Age and relatedness have an interactive effect on the feeding behaviour of helpers in cooperatively breeding sociable weavers

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Summary

In cooperative species, helpers often assist close relatives and kin selection is thought to be a major selective force underlying the evolution and maintenance of helping. However, in some cases helpers may be unrelated individuals, which require other types of explanation. Here, we used genetic analyses and observations of feeding behaviour to investigate the relationships between helping at the nest and relatedness in a species where helpers vary in their relatedness to the breeders, the sociable weaver, *Philetairus socius*. We also investigated the effect of age and breeding group size on feeding behaviour. We found no overall increase of feeding rate with relatedness. Instead, the relationship between helpers' feeding rate and relatedness changed with age. Yearling helpers, which were typically the offspring of one or both parents, did not feed significantly more often when more related to the nestlings or the breeding male or female but did bring larger prey when more related to the nestlings or breeding female. For adult helpers, contrary to the expectations of the kin selection hypothesis, the feeding rate and the size of the prey brought was negatively linked to their relatedness to the nestlings and the breeding female. These results suggest that the reasons for helping in this population change with age. Indirect benefits seem important for yearling helpers while direct benefits may influence the evolution and maintenance of helping behaviour in adult helpers.

Keywords: cooperative breeding, kin selection, *Philetairus socius*, direct and indirect benefits, birds, feeding behaviour.

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1. Introduction

The evolution and maintenance of altruistic behaviours is often explained by kin selection, where individuals gain indirect fitness benefits by helping relatives (Hamilton, 1964; Gardner et al., 2011). In cooperatively breeding species, where helpers assist to raise the offspring of others, groups often form through the delayed dispersal of mature offspring (Emlen, 1991). Hence, in these kin groups, high levels of relatedness between the helpers and the individuals helped can be a result of population viscosity (i.e., limited dispersal: Griffin & West, 2003; Cornwallis et al., 2009) and not a direct result of selection for helping kin. For example, there is increasing evidence of kin-structure in many species that do not breed cooperatively (Hatchwell, 2009). Although the two hypotheses are not exclusive (e.g., viscosity can favour kin selection), testing kin selection theory requires investigating whether helpers have an active preference for cooperating with kin and whether they adjust their helping effort to their level of relatedness to the individuals being helped.

Such a fine scale adjustment in helping preferences and behaviour has been shown for several species (e.g., Owens & Owens, 1984; Reyer, 1984; Curry, 1988; Komdeur, 1994; Wright et al., 2009; Nam et al., 2010). However, there is also a number of species where there is no correlation between helping effort and relatedness (Wright et al., 1999; Legge, 2000; Clutton-Brock et al., 2001; Canestrari et al., 2005; Le Vin et al., 2011). Finally, in at least two studies a negative correlation was found between relatedness and feeding rate: one on white-browed scrubwrens *Sericornis frontalis* (Magrath & Whittingham, 1997) and one on a cooperative fish *Neolamprologus pulcher* (Stiver et al., 2005).The lack of positive correlation between helping effort and relatedness can be explained in at least two ways. First, individual helpers may not always have accurate information regarding the degree of relatedness to the individuals helped. For example, where relatedness between groups is usually high, there might be less kin discrimination by helpers (Cornwallis et al., 2009), resulting in weaker correlations between amount of help provided and relatedness. Second, it is increasingly accepted that cooperation often arises through a combination of kin-selected and direct fitness benefits, which are not mutually exclusive (Bergmüller et al., 2007; Rutte & Taborsky, 2007), although evaluating the importance of the two types of benefits is often challenging.

