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ORIGINAL ARTICLE

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Kin associations and direct vs indirect fitness benefits in colonial cooperatively breeding sociable weavers *Philetairus socius*

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Abstract Indirect fitness benefits are believed to be an important force behind the evolution of cooperative breeding. However, helpers may associate with their relatives as a result of delayed dispersal, hence, kin associations might be a consequence of demographic viscosity rather than active choice. In addition, recent studies showed that helpers may have access to reproduction therefore direct benefits might also play an important role. Here, we investigate the possible roles of direct genetic benefits and kin associations on helping behavior in the sociable weaver *Philetairus socius*, a colonial and cooperatively breeding passerine. We used a microsatellite-based genotyping method to describe the genetic structure within nests and colonies. Within a colony, we found considerable genetic structure between males but not females. Sociable weaver colonies have several nests that are simultaneously active, giving individuals a choice of associating with a range of first-order kin to unrelated individuals. Helpers were significantly more related to the young in the helped nests than in other nests of the colony, suggesting an active choice for associating with kin. The helpers were generally offspring or first-order relatives of one (50%) or both (43%) breeders, although more infrequently, seemingly unrelated individuals also helped (7%). We found no supporting evidence of extrapair parentage and hence no direct genetic gains from helping in our population. This strong reproductive skew is contrary to theoretical models predicting conflicts over reproduction in stepfamilies. We discuss whether female decisions and/or other direct benefits of remaining in kin associations or helping might explain the high skew observed.

Keywords Extrapair paternity · Genetic structure · Helping behavior · Kin selection · Parentage · Reproductive skew

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Introduction

Understanding the adaptive basis of helping behavior requires a thorough account of the possible costs and benefits resulting from helping, which entails an investigation of the underlying genetic structure of groups. Individuals may gain genetic fitness in two ways: through their own reproduction (direct fitness) or through the reproduction of close relatives (indirect fitness; Hamilton 1964). In cooperatively breeding systems where sexually mature individuals forgo independent reproduction and instead help others to breed, indirect fitness benefits gained by the helpers have long been evoked as a basis for this type of behavior (Hamilton 1964). Indirect fitness benefits are appealing as an explanation because cooperative breeders often live in family groups where the receivers of help are close kin (Emlen 1997). This explanation was supported by some convincing studies (Russell and Hatchwell 2001; Baglione et al. 2003; Griffin and West 2003).

However, the simple observation that helping behavior is common among kin groups does not constitute enough evidence in favor of a role of indirect fitness in explaining this behavior (see also review in Griffin and West 2002). First, the demographic characteristics of the typical cooperative breeder result in limited dispersal and the formation of kin groups, in which case helping kin could be argued to be a result of demographic viscosity and not an active choice. This idea is supported by work on different vertebrate species showing that the amount of help given does not correlate with relatedness (Magrath and Whittingham 1997; Clutton-Brock et al. 2001; Canestrari et al. 2005; Doutrelant, Dalecky, and Covas, unpublished data; but see Dickinson 2004 for a counterargument). Second, in several species, helpers may have access to direct reproduction (reviewed in Cockburn 1998, 2004) even when helping relatives (Richardson et al. 2002, 2003; Webster et al. 2004), which suggests that direct genetic benefits might still be important when indirect benefits occur. Individuals in some species may also gain future genetic fitness benefits if by helping they acquire important skills (Komdeur 1996) or increase their chances of gaining access to mates (reviewed in Cockburn 2004). In any case, the possibility of promiscuity within groups complicates our understanding of cooperative breeding because evaluation of indirect fitness benefits based on assumed levels of relatedness could be erroneous unless the possibility of extrapair paternity or egg-dumping were ruled out by genetic tests (Richardson et al. 2001).

An understanding of the genetic benefits resulting from helping behavior therefore requires an investigation of whether helpers gain direct benefits [i.e., shared parentage, extrapair fertilizations (EPFs), or egg-dumping], indirect genetic benefits (i.e., increased production of nondescendant kin), or both. In addition, understanding the relative importance of the indirect component of kin selection in a species requires distinguishing between passive and active association with kin. Here, we investigate these issues in a cooperatively breeding passerine, the sociable weaver *Philetairus socius*. Establishing whether helpers have direct access to reproduction or are related to the breeders was made possible with the introduction of reliable molecular techniques (Queller et al. 1993). However, determining whether the association between kin is active or passive is usually a more difficult task due to the typical group structure and demography of cooperative species where young normally delay dispersal and remain in the family group (see Stacey and Koenig 1990 and several examples therein).

