ii) mating with a male who is himself highly heterozygous, as offspring and parental heterozygosity are often highly correlated (Mitton *et al.* 1993; Reid *et al.* 2006; Neff & Pitcher 2008; Fromhage *et al.* 2009; but see Aparicio 2011). Indeed, it may be the case that females seek to achieve both, preferring not only genetically dissimilar males but also those that are highly heterozygous (Hoffman *et al.* 2007).

In cooperatively breeding species, where individuals often help to rear young that are not their own (Cockburn 1998), delayed dispersal by offspring from previous broods can result in high within-group kin structure and an absence of unrelated (genetically dissimilar) breeding partners within the group (Koenig & Haydock 2004). Inbreeding avoidance is a well-described phenomenon in such species, and females will often mate exclusively with males from outside the group in the absence of unrelated within-group males (Sillero-Zubiri *et al.* 1996; Young *et al.* 2007; see also Koenig & Haydock 2004). Less known, however, are (i) whether social mate heterozygosity also drives the occurrence of extra-group mating in cooperative breeders, and more importantly (ii) if extra-group mating allows females to maximize offspring heterozygosity by maximizing both the heterozygosity of, and their dissimilarity to, their extra-group (EG) mate (e.g. Hoffman *et al.* 2007). Maximizing offspring heterozygosity via extra-group mating could be especially problematic in cooperative breeders, as individuals often demonstrate restricted natal dispersal that can result in a high concentration of relatives in the immediate neighbourhood of the natal territory as well (e.g. Double *et al.* 2005; Berg *et al.* 2009; Nelson-Flower *et al.* 2012; Rollins *et al.* 2012). While the rules for recognizing kin and avoiding inbreeding may be well developed at the within-group level (e.g. learning by association, Hatchwell *et al.* 2001), this may not be the case at the level of the population, where more sophisticated mechanisms may be required (Koenig & Haydock 2004) such as vocal kin recognition (Akçay *et al.* 2013). Relatively little is known about how, or if, females in cooperative species can secure genetically dissimilar males by mating EG within the local subpopulation (but see e.g. Cohas *et al.* 2008; Brouwer *et al.* 2011), though the extent to which they can will have marked implications for the heterozygosity of the resulting offspring. Accordingly, studies on both birds (e.g. Daniels & Walters 2000) and mammals (Dobson

et al. 1997) have provided evidence that individuals can be effective at minimizing inbreeding within social groups, but fail to do so at the level of the subpopulation where there is strong genetic structure due to the local dispersal of relatives (but see Brouwer *et al.* 2011). A key priority now should be to quantify the degree to which females are able to trade off increased heterozygosity with lower genetic similarity through extra-group mating in cooperative species.

Here, we use detailed genetic and ecological data to test the heterozygosity hypothesis in a cooperatively breeding bird, the white-browed sparrow weaver (*Plocepasser mahali*). White-browed sparrow weavers live in cooperatively breeding groups of 2–14 individuals in which reproduction is completely monopolized by a single dominant female, while subordinates of both sexes (typically offspring that have delayed dispersal from their natal group) help to rear her young (Lewis 1981, 1982; Harrison *et al.* 2013). Previously, we have shown that dominant males monopolize all within-group (WG) paternity (i.e. there are no WG opportunities for subordinate male reproduction), but that they concede 12–18% of reproduction to EG males (Harrison *et al.* 2013). The lack of within-group extra-pair paternity suggests that it is highly unlikely that females mate extra-pair to derive direct benefits (e.g. parental care, Rubenstein 2007; Townsend *et al.* 2010), which raises the possibility that any benefits of extra-group mating to females in this species may have a genetic basis. If female white-browed sparrow weavers employ EG mating to maximize the heterozygosity of their offspring, we predict that: (i) females will be more likely to mate EG when paired to social mates of low heterozygosity and / or high genetic similarity (relatedness) to the female; (ii) that EG-mating females will mate with EG males that are of higher heterozygosity and / or lower genetic similarity (relatedness) to the female than their social mates; and (iii) the offspring sired by EG males will be more heterozygous than their half-siblings sired by the within-group dominant male.

Methods

Study system and sample collection

Our study population comprises 40 cooperative groups of white-browed sparrow weavers, which defend small year round territories in an area of approximately 1.5 square kilometres, west of the Korranaberg mountains in Tswalu Kalahari Reserve in the Northern Cape province of South Africa (27°16'S, 22°25'E). Sparrow weaver social groups could be distinguished from one another as all group members typically foraged together each day, engaged in cooperative sentineling, offspring care,

weaving and territorial defence against neighbouring groups, and roosted together each night in individually woven chambers in a single tree or cluster of trees near the centre of their territory. Mean distance between neighbouring territories was 117.36 m (± 45.15 m SD, $n = 36$ territories, Harrison *et al.* 2013).

The dominant bird of each sex was determined by weekly monitoring of key dominance-related behaviours as described in previous studies of this species (e.g. Collias and Collias 1978; Voigt *et al.* 2007). Specifically, dominants of either sex more frequently demonstrated within-group aggression such as the chasing and displacing of other individuals, the dominant pair regularly produced synchronized duet song together and the dominant male consistently produced solo song at dawn throughout the breeding season.

All birds were fitted with a single metal ring and three colour rings for identification (under SAFRING license 1444) and records of group compositions were maintained with at least weekly visits. Genetic sampling was performed by taking a small amount ($<25 \mu\text{L}$) of blood from the wing vein and storing it in 96% ethanol at a minimum dilution of 1 part blood to 20 parts ethanol. All protocols were approved by the University of Pretoria ethics committee and complied with regulations stipulated in the Guidelines for the use of Animals in Research.

Genotyping and parentage assignment

We genotyped 607 birds at 10 microsatellite loci (Table S1, Supporting information) from samples collected over a 4-year period between 2007 and 2010. Genotyping repeatability was calculated by re-genotyping 10% of our samples from the DNA extraction stage, with 99% of alleles being scored identically between sets. We used the program COLONY v2.0 (Wang & Santure 2009) to assign parentage to the 385 offspring present in the sample of 607 birds (details in Harrison *et al.* 2013). This sample comprised 329 offspring of known natal origin (from 201 clutches laid in 36 groups) that had hatched from eggs in a monitored breeding attempt, in addition to 56 offspring whose origin was unknown because they were first discovered as fledglings after a break in monitoring. These latter individuals could have been either natal to the group in which they were first observed, or recent immigrants from elsewhere. We included these additional 56 because many are likely to have been siblings of the other 329 offspring, and larger sibships in the sample will improve the power that COLONY has to assign parentage (Wang & Santure 2009). For the 329 offspring of known origin, all females alive within the natal group at the time of the clutch being laid were included as candidate mothers, whereas all