Independently of the kin-selected benefits gained, helping may also provide direct fitness benefits such as increased survival mating or reproductive success (Cockburn, 1998; Clutton-Brock, 2002; Koening & Walters, 2011). Four main hypotheses, which overlap to some extent, have been suggested to explain by which mechanisms these direct benefits are obtained. (i) Group augmentation: This hypothesis proposes that the direct fitness benefits obtained by individual helpers are associated with being in large groups. Larger groups may allow obtaining larger territories and, thus, enhance access to food and survival. Under this hypothesis, helping increases the group's reproductive success and hence the future group size (Clutton-Brock et al., 1999; Kokko et al., 2001). This hypothesis predicts that helping effort is higher in smaller groups in order to increase reproductive success and thereby the number of young recruiting into the group; feeding effort is not expected to vary with relatedness to the recipients of help. (ii) Pay to stay: This hypothesis suggests that the direct fitness benefits the individuals get by helping are associated with having access to the communal resource of a group regardless of its size. These benefits vary from increased survival to joining a 'queue' to eventually become a breeder (either as a dominant breeder or through cuckoldry). Under this hypothesis, the helpers are expected to contribute towards feeding the nestlings in return for acceptance in the group, i.e., to pay a rent to be accepted in the group (Gaston, 1978; Kokko et al., 2002). Under this hypothesis, an effect of relatedness on individual contributions might be expected since parents should be more tolerant toward related helpers (i.e., their offspring) in order to allow them to benefit from group membership and/or to decrease the costs associated with helping, thereby contributing to improve their lifetime reproductive success. Hence, unrelated helpers may have to feed more (e.g., Stiver et al., 2005). (iii) Signalling: According to this hypothesis the direct fitness benefits the individuals get by helping are associated with the positive reactions of the receivers that observed the helping behaviour. Hence, helping would be performed in order to transfer information to conspecifics. The information provided by helping behaviour could be used in an 'image scoring' system (Bshary & Grutter, 2006), whereby helpers could benefit from reciprocal help in the future (Clutton-Brock, 2002; Griffin & West, 2002). In addition, since helping is a costly behaviour (Heinsohn & Cockburn, 1994; Clutton-Brock et al., 1998; Heinsohn & Legge, 1999), performing help could represent an honest signal of individual quality and could increase the chances of mating in the future

(Zahavi, 1995; Putland, 2001; Griffin & West, 2002; Doutrelant & Covas, 2007; but see McDonald et al., 2008). If helping is used to transfer information to potential mates inside the group, helping effort is expected to be negatively correlated with the level of relatedness to the breeders of the opposite sex. If the signal is directed to individuals outside the breeding group it should show no correlation with relatedness. (iv) Parental skills: Helping could improve parental skills and, thus, future reproductive success (Heinsohn, 1991; Komdeur, 1996). This parental skills mechanism does not predict any relationship between feeding effort and relatedness, but it predicts a positive age effect if young helpers are less efficient foragers, particularly in their first year, when they are feeding nestlings for the first time (Heinsohn & Cockburn, 1994; Komdeur, 1996; Woxvold et al., 2006).

The aim of our study was to determine whether sociable weavers *Philetairus socius* primarily adjust their feeding rate in relation to their relatedness to the brood or whether other factors like age or breeding group size might affect the feeding rate. The sociable weaver is a colonial cooperatively breeding bird inhabiting the semi-arid savannahs of Southern Africa. In our population, helpers do not have access to reproduction within or outside their group and hence helping behaviour cannot be explained by shared parentage and feeding own offspring (Covas et al., 2006). The number of individuals feeding the nestlings varies from 2 (i.e., the parents alone) to 7 (i.e., the parents plus five helpers) and, thus, group size might affect the reasons for helping. Previous results have shown that helpers are typically related to the breeders but there is variation in relatedness, with yearling helpers being typically closely related to the breeders while older helpers may be distant relatives or seemingly unrelated individuals (Covas et al., 2006). Age may, therefore, affect the relationship between relatedness and feeding rate in this system.

Specifically, for this system, we made the following predictions. Under kin selection hypothesis, the feeding investment of yearling and adult helpers is predicted to increase with relatedness. For yearling helpers that are typically highly related to the nestlings in sociable weavers, an alternative prediction is that the feeding rate is not correlated to relatedness if no fine discrimination occurs. Under this scenario yearling helpers should always feed their related kin as much as possible. Under the hypothesis that helping gives direct benefits, a negative relationship between relatedness and feeding investment is predicted (see the predictions of the pay to stay and signalling hypotheses above). Lastly, an effect of breeding group size is predicted if increasing breeding group size provides direct benefits.