Unlike most cooperative breeders, sociable weavers are colonial with colonies ranging from less than ten to more than 200 individuals (Maclean 1973b). Sociable weavers can breed in pairs or in groups with one to five helpers. Both sexes help but helpers older than 1 year were always males (Doutrelant et al. 2004). The number of breeding pairs varies within and between seasons, but a calc. 40–80% of the birds in a colony may breed simultaneously (Covas 2002; Covas et al. 2004). Hence, within a colony, sociable weavers have a choice of different nests at which they can help, comprising variable degrees of relatedness that likely range from first-order kin, such as their own parents or siblings, to unrelated individuals.

In this study, we combined field observations with a microsatellite-based genotyping method to determine the genetic structure underlying sociable weaver's social structure both at the colony and breeding group level. Specifically, we investigate: (1) the relatedness between individuals within a colony vs between colonies; (2) the relatedness between individuals attending the same nests; (3) the relatedness between helpers and nestlings in the same nest vs nestlings in the other nests within the same colony; and (4) whether helpers have direct access to reproduction.

Materials and methods

Study area and species

This study was conducted at Benfontein Game Farm about 6 km southeast of Kimberley in the Northern Cape Province, South Africa (approx. 28°53′S, 24°89′E). The study area covers approximately 15 km^2 of open savanna and contains a calc. 30 sociable weaver colonies.

Sociable weavers are 26–32 g passerines endemic to the semiarid savannas of Namibia and of South Africa's Northern Cape Province (Maclean 1973a; Mendelsohn and Anderson 1997). Sociable weavers build communally a large thatched structure (the colony), which is made mainly of *Stipagrostis* grasses and is most commonly built on acacia trees (Maclean 1973b; Mendelsohn and Anderson 1997). Colonies contain several independent nest chambers where breeding and roosting take place. In our study area, colony size ranged calc. 10–200 birds. Sociable weavers breed during the austral summer with breeding activity being closely linked to rainfall patterns. Clutch size varies between 2–4 eggs and successive clutches may be produced for up to 9 months as long as conditions are favorable (Covas 2002).

Field methods

The study was conducted from September 1999 to January 2001. During this period, 19 colonies were monitored for breeding activity and adults and nestlings at these colonies were marked with a uniquely numbered aluminum ring and a unique color combination. A significant proportion of adults in the population was already ringed as a result of a capture-recapture study initiated in 1993. The birds were normally captured with mist nets twice a year, at the beginning and end of the breeding season, to track juvenile dispersal and to mark immigrants.

To identify the individuals feeding at a given nest, we conducted a minimum of 3 h of observations per nesting attempt from a hide placed 2–5 m from the colony. If any of the individuals attending these nests were not previously ringed, we caught them individually at the nest using a hand net placed around the nest entrance before dawn.

We collected blood from 127 birds (including 61 nestlings) at 21 nests from ten colonies ranging in size calc. 12–40 birds. In six colonies, we sampled multiple nests (ranging 15–70% of the nests active in a given colony), allowing relatedness calculations among individuals from different nests within a colony. Blood samples were collected from the brachial vein using a sterile needle and a heparinized capillary tube. Blood was stored in ethanol or in buffer from a DNA extraction kit (DNAzol; Chomczynski et al. 1997). We excluded from analyses presented here the colonies or nests that were manipulated as part of experiments undertaken during the study period (Covas et al. 2004; Covas and du Plessis 2005).

Molecular methods

Genotypes were identified for each individual using four microsatellite markers, two isolated for house sparrows *Passer domesticus* (*PDO3* and *PDO5*; Griffith et al. 1999), and two for white-browed sparrow-weavers *Plocepasser mahali* (*WBS8* and *WBS9*; McRae and Amos 1999). In addition, we tested two other sparrow-weaver primers (*WBSW4* and *WBSW7*) but these were not sufficiently polymorphic in our population (two and three alleles, respectively).