sampled males alive in the study population at the time of egg laying were included as candidate fathers. For those offspring of unknown origin, we included all males and females in the population as candidate parents, to allow for the possibility that their natal origin was not identical to the group they were first recorded in as fledglings. To assign parentage, we performed three replicate runs with the following COLONY parameters: medium run length, full-likelihood estimation with high precision, and allowing for both male and female polygamy. Each run was performed with a different random number seed, with the expectation that true relationships would be reliably recovered in multiple runs, irrespective of the starting configuration of the search algorithm (Wang 2004). Conversely, spurious assignments may only occur in single runs and can thus be identified as such by their lack of consistency across runs. We specified a 1% error rate per locus for both the allelic dropout and stochastic (e.g. mutation, false alleles, mis-typing) error types, as parameterized from our repeat genotyping/error rate calculations. Allele frequencies for the COLONY run were calculated from the sample, and updated based on the inferred relationships. Assignments for both paternity and maternity were only accepted if at least two of the runs assigned the same parent with 95% confidence. We refer to assignments meeting this criterion as being assigned at the '95% consensus threshold'. In any case where there was a conflict in assignment across runs (i.e. >1 individual listed as the most likely candidate), that relationship was considered unassigned, irrespective of the probabilities associated with the relationships.

Our analyses of the drivers of extra-group mating used only the 292 offspring from 180 clutches in 34 social groups for which we knew that all males in the focal offspring's natal group had been successfully genotyped, so as to ensure that (i) 'unassigned' offspring (i.e. failing to reach the 95% consensus threshold for any candidate sire) are not erroneously assigned as EG when they are in fact the progeny of an unsampled within-group male and (ii) genotypes of offspring assigned to an EG male can be compared with the genotypes of within-group males using exclusion analysis, while accounting for the known maternal genotype, to check that no within-group males are equally compatible as sires. The latter can occur, for example, when the true *within-group* sire's brother (perhaps resident in another group) is erroneously assigned by COLONY, both having haplotypes compatible with the offspring's.

COLONY assigned 226 of these 292 offspring to the within-group dominant male at the 95% consensus threshold. A further 28 offspring were not assigned a sire at that threshold. Of these, 20 offspring had genotypes that were compatible with the within-group

dominant's genotype when allowing for up to 1 mismatch when discounting the maternal genotype (10 perfect matches & 10 with 1 mismatch), and so were conservatively assigned as within-group offspring. The remaining eight offspring with no assigned sire were presumed to be true EG offspring, as they mismatched all within-group males at two or more loci. COLONY assigned 38 offspring to EG sires at the 95% consensus threshold. Of these, nine had genotypes that were also compatible with the within-group dominant male (all perfect matches) and so were conservatively assigned as offspring from within-group paternity. Therefore, the final sample of 292 comprised a total of 37 EG offspring, 29 of which were assigned to sampled EG males, with the remaining eight offspring assumed to be the progeny of unsampled EG males as they had genotypes that were not compatible with any within-group males.

Heterozygosity, relatedness and morphometric data

Following Chapman *et al.* (2009), we used raw multilocus heterozygosity (MLH, number of heterozygous loci as a proportion of the total) as our measure of heterozygosity. Individuals with missing data for a particular locus were assigned the population mean observed heterozygosity (H_0) for that locus (Szulkin *et al.* 2010). Mean observed heterozygosity for the 10 loci employed in this study was 0.72 (± 0.045 SE). We employed the Queller & Goodnight moment estimator as our metric of relatedness (Queller & Goodnight 1989), calculated using the program COANCESTRY (Wang 2011).

Quantifying marker bias towards assignment of more heterozygous EG sires. Wetzel & Westneat (2009) and Wang (2010) found that employing the same set of markers to assign paternity and quantify heterozygosity could bias data towards finding that EG sires are more heterozygous than the social males they cuckold. To quantify the potential for such bias, we followed the methods outlined in Wang (2010) to calculate an 'hH' value for each marker employed, by calculating the mean EG sire heterozygosity for that marker (where each sire is scored as 1 or 0 for heterozygosity or homozygosity at that locus, respectively) and dividing it by the expected heterozygosity of that marker given the population allele frequencies (H_{EXP} in Table S1, Supporting information). A mean hH ratio over all markers of >1 suggests a bias in that panel towards assigning extra-group paternity (EGP) to more heterozygous sires (Wang 2010). The mean hH value for EG sires the 10 markers employed in this study was 0.98, and for all assigned sires was 1.02 (Table S2, Supporting information). This result concurs with our finding that EG sires had a

mean heterozygosity roughly equal to the population mean (see results), whereas in the case of significant assignment bias one might expect EG sires to have a mean heterozygosity above the population mean.

Inbreeding-heterozygosity correlations. Although inbreeding is expected to lead to a reduction in the heterozygosity of offspring, several studies have demonstrated that under certain circumstances, estimates of heterozygosity based on microsatellite loci correlate only weakly with inbreeding coefficients (Slate *et al.* 2004; Balloux *et al.* 2004; but see Forstmeier *et al.* 2012). To address this concern, we calculated the correlation between multilocus heterozygosity and marker-based estimates of inbreeding coefficients calculated using the R package 'adegenet' (Jombart & Ahmed 2011). Rather than use all 10 markers to calculate both heterozygosity and inbreeding, which would result in nonindependence of the two measures, we performed a randomization approach: for each permutation the markers were split into two randomly assorted sets of five, and one set was used to calculate heterozygosity and the other to calculate inbreeding. We performed 100 iterations in total and report the mean and 95% confidence interval of these randomizations. We found a significant negative correlation between heterozygosity and inbreeding coefficient estimates derived from randomly assorted subsets of loci (mean $r = -0.65$; 95% CI = -0.58 to -0.72). These data suggest that the variation in heterozygosity among individuals in our sample is also informative with respect to their inbreeding level.

Male mass and tarsus length. For the analyses of the effect of male morphometric traits on the probability of the breeding female mating EG, we used both body mass and tarsus length. Tarsus length was calculated as the mean value for all adult tarsus measurements taken per individual (mean number of measurements per individual: 4.7). For body mass, we computed the Scaled Mass Index (SMI) following Peig & Green (2009), which scales the mass of all individuals to values that would be expected if they were all of identical body size. We used 1021 records of male mass and tarsus length from 216 males over 5 years. We stress that this measure of mass is not a residual-based measure of 'body condition', which has recently been heavily criticized (see Labocha & Hayes 2012), but a measure of mass based on an inherent power relationship between mass and size modelled from our data (see Peig & Green 2009). Males were scaled to the mean male tarsus length (L_0) of 24.77 mm, using a Secondary Major Axis (SMA) slope of 2.6 (details in Peig & Green 2009). This resulting Scaled Mass Index is hereafter referred to as 'body mass'. Where multiple measures of body mass

existed per individual per year, we computed a mean value to be used in subsequent analyses.