2. Material and methods

2.1. Study species and population

This study was conducted at Benfontein Game Farm near Kimberley, in the Northern Cape Province, South Africa (approx. 28°53′S, 24°89′E). The resident birds at the study colonies were captured with mist nets twice a year, at the beginning and end of the breeding season to track juvenile dispersal and to mark immigrants. The weavers' age was known if individuals were marked as nestlings or adults in the years preceding this study. All the individuals feeding at the focal nest were colour ringed with a unique colour combination.

In our population, sociable weavers breed in pairs or with one to five helpers (average breeding group size is 3.1; Covas et al., 2008). The helpers we followed always remained with the same pair during the entire breeding season. They may help for one or consecutive seasons. Helpers older than one year are invariably males, one year old helpers can be males or females but are predominantly males (Doutrelant et al., 2004). One year old male and female helpers have similar feeding rate (Doutrelant et al., 2004). On average, helpers feed as much as the breeding female and slightly less than the breeding male (Doutrelant & Covas, 2007). Helpers have been shown to have a positive influence on the reproductive success of the breeding pairs under some circumstances (i.e., when rainfall is low or in large colonies), and parents have been shown to decrease their feeding rate in the presence of helpers (Covas et al., 2008).

2.2. Behavioural observations

When conducting field observations during two years (1999 and 2000), the observers did not know the identity and the sex of the feeder (helper, mother or father). This was determined later through genetic parentage analyses with a likelihood-based approach using the Cervus software (Covas et al., 2006). Sex determination was done by molecular techniques (Doutrelant et al., 2004) using the P2 and P8 universal primers of Griffiths et al. (1998).

All nest-chambers in each study colony were individually identified with a numbered plastic tag. During the breeding season, all nest chambers were inspected every 4 days to detect initiation of new clutches. Nests were then visited daily near the hatching date until all nestlings had hatched. When the nestlings were around 6 days old, we conducted 1–2 h of daily observations for two to three consecutive days to identify the individuals feeding at a given nest. Subsequently, to record each individual's feeding rate, we conducted one hour of observations on three consecutive days (i.e., when the nestlings were typically 8–13 days old). We noted the identity of the birds feeding at a given nest, the number of visits per hour and the food size. Food size was scored from 1 to 4 relatively to the size of the beak.

We obtained data for 22 nests and 34 helpers: 26 males and 8 females. Male helpers were both yearlings ($N = 15$) and adults ($N = 11$). Female helpers were all yearlings ($N = 8$). For the statistical analyses, we averaged the values obtained during the three days of observations. Preliminary analyses showed that the feeding rate and the size of the food brought by the helpers was not affected by rainfall (in mm, corresponding to the total of rain collected over the 30-day period before the nestlings were 17 days old), the number and age of the nestlings (all $p > 0.30$ in a GLMM model with nests as a random factor). These preliminary analyses also showed that the feeding rate was significantly different between 'seasons' ($p = 0.02$) and that food size was positively linked to the size of the colony ($p = 0.04$). We, thus, entered respectively 'year' and colony size' in the statistical models testing the effects of relatedness, breeding group size and age on the variation in the feeding rate and the food size brought by the helpers (see Statistical methods section). In these full statistical models, these two factors were however no more significant.

2.3. *Estimates of kinship relationships and relatedness between helpers and individuals helped based on microsatellite analyses*

Details on microsatellite genetic data are given in Covas et al. (2006). Individuals were genotyped at four highly polymorphic microsatellite loci (gene diversity H_E: 0.852–0.865; see Covas et al., 2006 for details). Regression relatedness b was estimated using microsatellite loci between classes of individuals following the method of Queller & 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.