Amplifications were performed in a volume of 10 µl containing 1 µl of extraction product, 0.48 µl (*PDO3* and *WBS9*) or 0.6 µl (*PDO5* and *WSB8*) of 25 mM $MgCl_2$, 1 µl of 10× buffer (10 mM Tris–HCl, 50 mM KCl, and 0.1% Triton X-100), 0.4 U of *Taq* polymerase (Promega), 0.4 µM of each primer, 1 µCi of $[\alpha^{33}P]$-dATP (ICN), 75 µM of dBTP, and 6 µM of dATP. Amplifications were carried out in a PTC 100 thermocycler (MJ Research) using a “touch down” procedure (Don et al. 1991). After an initial denaturing step of 94°C for 3 min, 10 cycles were performed each consisting of 92°C for 20 s, 30 s of annealing starting at 60°C and dropping by 1°C per cycle, and an extension step of 72°C for 30 s. We also included a further 20 cycles consisting of 92°C for 30 s, 30 s of annealing at 50°C and 72°C for 30 s, and a 10-min extension step at 72°C after the last annealing step. Amplification products were ran for 3 to 6 h on 6% polyacrylamid denaturating gels and were visualized by autoradiography.

Sociable weavers are sexually monomorphic and sex determination was done by molecular techniques (Doutrelant et al. 2004) through amplification of chromo-helicase-DNA-binding genes located on the W and Z sex chromosomes using the P2 and P8 universal primers of Griffiths et al. (1998).

Parentage analysis

Parentage was determined by analyzing the genotypic data with a likelihood-based approach using the CERVUS software version 2.0 (Marshall et al. 1998; see Jones and Ardren 2003 for review). For each nestling, parentage is assigned to an adult individual if the logarithm of the likelihood (LOD) ratio is large relative to the LOD ratios of alternative adults. Simulation of parentage inference with CERVUS—assuming that candidate parents other than the true parents are unrelated to the mother-father-offspring trio—was used to estimate the required critical difference in LOD scores between the first and second most likely candidate parents at the levels of 95 and 80% confidence.

In species with helper-at-the-nest that are offspring from previous years, full and half siblings of the nestlings have on average higher LOD scores than true parents (Marshall et al. 1998). Consequently, the ability to assign parentage unambiguously is reduced. To minimize this problem, we adapted the framework proposed in the cooperatively breeding Seychelles warbler *Acrocephalus sechellensis* by Richardson et al. (2001). Parentage was assigned in a series of steps, as follows.

First, we attempted to assign paternity to an adult male within a given nest. Then, when a male was assigned, we attempted to assign maternity to an adult female within this nest. The number of candidate parents was set at four for males and three for females—the maximum number of same-sex adults within a nest in our sample. The proportion of candidate parents sampled was set at 75% to simulate the chance that an unknown or nonnest individual might be the parent. Simulation parameters were as follows: 99.2% of loci typed, 1% rate of typing error, and 10,000 simulated offspring. In this paper, the “dominant” male and female were defined as the pair-bonded male and female in a given nest. The term “helper” included adult birds, which attended a given nest when we knew that they were offspring of the dominant pair from a previous brood or all nonbreeding adults attending a nest after the genetic results became available (see below). In an attempt to avoid the incorrect parentage assignment of a sibling, cases where more than one adult male had LOD scores above zero were examined. Following Richardson et al. (2001), a summed LOD score was obtained in such cases for each combination of a candidate male plus the female subsequently assigned in conjunction with this male and the summed LOD scores were compared. The pair yielding the highest combined LOD score was assigned.

Relatedness estimation

Regression relatedness (b) was estimated both within and between classes of individuals following the method of

Queller and Goodnight (1989) with the program relatedness 5.0 (Goodnight 2000), i.e., as the probability of allele sharing among individuals beyond the baseline probability set by the frequency of the allele in the population. Nests were weighed equally for allele frequency and relatedness calculations. Mean relatedness (±SE) was estimated by jack-knifing over nests or loci. Jack-knifing results in a normal distribution for the error around the mean. Significance for either positive or negative relatedness estimates were thus tested with one-tailed *t* tests (p. 230 in Sokal and Rohlf 1981) and the differences between two relatedness estimates were tested with two-tailed *t* tests (p. 411 in Sokal and Rohlf 1981) with number of nests-1 or number of loci-1 degrees of freedom. Genotypes of individuals present within a nest were further analyzed in terms of disjunctions assuming Mendelian inheritance. This information was combined with field observations—pedigree relationships inferred from clutches monitored in previous years—to determine whether genotypes were best explained by individuals being first-order relatives (no mismatch between the genotypes of the two individuals considered) or more distantly related to the breeding pair (two or more mismatches).