Distance between territories. Distance between territories was calculated as the Euclidean distance between the territory centres of social groups, where territory centres are defined as the GPS coordinates of the roost trees. Where >1 roost tree was regularly used, the average coordinates for these trees were taken and used in subsequent calculations.

Statistical analysis

What factors predict when a female will mate extra-group?. We fitted a mixed effects model with binomial error structure and logit link (see 'Statistical Modelling' section below), using data from 180 clutches from 34 groups. We fitted 'EG mating' as a binary response term to indicate if that clutch contained a chick sired by an EG male. We fitted the following traits of the resident-dominant male as input variables: multilocus heterozygosity (MLH), relatedness to the dominant female, body mass and tarsus length. We also included group size at the time the clutch was laid. We fitted maternal ID as a random effect to account for multiple clutches originating from a single female. We did not include a random intercept term for the ID of the resident-dominant male, as in the majority of cases dominant male and female pairs were unique, leading to convergence problems when trying to estimate a crossed random effect.

What factors predict the identity of the extra-group sire?. We fitted a mixed effects model with binomial error structure and logit link, using the 19 clutches containing 29 EG-sired chicks for whom we had been able to identify the extra-group sire. For each clutch, we extracted all EG males alive at the time of the paternity in our study population that were in their second year or older (i.e. excluding juvenile birds in their first year of life). We fitted 'paternity' as a binary response term, where the EG sire that gained the paternity was scored as '1' and all other males as '0'. We fitted the following traits of the EG male as input variables: MLH, dominance status (dominant or subordinate), relatedness to female, tarsus length, body mass, distance of his territory centre from the maternal territory centre and distance² (to allow for a nonlinear effect of distance). We specified random intercept terms for Clutch ID and EG Male ID. All models containing the quadratic distance term were always fitted with its component linear term.

Does extra-group mating result in pairing with higher quality mates?. To investigate whether EG mating afforded

females access to males with higher trait values than the social mates they cuckolded, we performed tests to compare the trait values of cuckolded social mates and EG sires. Such analysis is crucial, as if females are mating EG to pursue 'benefits', then we would predict that she should do so with higher quality mates than her social male. However, few studies are able to do so because they lack information on the identity of the EG sire. We focused exclusively on the genetic traits (heterozygosity and relatedness) because they were identified as significant predictors of female EG-mating probability (see above). Wetzel & Westneat (2009) found that pairwise tests between traits could be biased because the two classes of males (cuckolded social mates and EG sires) are not from separate statistical populations (i.e. in 1 case in our data set a cuckolded social mate also gained extra-pair paternity). They suggested that randomization approaches could circumvent this problem (Wetzel & Westneat 2009), and so we adopt this approach here. The analysis used paired trait values for the cuckolded within-group males and their extra-group cuckolds for the 19 clutches for which we were able to assign the EG sire. To conduct these tests, for each permutation, we randomly assigned the order that each trait value would appear within pairs for the whole data set (i.e. pairwise values are always preserved and never separated, but randomly shuffled). We performed 10 000 permutations in total. We then performed a paired *t*-test using the randomized data set, by comparing the true *t* value derived from a paired *t*-test on the empirical data to the distribution of *t* values generated by the randomization.

Can random pairing explain the observed traits of the extra-group sires?. We performed randomizations to test whether: (i) the proportion of EGP obtained by dominant males, (ii) the mean heterozygosity of EG sires and (iii) the mean relatedness of EG sires to dominant females were consistent with females, when they do mate EG, simply pairing at random with an EG male from across our study population. All *P*-values reported from randomizations are 2-tailed unless otherwise stated and employ 10 000 permutations of the data, which are used to create a null distribution of a test statistic from which we derive a *P*-value using the equivalent-test statistic from the observed data.

To test (i) whether the proportion of EGP assigned to dominants was consistent with random EG pairing by the female, we randomly assigned an extra-group sire to each of the 19 EGP clutches from the pool of dominant and subordinate adult males present in other groups in the study population at the time of the paternity. We used raw proportion of paternity by dominants as our test statistic.

To test (ii) whether the observed pattern of heterozygosity of the EG sires was consistent with random selection of EG mates from across the study population, we randomly assigned an EG sire for each clutch as for (i), but specified a 15.8% chance of paternity being gained by a subordinate (the observed proportion). For each permutation of the data set, we computed the mean heterozygosity of the chosen males and compared this to the actual data set mean.

To test (iii) whether the patterns of relatedness between the dominant female and EG sire were consistent with random selection of EG mates from across the study population, we repeated the randomizations as for (ii), but instead extracted the Queller & Goodnight relatedness estimator between dominant female and randomly chosen male and used the data set mean as a test statistic.

To test (iv) whether pairs of dominant males and females were less related than expected by chance, for 35 known breeding pairs (dominant males and females), we simulated random mate choice by the dominant female by randomly selecting a male from the pool of adult EG males alive in the population at the beginning of that female's dominance tenure. Following Bretman *et al.* (2011), we used $r \geq 0.25$ as the threshold to categorize a male as closely related to the breeding female, and used the frequency of closely related males present in the sample at each permutation as a test statistic. We used a one-tailed test to derive a *P*-value as (i) the alternative hypothesis was directional – that social mates were *less* related than expected by chance and (ii) neither a nonsignificant result, nor a significant result in the opposite direction would be consistent with our result regarding the relatedness of EG sires, and therefore can be treated as identical outcomes (see Ruxton & Neuhäuser 2010).

Are extra-group offspring more heterozygous than intragroup offspring? We employed a paired within-female comparison to test for heterozygosity differences between offspring resulting from mating with the social mate vs. extra-pair males for those females that did mate EG. Such differences might arise either from differences in heterozygosity of, or pairwise relatedness to, EG sires vs. the social mate.

Tests of Observed Offspring Heterozygosity: We used 164 genotyped offspring (27 extra-group and 136 intragroup) from 53 clutches from seven dominant females, and averaged the data to yield a mean heterozygosity of the offspring that each female produced when she mated either within-group or extra-group. We excluded 10 EG offspring from one female who mated exclusively EG and so had no within-group offspring to be compared with. We performed a randomized paired *t*-test on the data.

Tests of Simulated Offspring Heterozygosity: For each pair of cuckolded social mate and assigned EG sire ($n = 17$), we simulated 20 offspring from the maternal (dominant female) and paternal genotypes, and calculated a mean heterozygosity per mating type (i.e. 20 offspring from the female/social mate pairing and 20 from the female/EG sire pairing for each female). This approach prevents a bias towards finding that the group with the smaller sample size (i.e. EG offspring) has a higher heterozygosity (see Wetzel & Westneat 2009), which can lead to the erroneous conclusion that such matings confer benefits to females when in fact there is no difference between groups. It also accounts for the fact that low heterozygosity offspring may experience lower survival or egg viability, which could in turn bias our sample whereby we observe only the higher heterozygosity siblings that survived to be sampled. Where parental genotype data was missing for a locus, we replaced that locus in the offspring with the mean heterozygosity for that locus (Szulkin *et al.* 2010). We performed a randomized within-female paired *t*-test on these means.