In a previous study (Covas et al., 2006) we estimated average relatedness and Standard Error ($\bar{b} \pm$ SE) that can be estimated with reasonable accuracy even with a low number of loci (Queller & Goodnight, 1989), 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 tested with one-tailed t-tests (p. 230 in Sokal & Rohlf, 1981) and the differences between two relatedness estimates were tested with two-tailed t-tests (p. 411 in Sokal & Rohlf, 1981) with number of nests-1 or number of loci-1 degrees of freedom. The analysis of Covas et al (2006) showed that helpers were significantly positively related to the nestlings they were tending ($\bar{b} \pm \mathrm{SE} = 0.228 \pm 0.039$ (95% confidence interval (CI) 0.146–0.310); $t_{20} = 5.7$, one-tailed $p < 0.001$) and significantly more related to these nestlings than to nestlings from different nests within a colony ($\bar{b} \pm \mathrm{SE} = 0.020 \pm 0.031$ (95% CI −0.078–+0.117); $t_{17} = 4.2$, two-tailed $p < 0.001$). On average, it also showed that helpers were related to the breeding pair and that helpers were not more often related to the breeding female than the breeding male ($\bar{b} \pm \mathrm{SE} = 0.323 \pm 0.081$ (95% CI 0.151–0.495) and 0.273 ± 0.059 (95% CI 0.149–0.396), respectively; $t_{28} = 0.50$, two-tailed $p = 0.63$).

Based on this genetic structure, we can infer kinship relationship between pairs of individuals within nests. Two methods could have been used. First, relatedness estimates could be calculated between pairs of individuals based on their multilocus genotypes. However, in contrast to average estimates within groups, these pairwise relatedness estimates are expected to show a high sampling variance, particularly when the number of loci is low (Queller & Goodnight, 1989). Indeed, up to tens of microsatellite loci are needed to obtain even moderate confidence around a single pairwise estimate (Blouin, 2003). Although both methods give similar results here (not shown), with fewer loci an alternative and more prudent method is to infer relationship between pairs of individuals with a maximum likelihood approach. In this approach, the probability of occurrence of the multilocus genotypes data is calculated under a priori competing relationship categories, and the category giving the highest likelihood is chosen (Goodnight & Queller 1999; Blouin, 2003; Wright et al., 2009). To confirm our previous results on relatedness structure within nests inferred from pedigree relationships and disjunction analysis assuming Mendelian inheritance (Covas et al., 2006), and to provide statistically robust kinship relationships, we used here this second method.

Within each nest, multilocus genotypes were used to assign pairs of individuals to specified categories of relationships with the software KINGROUP v.2 (Konovalov et al., 2004) following the method of Goodnight & Queller (1999) at a significance level of $p < 0.05$ based on 10 000 simulated pairwise comparisons. Classes of relatedness, b, between helpers and nestlings were assessed as follows.

We calculated likelihoods of helpers and breeders being either close relatives (test 1 = primary hypothesis H_1: parent–offspring vs. null hypothesis H_0: unrelated; test 2 = H_1: full-sibs vs. H_0: unrelated) or unrelated (test 3 = H_1: unrelated vs. H_0 (parent–offspring or full-sibs)). Relationships between helpers and the breeders could be assigned with statistical significance to one of these categories: (i) unrelated $b = 0.0$ (tests 1 and 2: $p > 0.05$, test 3: $p < 0.05$); (ii) closely related $b = 0.5$ (tests 1 and/or test 2: $p < 0.05$, test 3: $p > 0.05$); or (iii) unresolved $b = 0.25$ (tests 1, 2, 3: all $p > 0.05$).