Results

The proportion of birds breeding in pairs or groups varied between and within years. In the first year, only 30% of the breeding pairs had helpers at the beginning of the season, but this percentage increased to 46% at the end of the breeding season as some pairs successfully raised young, which became helpers at the subsequent broods of their parents (*n*=43 groups; the juvenile helpers were not considered in the analyses presented below). In the second year, 82% of the breeding pairs were assisted by adult helpers only (*n*=51). The group size varied between 2–7 birds. Normally, helpers remained with the same pair during the entire breeding season. However, in one case, one individual was breeding and helping simultaneously and in another case, one individual was helping simultaneously at two different nests.

Most helpers were males (24 of 32 helpers sexed; see also Doutrelant et al. 2004). Helpers' age varied from 1 to more than 5 years old in both years, although helpers were markedly younger in the second year, presumably as a result of the exceptionally good breeding conditions in 1999 (Covas 2002; Covas et al., unpublished data).

The four loci were highly polymorphic in our sociable weaver sample (Table 1). Using one randomly sampled nestling per clutch, we did not detect any evidence for genotypic linkage (all $P \geq 0.08$) or Hardy–Weinberg (all $P \geq 0.12$) disequilibria with the program genepop version 3.3 (Raymond and Rousset 1995). The loci were thus suitable for parentage and relatedness analyses.

Table 1 Genetic variation at the four microsatellite loci over 127 individuals in a *Philetairus socius* population

Locus	na	H_O	H_E	Excl(1)	Excl(2)
PDO3	10	0.887	0.859	0.551	0.713
PDO5	12	0.865	0.856	0.545	0.708
WBS8	10	0.858	0.850	0.529	0.695
WBS9	10	0.882	0.860	0.554	0.715

na Number of observed alleles, H_O observed proportion of heterozygous individuals, H_E Nei's gene diversity, Excl(1) exclusion probability of the locus for the first parent, and Excl(2) exclusion probability of the locus for the second parent (with first parent assigned)

Parentage

The overall probability of excluding a randomly chosen individual from parentage as calculated in CERVUS version 2.0 was 0.957 for the first parent and 0.993 for the second parent. The critical difference in LOD scores (and success rate) for assignment of parentage at 80 and 95% confidence, respectively, were (1) paternity to a nest male-maternity not known: 0.00 (88%) and 1.31 (55%) and (2) maternity to a nest female-paternity assigned: 0.00 (81%) and 0.70 (77%).

Paternity

For male parentage analyses, we used 56 nestlings from 20 clutches (four additional nestlings from one clutch were not included as the breeding male in this nest was not captured). We assigned 100% of these nestlings to a male present in their nest, 28 at 95% confidence and 56 at 80% confidence. Globally, we did not obtained any convincing case of paternity sharing among feeding males and or extrapair paternity. The detailed results are as follows.

In two nests (six nestlings), a single adult male was feeding and was assigned paternity on the basis of having a positive LOD score. In 18 nests (50 nestlings), more than one adult male was feeding. In 11/50 cases, all but one male were excluded on the basis of having a negative LOD score. Among the 39 remaining nestlings, the male with the highest LOD score could be assigned at 95% confidence in 15 cases and at 80% confidence in 39 cases. Based on the highest LOD scores, 30 of these nestlings were assigned to the male that is thought to be the primary male based on pedigree data and the other nine (from seven clutches) to a male that is thought to be the helper based on pedigree data.

To avoid the incorrect parentage assignment of a sibling, we examined the summed LOD score of each candidate male with positive LOD score plus the female subsequently assigned in conjunction with this male. This summed LOD scores were compared in the 26 cases where the breeding female was captured, including seven nestlings initially assigned to a male helper and 19 to the dominant male. Among these seven cases, the dominant male was finally assigned as the father for all but one nestling. This case of paternity assignment to a helper is highly questionable as

(1) differences in LOD scores were small (helper vs primary male LOD=1.99 vs 1.60; combined male + female LOD=3.68 vs 3.59) and (2) the nestling showed a mismatch with the male helper–mother pair but none with the dominant male–mother pair. Of the 19 other nestlings, the initially assigned dominant male was confirmed for all but one nestling, though again this case of paternity assignment to a helper is questionable as (1) differences in LOD scores were small (helper vs primary male LOD=1.30 vs 1.31; combined male + female LOD=3.43 vs 3.37) and (2) the nestling showed a mismatch with the male helper but none with the dominant male.