Is heterozygosity heritable? We conducted simulations using the genotypes of 35 dominant breeding females to test whether heterozygosity was heritable, assuming that females were mating with unrelated males. Specifically, we wanted to know if simulated offspring from a more heterozygous sire are themselves more heterozygous than if they were the product of a less heterozygous sire. These data are presented in Fig. S2 (Supporting information).

Statistical modelling. We employed an information-theoretic (IT) approach to investigate (i) the factors that predict a female's propensity to mate with extra-group males; and (ii) the factors that predict which male she mates with (from all available males in the population). The strength of the IT approach is its ability to formally evaluate model selection uncertainty, where multiple competing models may be equally well supported by the data (Burnham & Anderson 2002). Models were ranked by AICc for all analyses and we considered any models within $\Delta 6$ units AICc of the top model to be equally well supported (Richards 2008; Richards *et al.* 2011). However, to avoid the retention of overly complex models, we also applied the 'nesting rule' (Richards 2008; Richards *et al.* 2011) whereby we discarded models in the $\Delta 6$ AICc model set that was more complex versions of simpler (nested) models with lower AICc values. This reduces the chance of considering models containing variables with no explanatory power, as the addition of an uninformative parameter to a well-supported model can often yield a change in AICc

of ≤ 2 units and thereby erroneously inflate the size of the candidate model set (see Arnold 2010). All model sets contained an intercept-only model for comparison. Full model tables are provided in Online Supplementary Material.

Models were fitted using the 'lme4' package (Bates *et al.* 2013) in R v2.15 (R development Core Team 2013). Prior to model selection, all variables in the global model were standardized to have mean of 0 and standard deviation of 0.5 following Gelman (2008) using the 'standardize' function in the 'arm' package (Gelman & Su 2013). As all predictors were standardized, final model-averaged coefficients are on a common scale and representative of effect size (see Gelman (2008) & Schielzeth (2010) for a discussion of the importance of standardizing regression predictors). We performed all-subsets selection of the global model using the 'MuMIn' package (Bartoń 2013) using AICc as our ranking criterion.

To assess the fit of the models employed, we report the marginal r^2 of the top model in each analysis following Nakagawa & Schielzeth (2012). This assesses the total variance explained by the fixed effects of a model while controlling for the random effects, but not allowing those random effects to contribute to the explained variance (unlike conditional r^2 , Nakagawa & Schielzeth 2012).

Results

Patterns of extra-group paternity

We detected 37 EG offspring in 25 of 180 clutches (13.8%), occurring in eight of 34 (23.5%) social groups (modal clutch size is 2, range 1–4, Harrison *et al.* 2013). Twenty-nine of the 37 (78.3%) EG offspring could be assigned a father from the pool of sampled males from across the study population at the 95% consensus threshold (see methods). The remaining eight EG offspring (from six clutches in five groups) could not be assigned a father at the 95% consensus threshold and also mismatched the within-group dominant male by two or more loci and so were presumed to be sired by unsampled males from outside the study population. Of the 40 dominant females from 34 groups that were successfully genotyped (some groups had experienced dominance turnover), 8 (20%) were found to engage in EG mating. Mixed-paternity clutches were rare: of the 38 clutches produced by the eight EG-mating females containing two or more eggs, only 5 (13%) contained progeny from >1 sire. In these five cases, offspring were always sired by the social mate and a single EG sire (there were no cases where multiple EG males shared paternity of a clutch). However, females did mate with

multiple EG sires across clutches in some cases (range 1–3 distinct EG sires, assuming conservatively that unassigned paternities count as only 1 additional EG sire). The mean distance (\pm SD) over which EGP occurred (for those cases where the EG sire could be assigned; $n = 19$ clutches) was 640 m (± 294 m) which corresponds to crossing approximately five territories (see methods); range: 280–1242 m.

What factors predict whether females mate extra-group?

The $\Delta 6$ AICc set contained 16 competing models (Table 1). The best-supported model contained an effect of both the resident-dominant male's multilocus heterozygosity (MLH) and his relatedness to the dominant female. The marginal r^2 of the top model was 0.33.

After applying the nesting rule, only two models were retained as follows: the best-supported model and a model containing only the effect of MLH (Δ AICc = 1.04, Table 1). MLH was the strongest predictor of the occurrence of extra-group mating, appearing in both retained models, whereby females are more likely to mate EG when their social mates are less heterozygous (Fig. 1). There was some support in the data for a positive effect of the female's relatedness to her social mate on her likelihood of mating EG. No models containing terms for group size, social mate tarsus and social mate body mass were retained, as they were all more complex versions of nested models containing fewer parameters with lower AICc values (Richards 2008).

What factors predict the identity of the extra-group sire?

There were 42 competing models within the $\Delta 6$ AICc candidate set (Table 2). The best-supported model contained the dominance status of the EG sire as the sole predictor of a male's likelihood of siring EG young, with dominant males being substantially more likely to secure paternity of a clutch via EG mating than subordinates (dominants were 7.6 times more likely to secure an EG paternity compared with subordinates, 95% CI 3.6–12.4 times). This is supported by the observation that the EG chicks in 16/19 (84%) of clutches were sired by an EG dominant, despite the fact that there were similar numbers of adult subordinate and dominant males in the population at the time of each clutch. Subordinates sired the remaining three chicks. The marginal r^2 of the top model was 0.24. However, as dominance status was present in all 42 models in the $\Delta 6$ set (Table 2), only the top model was retained after the application of nesting rule, as all other models were

Table 1 Competing models in the $\Delta 6$ AIC_C set detailing the factors associated with a female's propensity to mate with extra-group males

Int.	Mass	MLH	Rel.	Tarsus	Group Size	k	logLik	AICc	Δ AICc	Retained
-5.76		-5.41	2.83			4	-50.23	108.7	0	✓
-6.62		-6.39	3.11		-1.00	5	-49.45	109.2	0.57	
-3.95		-3.64				3	-51.79	109.7	1.04	✓
-4.28		-4.19			-0.83	4	-51.11	110.5	1.77	
-5.72		-5.30	2.86	-0.51		5	-50.16	110.7	1.99	
-5.65	-0.24	-5.28	2.76			5	-50.20	110.7	2.07	
-6.50		-6.18	3.09	-0.59	-1.00	6	-49.39	111.3	2.58	
-6.53	-0.22	-6.27	3.04		-1.00	6	-49.43	111.4	2.67	
-3.91	-0.33	-3.53				4	-51.71	111.7	2.98	
-3.95		-3.60		-0.36		4	-51.73	111.7	3.01	
-4.21	-0.36	-4.06			-0.84	5	-51.03	112.4	3.72	
-4.26		-4.13		-0.42	-0.84	5	-51.03	112.4	3.73	
-5.41	-0.64	-4.87	2.67	-0.93		6	-50.04	112.6	3.89	
-6.13	-0.61	-5.69	2.88	-0.97	-0.97	7	-49.29	113.2	4.55	
-3.82	-0.71	-3.32		-0.81		5	-51.48	113.3	4.63	
-4.09	-0.78	-3.79		-0.92	-0.86	6	-50.75	114	5.31	