For 13 of these 39 nestlings—two initially assigned to a male helper and 11 to the dominant male—the breeding female was not captured so maternity was not determined. Among the 11 nestlings initially assigned to the dominant male, six were assigned to the dominant male at 95% confidence and 11 at 80% confidence. For the two nestlings—each from a different clutch—initially assigned to a male helper, the difference between the candidate male LOD scores was small (helper vs primary male LOD=1.45 vs 1.01 and 1.51 vs 1.16. However, it should be noted that we expect siblings of the offspring to have higher LOD than the true father when the mother genotype is unknown (Marshall et al. 1998). Pairwise relatedness estimates *b* are compatible with these helpers being half siblings of the nestlings (helper-nestling *b*=0.53 and 0.49 and helper-primary male *b*=0.07 and −0.13). So we cannot exclude paternity by the primary males for these two nestlings. Close examination of multilocus genotypes confirmed this conclusion: (1) there was no mistmatch between nestlings and primary males at the four loci and (2) though there was no mismatch between nestlings and helpers, one of the helpers was genotyped at only three loci.

Maternity

Female parentage analyses are based on 41 nestlings from 15 clutches (19 additional nestlings from six clutches were not included as the breeding females in these nests were not captured). We assigned 100% of the nestlings to a female present in their nest, 38 nestlings with 95% confidence and 41 with 80% confidence. Globally, we did not detect any convincing case of shared maternity or egg dumping. In detail, we obtained the following.

In ten nests (28 nestlings) a single adult female was feeding and was assigned maternity on the basis of having a positive LOD score. In five nests (13 nestlings), there was more than one adult female feeding. For six of these 13 nestlings, all but one female were excluded on the basis of having a negative LOD score. Among the seven remaining nestlings, the female with the higher LOD score could be assigned at 95% confidence in five cases and at 80% confidence in seven cases. Based on the highest LOD scores, all but one nestling were assigned to the female, which is believed to be the primary female. In this one case where a female helper—a young from the previous brood—was assigned as the mother of the nestling, the primary female could not be excluded and the difference between the candidate female LOD scores were small (helper vs primary female LOD=4.35 vs 3.89).

Hence, with our data we found no supporting evidence of extrapair parentage (EPP). In our population, helpers are therefore unlikely to have direct access to reproduction. This is also suggested by the fact that relatedness estimates between nestlings within a nest, *b*=0.478, was not significantly different from the value expected between full sibs (0.50, t_{19}=0.69, two-tailed *P*=0.50). Relatedness estimates of the breeding female and male to the nestlings within their nest, *b*=0.474 and 0.510, respectively (Table 2), were not significantly different from 0.50, the value expected between parent and offspring (t_{15}=1.03, two-tailed *P*=0.32 and t_{19}=−0.31, two-tailed *P*=0.76).

Relatedness

Within a nest, the breeding male and female were not significantly related to each other (*b*=0.064, t_{15}=1.2, one-tailed *P*=0.12; Table 2), which suggests that inbreeding is rare, if occurring at all. Helpers were on average positively related to each other (*b*=0.293, t_{10}=3.2, one-tailed *P*=0.005). In general, there was significant kinship between helpers and one or both breeders (Table 2). Helpers were significantly more related to the young they were tending (*b*=0.228, t_{20}=5.7, one-tailed *P*<0.001; Table 2) than to other nestlings in the colony (*b*=0.020, t_{17}=4.2, two-tailed *P*<0.001; Fig. 1), suggesting an active association with kin.

Male and female helpers were equally related to the nestlings they were tending (*b*=0.228 and *b*=0.235, respectively; t_{21}=0.12, two-tailed *P*=0.91) and we also found no evidence of helpers being more often related to

Table 2 Relatedness among individuals within nests

Relatedness within nests	*b*±SE	95% CI	Number of nests
Breeding pair	0.064±0.050	−0.044 to 0.171	16
Breeding female–nestlings	0.474±0.025	0.421 to 0.526	16
Breeding male–nestlings	0.510±0.031	0.445 to 0.575	20
Adult helpers	0.293±0.089	0.094 to 0.492	11
Nestlings	0.478±0.031	0.412 to 0.543	20
Adult helpers–nestlings	0.228±0.039	0.146 to 0.310	21
Female helpers–nestlings	0.235±0.038	0.142 to 0.328	7
Male helpers–nestlings	0.228±0.047	0.130 to 0.326	19
Father–adult helper	0.273±0.059	0.149 to 0.396	20
Mother–adult helper	0.323±0.081	0.151 to 0.495	16

The standard errors of the relatedness estimates were obtained by jack-knifing over nests

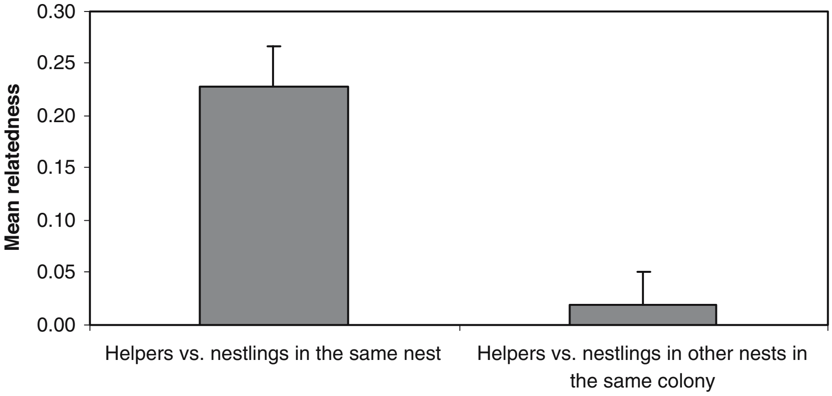

Fig. 1 Mean-relatedness between adult helpers and the nestlings they were tending was higher than the relatedness between those same helpers and nestlings in other nests in the colony

the dominant female or male (b=0.323 and 0.273, respectively, t_{28}=0.50, two-tailed P=0.63; Table 2).

Ninety-three percent of helpers (n=30) were first-order relatives of one or both breeders; in two cases, the helpers were either more distant relatives or unrelated to the dominant pair (Table 3). Based on ringing data, we know that the second year that followed a highly successful reproductive season, most helpers aided their social parents but in at least two cases (two helpers at one nest), helpers assisted apparent brothers they first encountered as nest mates.

Overall relatedness values among individuals from different nests within colonies are given in Table 4. Our results revealed a significant degree of genetic structure within colonies. We found a significantly positive relatedness estimate b of 0.171 among breeding males within a colony (t_4=−2.4, one-tailed P=0.036). There was, however, no structure among breeding females, which were negatively related, though not significantly, to each other within the colonies (b=−0.130, t_4=1.9, one-tailed P=0.064; Table 4). These results are in agreement to what is expected if females breeding within a colony are immigrants, but breeding males are typically philopatric individuals.

Table 3 Number and percentage of helpers falling into different categories of kinship relationship to the breeders

	Helpers (both sexes) N (%)	Female helpers	Male helpers
Offspring of both breeders	13 (43%)	3 (10%)	10 (33%)
First-order relative of breeding female only	7 (23%)	2 (7%)	5 (17%)
First-order relative of breeding male only	8 (27%)	1 (3%)	7 (23%)
Second-order or more distantly related	2 (7%)	0 (0%)	2 (7%)
Total	30 (100%)	6 (20%)	24 (80%)

The relationship between helpers and each breeder was established by combining multilocus genotypes from microsatellite data with field observations of 30 helpers in 19 nests

Discussion

We found two levels of genetic structure in sociable weavers underlying their social structure: the breeding group and the males within a colony. The breeding group always comprised a dominant pair that appeared to control reproduction; this pair could be assisted from zero to five helpers. The helpers were usually (but not always) first-order relatives of one or both parents. Very low levels of EPP also seem to occur in another sociable weaver population in Namibia. Allowing for one mismatch at microsatellite loci, the results obtained by Marsden (1999) indicate calc. 2% egg dumping (N=101) and calc. 4% EPFs (N=70). This monogamous genetic mating system of sociable weavers markedly differs from the polygynandrous system of the only other colonial cooperative weaver for which molecular data is available, the red-billed buffalo weaver *Bubalornis niger* (Winterbottom et al. 2001).