Values in the first six columns are parameter estimates, calculated as effect size following Gelman (2008) and on the logit scale. 'Int': Intercept, 'Mass': Scaled Mass Index, 'MLH': multilocus heterozygosity; 'Rel.': Queller & Goodnight relatedness estimator. 'k': number of estimated parameters, including a random intercept for maternal ID; 'logLik': log-likelihood; 'delta': change in AICc value from the top model. Blank cells indicate that a term was absent from that model. Sample size for the analysis was 180 clutches.

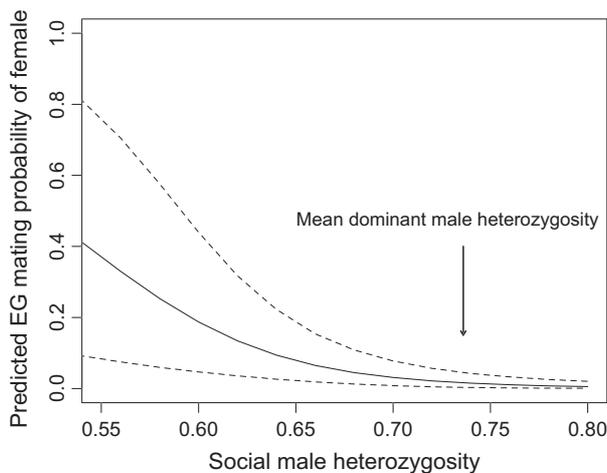


Fig. 1 Predicted probability that a female's clutch contains one or more young sired by an EG male as a function of the heterozygosity of her social mate. Solid line is the mean predicted probability. Dashed lines are 95% credible intervals. Parameter estimates for prediction are derived from a Bayesian parameterization of the top model from Table 1, and predictions were made at the average value for pairwise relatedness between social mates and females.

more complex versions of the top model for which there was nevertheless weaker support (see Richards 2008). Despite social mate heterozygosity being the principal predictor of the occurrence of EG mating (see above), there was no support for more heterozygous

males being more likely to secure EGP nor any support for an effect of male morphological traits or relatedness.

Does extra-group mating result in females pairing with higher quality mates?

Heterozygosity. Extra-group sires were significantly more heterozygous than the males that they cuckolded (Randomized paired *t*-test, $n = 19$, $P < 0.01$, Fig. 2a). Conversely, there was no difference in the mean heterozygosity between EG sires and the social mates of females for which there was no evidence of EG mating (randomized *t*-test, $n = 17$ EG sires/33 uncuckolded social mates, $P = 0.13$, Fig. 2a).

Relatedness. Females who mated EG were actually significantly *more* related to the EG sire than they were to their social mates (Randomized paired *t*-test, $n = 19$, $P = 0.048$, Fig. 2b). There was, however, no significant difference in relatedness to social mate between females that did and did not engage in EG mating (randomized *t*-test, $n = 17$ EG sires/33 uncuckolded social mates, $P = 0.26$; Fig. 2b).

Can random pairing explain the observed traits of the extra-group sires?

Dominance. We further explored the effect of dominance status on the probability of siring EG offspring by

Table 2 Competing models in the $\Delta 6$ AIC_C set examining the factors predicting the identity of the extra-group sire when extra-pair paternity was detected within nests

Int.	Status	Dist.	Dist. ²	Mass	MLH	Rel.	Tarsus	k	logLik	AICc	Δ AICc	Retained
-5.12	-2.25							4	-86.20	180.4	0	✓
-5.12	-2.32				-0.61			5	-85.68	181.4	0.98	
-5.17	-2.22					0.40		5	-85.85	181.8	1.33	
-5.12	-2.18						0.44	5	-85.94	181.9	1.51	
-5.14	-2.25	0.27						5	-86.07	182.2	1.76	
-5.11	-2.24			0.10				5	-86.18	182.4	1.98	
-5.13	-2.25				-0.64		0.48	6	-85.37	182.8	2.38	
-5.16	-2.28				-0.54	0.32		6	-85.46	183	2.57	
-5.14	-2.00			0.72			0.98	6	-85.48	183	2.61	
-5.15	-2.33	0.32			-0.65			6	-85.50	183.1	2.64	
-5.20	-2.21	0.37				0.46		6	-85.64	183.3	2.91	
-5.12	-2.30			0.10	-0.61			6	-85.66	183.4	2.97	
-5.17	-2.16					0.36	0.38	6	-85.67	183.4	2.98	
-4.94	-2.23	0.42	-0.95					6	-85.69	183.4	3.02	
-5.17	-2.19			0.15		0.42		6	-85.82	183.7	3.27	
-5.14	-2.17	0.27					0.44	6	-85.82	183.7	3.28	
-5.15	-2.06			0.75	-0.68		1.03	7	-84.86	183.8	3.37	
-4.92	-2.34	0.49	-1.06		-0.71			7	-85.02	184.1	3.71	
-5.14	-2.23	0.29		0.13				6	-86.04	184.1	3.72	
-5.16	-2.25	0.32			-0.69		0.48	7	-85.19	184.5	4.04	
-5.21	-2.29	0.40			-0.58	0.38		7	-85.20	184.5	4.07	
-5.19	-1.98			0.73		0.36	0.93	7	-85.21	184.5	4.09	
-5.17	-2.23				-0.59	0.27	0.43	7	-85.23	184.5	4.11	
-5.01	-2.20	0.50	-0.89			0.44		7	-85.30	184.7	4.25	
-5.17	-1.99	0.32		0.77			1.02	7	-85.30	184.7	4.27	
-4.94	-2.14	0.42	-0.95				0.44	7	-85.43	184.9	4.52	
-5.16	-2.26			0.14	-0.54	0.34		7	-85.43	185	4.53	
-5.20	-2.15	0.35				0.42	0.37	7	-85.47	185	4.6	
-5.15	-2.32	0.34		0.13	-0.65			7	-85.47	185	4.6	
-5.21	-2.19	0.39		0.20		0.48		7	-85.57	185.2	4.81	
-5.18	-2.06	0.39		0.81	-0.74		1.08	8	-84.59	185.3	4.87	
-4.94	-2.22	0.43	-0.94	0.12				7	-85.67	185.4	5	
-4.93	-2.24	0.50	-1.09		-0.76		0.51	8	-84.68	185.5	5.05	
-5.19	-2.03			0.75	-0.62	0.26	0.99	8	-84.72	185.5	5.12	
-4.99	-2.29	0.55	-1.00		-0.64	0.35		8	-84.78	185.7	5.24	
-4.96	-1.96	0.48	-0.93	0.77			1.02	8	-84.92	186	5.53	
-5.23	-1.97	0.41		0.78		0.42	0.96	8	-84.94	186	5.57	
-5.21	-2.23	0.38			-0.62	0.33	0.42	8	-84.98	186.1	5.65	
-4.92	-2.32	0.50	-1.05	0.11	-0.70			8	-85.00	186.1	5.7	
-4.95	-2.04	0.57	-1.08	0.82	-0.81		1.11	9	-84.08	186.3	5.88	
-5.01	-2.12	0.49	-0.90			0.40	0.38	8	-85.12	186.3	5.92	
-5.21	-2.26	0.42		0.19	-0.58	0.40		8	-85.14	186.4	5.97	