At a higher social level, we found significant relatedness linking sociable weaver males within a colony. Similar results showing a genetic structure underlying the social structure at different levels were reported for the colonial cooperatively breeding bell miner *Manorina melanophrys* by Painter et al. (2000). Within each colony, sociable weaver helpers were significantly more related to the nestlings they were tending than to the nestlings in the other nests, suggesting an active choice for associating with kin, as opposed to a passive consequence of place of birth and demographic viscosity. Evidence suggesting an active

Table 4 Relatedness among individuals from different nests within a colony

Relatedness between nests within a colony	b±SE	95% CI	Number of colonies
Breeding males	0.171±0.064	−0.034 to 0.375	5
Breeding females	−0.130±0.062	−0.326 to 0.067	5
Adult helpers	0.121±0.009	0.092 to 0.151	5
Adult helpers–nestlings	0.020±0.031	−0.078 to 0.117	5
Nestlings	−0.032±0.030	−0.126 to 0.062	5

The standard errors of the relatedness estimates were obtained by jack-knifing over loci association with kin was seldom obtained for cooperative breeders with the exceptions of long-tailed tits *Aegithalos caudatus* (Russell and Hatchwell 2001; Sharp et al. 2005) and carrion crows *Corvus corone* (Baglione et al. 2003). Helping by European bee-eaters *Merops apiaster* also appears to fit this pattern (Lessells et al. 1994).

We found no supporting evidence for extrapair parentage in our population. The likelihood-based approach allowed assigning paternity to the dominant male of a given nest in 93% of cases. Although for four nestlings from different clutches paternity was assigned to a male helper, these cases do not necessarily represent evidence for extrapair paternity because in all cases, paternity by the dominant male was never excluded and its likelihood was at least of the same magnitude or higher as that of helpers. The likelihood-based approach also allowed assigning maternity to the dominant female in all but one case. For this nestling, maternity was assigned to a female helper at the nest, but again, this does not necessarily constitute evidence for EPP because maternity by the dominant female was never excluded and its likelihood was of the same magnitude or higher as that of the helper.

EPP, whether in the form of egg dumping or EPF, varies widely across and within species, but is generally common being found in calc. 90% of bird species (Griffith et al. 2002). In cooperatively breeding species, there is wide variation in EPP levels, from an apparent absence of shared parentage in laughing kookaburras *Dacelo novaeguineae* (Legge and Cockburn 2000) to the very high promiscuity of Maluridae wrens (Dunn and Cockburn 1999; Webster et al. 2004). In a survey of 23 cooperative species for which molecular parentage data is available, Cockburn (1998) found that shared reproduction within the group occurred in at least 17 species (calc. 74%), suggesting that the direct fitness benefits resulting from shared reproduction could be an important selective force promoting cooperative breeding.

Our failure to find evidence for EPP in our sample suggests that contrary to many cooperative breeders, reproductive sharing is not an important strategy for sociable weavers. Reproductive sharing seems to be inversely correlated to relatedness among same-sex group members (e.g., Whittingham et al. 1997; Heinsohn et al. 2000; Vehrencamp 2000), presumably because the subordinate gains higher indirect fitness benefits when relatedness is higher. This could help explain our findings, given the close relatedness of sociable weaver groups. However, Richardson et al. (2002) found high levels of reproductive sharing among mother and daughter in the Seychelles warbler and reproductive sharing among females with different degrees of relatedness was also reported in other species (reviews in Cockburn 1998; Vehrencamp 2000). In many species, reproductive sharing among females might be constrained by hatching synchrony and clutch size (Chao 1997; Cant 1998; Cockburn 1998). This constraints could be important in sociable weavers because clutch size and reproductive success are highly variable as a result of unpredictable rainfall (Covas 2002). In particular, brood reduction is common both in natural (Covas 2002) and artificially enlarged clutches (Covas and du Plessis 2005), suggesting that egg dumping by helper females could substantially decrease fledging success and/or condition of the brood. Given that in this study the female helpers were always offspring of one or both breeders, by reducing breeding success they would also reduce their own indirect fitness benefits (see also Cant 1998).