Values in the first 8 columns are parameter estimates, calculated as effect size following Gelman (2008) and on the logit scale. 'Int.': intercept; 'status': the effect of being a subordinate. 'Dist./Dist²': linear and quadratic terms for distance; 'Mass': Scaled Mass Index; 'MLH': multilocus heterozygosity; 'k': number of estimated parameters, including random intercept terms for clutch and male ID; 'logLik': log-likelihood; ' Δ AICc': change in AICc value from the top model. Blank cells indicate that a term was absent from that model. 'Retained': indicates the model(s) in the $\Delta 6$ AICc model set that are retained using the 'nesting rule' Richards (2008) whereby models are removed if they are more complex models of nested (simpler) models higher up in the table. As the effect of status is present in all models in the $\Delta 6$ set, and the top model contains only that term, all other models are considered more complex versions of the top model and removed.

randomly drawing a sire for each clutch that contained EG young from the pool of all available EG males (both dominant and subordinate) at the time of paternity to

derive a null distribution of the proportion of paternity attained by dominants. We observed a significantly higher proportion of extra-group offspring sired by

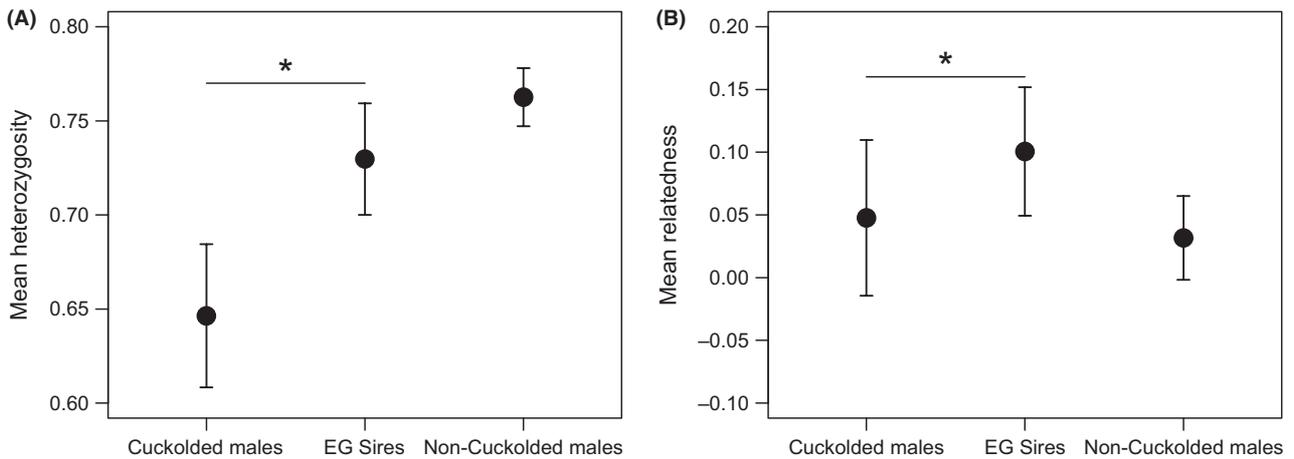


Fig. 2 Plots showing: (a) differences in mean heterozygosity and (b) differences in mean relatedness among three groups of male. 'Cuckolded Males': social mates that lost paternity to EG males; 'EG Sires': the males that gained extra-group paternity and 'Noncuckolded Males': social mates for which there was no evidence of being cuckolded. EG sires were significantly more heterozygous than the social mate they cuckolded, but were also significantly more closely related to the female than the social mate. '*' indicates a significant difference at the $P < 0.05$ level. Bars are \pm SE. P -values were derived from *pairwise tests* on the genetic trait values of social mates and the EG sires that cuckolded them (see Results), rather than on the group means presented above. Paired plots of these data are present in Fig. S1 (Supporting information). There was no significant difference between the group means of EG sires and noncuckolded males for either heterozygosity or relatedness to the female (these tests were conducted as group means because there is no inherent paired structure to the data for these two classes of male).

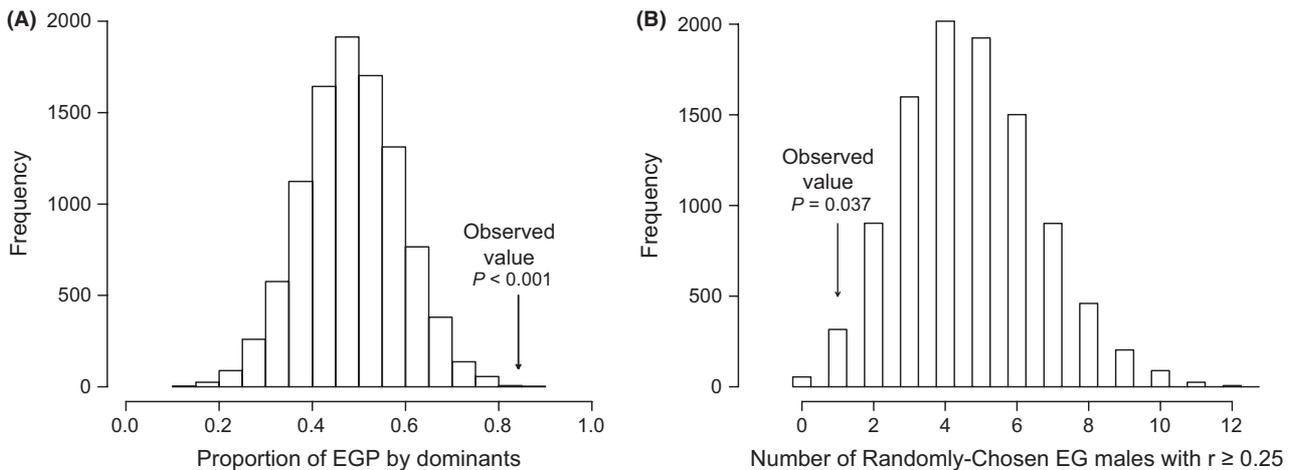


Fig. 3 Randomization histograms of (a) the null expectation of proportion of extra-group paternity by dominants; (b) the null expectation of the frequency of social mates being related to the dominant female at the level of $r \geq 0.25$, if females were to randomly pair with adult EG males from the local population. We observed that (a) dominant males secured 84% of EG paternities in a sample of 19 clutches sired by EG males, which was significantly higher than expected by chance ($P < 0.001$); and (b) in a sample of 35 dominant breeding pairs, only 1 male–female dyad had a pairwise relatedness value greater than 0.25, which was significantly lower than expected by chance (1-tailed $P = 0.036$).