The apparent lack of reproductive sharing among males in our population is somewhat more surprising because EPF does not bear such risks of reducing reproductive success. More than a third of the 24 male helpers in our study did not appear related to the dominant female and could have attempted to breed (cf. Table 3). In cooperative groups composed of close family members, incest avoidance is expected to prevent subordinates from attempting to breed with one of the parents or other breeding members (Koenig and Pitelka 1979; Koenig et al. 1999). However, conflicts over reproduction are expected when changes in group composition alter the relatedness between individuals (Keller and Reeve 1994; Emlen 1997; Cockburn 2004). For example, if the breeding female is replaced through death or divorce, male helpers will no longer be related to the new breeding female and could seek copulations with her (e.g., Koenig and Pitelka 1979; Whittingham et al. 1997; Webster et al. 2004). However, reproduction by male helpers is expected to increase as their relatedness to the breeding male decreases because where helpers have a positive effect on reproductive output, breeders should concede some reproduction to retain unrelated helpers in the group (Keller and Reeve 1994; Emlen 1997). The rationale behind this suggestion is that helpers would gain smaller indirect fitness benefits when they are less related to the breeder. In this study, helpers that were in position to attempt reproduction (i.e., that were of the opposite sex of the “stepparent”) were in all but two cases, first-order relatives of the other parent. Hence, the majority of helpers in our sample could still gain significant indirect fitness benefits by assisting the breeding pair. In sociable weavers, the presence of helpers improved reproductive success under adverse conditions (Covas, Doutrelant, and du Plessis, unpublished data) and under an artificial brood enlargement (Covas and du Plessis 2005). Hence, by staying in the group, helpers contribute to increase the production of nondescendent kin, at least under some circumstances. In addition, an experimental manipulation of breeding conditions showed that sociable weavers are less likely to breed independently and more likely to help when breeding conditions are poor (Covas et al. 2004). Hence, in sociable weavers, helping under adverse conditions might be particularly beneficial, while attempting to breed can be costly.

Nonetheless, the direct fitness benefits obtained in the event of shared reproduction would be at least twofold higher in terms of genetic fitness gain. So it is still important to explore other possible explanations for why sociable weavers in our population appeared to have no shared parentage. Two factors were overlooked in studies of reproductive sharing and conflict (see also Magrath and

Heinsohn 2000). First, in addition to any kin selected fitness benefits, there is a range of other important direct benefits associated with group membership, which are often ignored. For example, helper survival might increase in larger groups in which case helpers would gain significant benefits by contributing to group augmentation (Clutton-Brock et al. 1999). Furthermore, when in family groups, subordinate individuals probably benefit from increased survival and lifetime reproductive success resulting from parental nepotism toward offspring (Ekman et al. 1999–2001; Green and Cockburn 2001). Other possible benefits might include gaining experience (Komdeur 1996), signaling to other group members (Zahavi 1995; Putland 2001; Doutrelant and Covas, unpublished data), and gaining increased access to territories or mates (Clarke 1989; see also reviews in Cockburn 1998, 2004). Signaling to other group members might be an important benefit of helping in sociable weavers (Doutrelant and Covas, unpublished data) although at present we lack data to evaluate the magnitude it might have. Second, most models dealing with reproductive sharing assume there is a conflict between males, but do not consider the role of female choice and decision (Magrath and Heinsohn 2000). In species where there is strong competition for breeding vacancies, females might already be paired to a top quality male and not gain from EPFs (Quinn et al. 1999). In addition, where the dominant male performs the bulk of the nestling care, females might trade faithfulness for care and it might be more advantageous for them to benefit from higher male investment than from EPFs (Legge and Cockburn 2000; Cockburn 2004). In sociable weavers, dominant males contribute more to feed the nestling than dominant females or helpers individually (Doutrelant, Dalecky, and Covas, unpublished data). Similarly, in genetically monogamous laughing kookaburras, males contribute more than females to brood care (Legge and Cockburn 2000). These observations suggest that a “faithfulness for care” deal could play a role in explaining EPF levels. However, although paternity and male care are often positively related (Møller and Birkhead 1993), many studies found no relation between the two (Sheldon 2002; Dickinson 2003). Data from more species is therefore necessary to establish whether this explanation is valid.

In conclusion, sociable weaver helpers do not appear to have access to reproduction, suggesting that immediate reproductive benefits are not an important selective force behind cooperative breeding in this species. Indication of an active choice for associating with kin suggests that kin selection plays an important role in the maintenance of helping behavior (and high reproductive skew) in this species. However, other direct, albeit non-reproductive benefits of remaining as a helper, as well as female decisions, could play an equally important role, but this remains largely unknown. More data is needed to understand the role of nonreproductive direct benefits and female decisions in this species and cooperative breeders in general.

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