dominants than expected by chance (observed value = 0.842, null distribution mean = 0.482, $P < 0.001$; Fig. 3a).

Heterozygosity. Given that heterozygosity of her social mate was a strong predictor of a female's propensity to mate EG (Table 1; Fig. 1), but received no support as a factor predicting identity of the EG sire (Table 2), we

performed randomization tests to further explore whether male heterozygosity influences his probability of becoming an EG sire. Our randomizations reveal that the mean heterozygosity of EG sires was consistent with the null expectation of sires being randomly selected from the pool of available males, while controlling for the fact that dominant males sire 84% of EG young (observed mean MLH of sires = 0.712, null distribution

mean = 0.736, $n = 19$, $P = 0.33$). This result was robust to the use of a simpler null model whereby we used only the 16 clutches sired by dominants and randomly assigned sires from only the pool of available dominant males (observed mean MLH of sires = 0.705, null distribution mean = 0.74, $n = 16$, $P = 0.17$).

Relatedness. The mean relatedness of observed EG sires to the female who mated EG was consistent with random pairing with mates from the pool of available EG males, while controlling for the fact that dominant males sire 84% of EG young (observed mean relatedness to EG sires = 0.087, null distribution mean = 0.046, $n = 19$, $P = 0.33$). This result was also robust to the use of a simpler null model whereby we used only the 16 clutches sired by dominants and randomly assigned sires from only the pool of available dominant males (observed mean relatedness to EG sires = 0.056, null distribution mean = 0.051, $n = 16$, $P = 0.91$). In support of our finding that EG-mating females are actually more distantly related to their social mates than their EG mates (Fig. 2b), we found that dominant females were also significantly more distantly related to their social mates than they were to males drawn at random from the population. In a sample of 35 dominant breeding pairs, only 1 of the pairs had a relatedness value of ≥ 0.25 . This observed frequency was significantly lower than the null expectation of females randomly choosing social mates from the pool of available EG males at the beginning of their dominance tenures (1-tailed $P = 0.037$ Fig. 3b).

Are extra-group offspring more heterozygous than intragroup offspring?

There was no difference in the mean heterozygosity of the offspring arising from intra- and extra-group matings, using paired within-female comparisons (randomized paired t -test, $n = 7$ females who produced both WG and EG young, $P = 0.33$, 1 female was excluded because she mated exclusively EG). Nor was there a difference in the mean heterozygosities of offspring simulated from the parental genotypes of the dominant female and her social mate and the dominant female and her assigned EG sire (randomized paired t -test, $n = 17$ unique pairs, $P = 0.51$).

Discussion

Our results suggest the principal factor that predicts a female's propensity to engage in extra-group mating is being paired with a social mate of low heterozygosity. EG mating afforded females access to mates of significantly higher heterozygosity than their own social mates, but also exposed them to mates that were of

higher pairwise relatedness. The consequence of such a pattern was that offspring resulting from EG matings were no more heterozygous than their half-siblings from the within-group dominant male. Below, we first discuss our findings in the context of the 'female benefits' hypotheses for the evolution of EG mating and then highlight their consistency with a key role instead for male-male competition in driving the patterns of EG mating in this species (which would not require benefits to females). Finally, we consider the complications that may be associated with EG mating at a restricted spatial scale in cooperative breeding vertebrates, where a high degree of local population kin structure could actually expose EG-mating individuals to a risk of inbreeding.

We found that dominant males of low heterozygosity were far more likely to be cuckolded, and that those females that secured EGP did so with males that were significantly more heterozygous than their social mates. By contrast, females for which there was no evidence of EG mating had social mates with heterozygosities comparable with those of the EG sires, suggesting that EG mating for mate heterozygosity benefits would not have been advantageous for these females. These findings add to a now growing body of evidence consistent with a female preference for mating with more heterozygous males even in the absence of scope for direct benefits (e.g. Hoffman *et al.* 2007; Gohli *et al.* 2013; see also Kempnaers 2007). We consider three potentially general mechanisms that could explain why males that gain EGP are significantly more heterozygous than the social mates that they cuckold. First, one controversial hypothesis posits that females stand to gain 'indirect' genetic benefits from selecting sires based purely on their heterozygosity (Tregenza & Wedell 2000; Kempnaers 2007; Aparicio 2011). Highly heterozygous males are more likely to carry rare alleles and so have been suggested to increase the likelihood that the offspring that their sire will also be heterozygous (e.g. Mitton *et al.* 1993; Hoffman *et al.* 2007; but see Lehmann *et al.* 2007). Sire-offspring heterozygosity can indeed be correlated under certain circumstances in our study population (Fig. S2, Supporting information), but large between-sire differences in heterozygosity (over 25%) translate into only modest differences in offspring heterozygosity (approximately 4%). Even to achieve this small increase in offspring heterozygosity, females would have to consistently mate with males with a mean heterozygosity >1 standard deviation above the population mean, whereas our data suggest that EG sires have a mean heterozygosity roughly equal to the population mean (Fig. 2a). These data, coupled with our observation that the offspring of EG sires were no more heterozygous than their half-sibs sired by the within-group dominant

male (using both real and simulated offspring genotypes), strongly suggest that EG mating in white-browed sparrow weaver societies does not currently function to increase offspring heterozygosity.

Second, females may choose males based on performance-related traits that have heritable variation because of 'good genes' effects (Neff & Pitcher 2005), but that are also impacted by nonheritable variation in male heterozygosity (for associations between heterozygosity and traits that may reflect male quality see: Aparicio *et al.* 2001; Foerster *et al.* 2003; Seddon *et al.* 2004; Reid *et al.* 2005; but see Chapman *et al.* 2009). As the preferred males may thereby tend to be more heterozygous, one might then detect an apparent pattern of female preference for male heterozygosity that is merely a by-product of a heritable good gene effect. A potential mechanism by which female white-browed sparrow weavers may assess male quality is through song (Seddon *et al.* 2004; Reid *et al.* 2005), as dominant male white-browed sparrow weavers sing a complex dawn solo song (Voigt *et al.* 2007), and while subordinate males do often sing a solo song they are invariably out-sung by their dominants (York 2012).

Third, while studies seeking adaptive explanations for EG mating typically focus on the nature of the benefits that females might accrue from doing so, our findings are also consistent with a key role for male-male competition in driving EG mating in this species. If more heterozygous male white-browed sparrow weavers are more competitive, they may simply dominate less heterozygous males in competition for females. This explanation does not require a mechanism of female 'choice' of EG sire nor does it require that females gain a net benefit from EG mating. The differential success of more heterozygous males could arise because they are more likely to secure access to matings with fertile females and/or because they may dominate post-copulatory sperm competition for fertilizations (Kempnaers & Dhondt 1993). Such male-driven patterns could arise even if EG mating entailed a cost for females, if, for example, EG mating averted potentially higher costs for females arising from prolonged harassment by males (Westneat & Stewart 2003). Alternatively Forstmeier *et al.* (2011) showed that promiscuity can evolve in females as the product of a genetic constraint, where selection on males for multiple mating leads to a genetically correlated increase in frequency of multiple mating in females. Observations of copulations are rare (Harrison *et al.* 2013), and so we cannot currently distinguish between the alternative hypotheses that females actively solicit mating from EG males, or that copulations are forced via harassment. Whichever of these two mechanisms is in operation, our data are consistent with the hypothesis that observed patterns of EG

mating in white-browed sparrow weavers are the product of male competition.

We found that females who mated EG were on average significantly *more* related to the EG sire than to their own social mate. This result is in contrast to studies on other cooperatively breeding species that have found support for the genetic compatibility hypothesis, whereby females have been found to be less related to their extra-pair sires than their social mates (Tarvin *et al.* 2005; Cohan *et al.* 2008; see also Kempnaers 2007). Using simulations, we showed that heterozygosity was only weakly heritable under conditions where female relatedness to the EG sire was constrained to be <0.2 . That offspring resulting from EG matings were no more heterozygous than their half-siblings from the within-group dominant male could have arisen as a result of the fact that some females mated with males with a pairwise relatedness above this value, being more likely to share alleles with these males and therefore pass on identical copies to offspring. Our randomizations suggest that such elevated relatedness between females and their EG sires could arise simply from random EG mating by females, because (i) the observed levels of relatedness between females and their EG sires were consistent with EG-mating females choosing EG sires at random, and (ii) dominant females and their social mates were significantly less related to each other than would be expected on the basis of random pairing across the population. As such, these results suggest that white-browed sparrow weavers are effective at avoiding close relatives as social mates, but that EG-mating females are not as effective at avoiding relatives among EG sires that may require more complicated mechanisms (Koenig & Haydock 2004; though evidence suggestive of such an ability *has* been reported elsewhere; Foerster *et al.* 2003; Brouwer *et al.* 2011). Moreover, there is some evidence from other species that females are able to avoid inbreeding by employing postcopulatory mechanisms to bias paternity away from relatives (e.g. Bretman *et al.* 2009; Brekke *et al.* 2012) or achieve optimal dissimilarity between genotypes (Tyler *et al.* 2013).

That EG mating exposes females to an increased risk of inbreeding suggests that, as with many cooperatively breeding species, there is significant local kin structure in our study population (Koenig & Haydock 2004; Double *et al.* 2005; Berg *et al.* 2009; Nelson-Flower *et al.* 2012). Both male and female white-browed sparrow weavers have been shown to disperse <300 m from their natal territory (Lewis 1982), and so, EG mating over the distances described in this study could certainly expose females to a risk of mating with relatives because of their restricted dispersal (Harrison & Young, unpublished data) and the spatial structuring of kin that results (Stopher *et al.* 2012). In addition, our results

add to a growing number of studies demonstrating that individuals do not simply avoid relatives as extra-pair mates (Kleven *et al.* 2005; Wang & Lu 2011 see also Szulkin *et al.* 2012), suggesting inbreeding avoidance and extra-pair mating strategy are not uniform among populations and species (Szulkin *et al.* 2012).

Conclusion

While patterns of EG mating in white-browed sparrow weavers could be driven by 'female benefits', it is unlikely that these benefits arise through increased offspring heterozygosity. EG-mating behaviour in the population could be driven by 'good genes' benefits to females who seek to mate with more attractive sires, but the maintenance of EG mating by females will depend on the relative frequency of females who manage to secure males who both carry 'good genes' and to whom they are genetically dissimilar. Our findings are also compatible with the hypothesis that EG mating could be of no net benefit to females, but arise purely as a result of competition among males to secure EG matings. Future work will test the prediction of the 'good genes' hypothesis that offspring from EG matings should be fitter than their within-group half-siblings. Finally, cryptic local kin structure has also been described in a variety of noncooperative species (e.g. Harrison *et al.* 2010; Bretman *et al.* 2011) and may be more widespread than previously thought (reviewed in Hatchwell 2010). As such, the patterns that we describe here, where even EG mating with males from the local pool of available mates can expose females to a risk of breeding with relatives (e.g. Bretman *et al.* 2011), may have implications for a wide number of species, irrespective of their level of sociality.

Acknowledgements

We are grateful to our many field assistants during this period for their tireless efforts under the Kalahari sun, to Northern Cape Conservation for permission to conduct the research, to E.O. & Son and all at Tswalu Kalahari Reserve for their exceptional support in the field, to Nigel Bennett for logistical support, to Shane Richards for statistical advice, and Tom Tregenza, Jinliang Wang and Andrew Russell for useful discussion on the manuscript. Finally, we thank two anonymous reviewers for constructive comments that improved an earlier version of this manuscript. This study was funded by BBSRC David Phillips and NERC Blue Skies research fellowships to AY.

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Data accessibility

Genotyping data and R scripts for (i) simulation of offspring heterozygosity and (ii) analysis of paired data by randomization test are uploaded on the Dryad data repository, doi:10.5061/dryad.v8q6c.

Supporting information

Additional supporting information may be found in the online version of this article.

Fig. S1 Pairwise plots of (A) Heterozygosity and (B) Pairwise relatedness to the breeding female of ‘Cuckolded Male’: the social mate that lost paternity to an EG male, and the ‘Extra-Group Sire’: the male from outside the social group that cuckolded the resident dominant male. Extra-Group sires were

significantly more heterozygous than the social mates they cuckolded, but were also significantly more related to the breeding female than she was to her social mate.

Fig. S2 Graph showing the mean differences in offspring heterozygosity for offspring produced by dominant females when mated to males of varying heterozygosity.

Table S1 Marker data for 13 microsatellite loci employed in the study.

Table S2 Quantification of assignment bias towards more heterozygous males following Wang (2010).