Relatedness to both the breeding male and the breeding female were combined to give for each helper an estimate of relatedness to the nestlings following Wright et al. (2009). For a subset of helpers, however, breeder genotypes were not available for either female (five nests) or both male and female (one nest), preventing the assignment of relationships between seven helpers and the two breeders. For this subset of helpers, we used nestling genotypes instead. We calculated likelihoods of helpers and nestlings being either close relatives $b = 0.5$ (test A = H_1: full-sibs vs. H_0: unrelated; test B = H_1: full-sibs vs. H_0: half-sibs), moderately distant relatives $b = 0.25$ (test C = H_1: half-sibs vs. H_0: unrelated; test D = H_1: half-sibs vs. H_0: full-sibs) or unrelated $b = 0.0$ (test E = H_1: unrelated vs. H_0: full-sibs; test F = H_1: unrelated vs. H_0: half-sibs). For each helper the different nestlings were considered as independent replicates and a combined probability for tests A–F separately was constructed using Stouffer's Z-transformed method following (De Meeûs et al., 2009; see also Whitlock, 2005). The following information on relationships between helpers and the genotyped parent was used when available (inferred previously, see tests 1, 2 and 3). (1) When relationships between helpers and the single genotyped breeder was assigned to 'unrelated' (two cases) we performed tests C and F, and relationships between helpers and the nestlings could be assigned with statistical significance to (i) 'seemingly unrelated' $b = 0.0$ (tests C: $p > 0.05$, test F: $p < 0.05$; one case) and (ii) 'moderately distant relatives' $b = 0.25$ (tests C: $p < 0.05$, test F: $p > 0.05$; one case). (2) When relationships between helpers and the genotyped breeder was assigned to 'closely related' (three cases) we performed tests B and D, and relationships between helpers and the nestlings could be assigned with statistical significance to: (i) 'close relatives' $b = 0.5$ (tests B: $p < 0.05$, test D: $p > 0.05$; one case) and (ii) 'moderately distant relatives' $b = 0.25$ (tests B: $p > 0.05$, test D: $p < 0.05$; two cases). (3) Otherwise all tests were implemented, and relationships between helpers and the nestlings were assigned to (i) unrelated $b = 0.0$ (tests A, B and C: $p > 0.05$, tests D, E and F: $p < 0.05$; one case) or (ii) unresolved between unrelated and moderately distant relative, $b = 0.125$ (tests B, C and F: $p > 0.05$, tests A, E and D: $p < 0.05$; one case). Relationships between helpers and the unsampled breeders were deduced from relationships between helpers and the genotyped breeders and nestlings.

Lastly, for a single helper, its genotype was not available and relatedness to the nestlings was inferred from pedigree: in this nest the breeding pair remained unchanged from year to year and this helper was ringed as a nestling the year before our behavioural observations of feeding rate. We, thus, deduced that this helper was an offspring of both breeders and a full-sib of the current nestlings (expected $b = 0.5$), assuming no paternity sharing, egg-dumping, extra-pair parentage (see Covas et al., 2006).

2.4. *Statistical methods*

Our aim here was to test the predictions of the five main hypotheses that could explain the evolution of helping in this species (kin selection, group augmentation, pay to stay, signalling and improve parental skills, see introduction). The dependent variables were the feeding rate and the food size of the helpers and the factors we tested were: relatedness, age, group size, and the interactions between age and relatedness, and age and group size (varying from 3, i.e., 2 breeders and the helper, to 7, i.e., two breeders and 5 helpers). We run general linear mixed models (GLMM). These models all included the random co-variable 'nest' since 10 out of 22 nests had more than one helper. For model selection we used backward selection procedures and Type III errors in SAS v9.

2.4.1. Preliminary analyses

Given that no females older than one year were helping, we conducted a preliminary analysis to test whether male and female yearling helpers have different feeding behaviours or can be lumped in one class, the yearling helpers for some analyses. On a sample containing only male and female yearling helpers, we tested the effects of sex and found no significant effect of this variable on helpers' feeding rate and food size ($p = 0.17$ and $p = 0.41$, respectively). We also tested whether yearling helpers' feeding rate and food size was affected by the interactions between sex and class of relatedness ($b \leqslant 0.125$, $b = 0.25$ and $b = 0.5$) and sex and breeding group size. These interactions were not significant (feeding rate: all $p > 0.15$; food size: all $p > 0.41$). We concluded that male and female yearling helpers have similar feeding behaviours and can be lumped in one class, the yearling helpers in some of the main analyses below.

2.4.2. Main analyses

We examined the factors affecting the variation in the feeding rate and the food size brought by adult and yearling helpers. We used two data sets: one was the full data set that contains both male and female helpers; one was a restricted data set that contains only male helpers. The analyses conducted on the full data set tested the effects of class of relatedness with the nestlings (in three classes: $b \leqslant 0.125$, $b = 0.25$ and $b = 0.5$), 'helper age' (yearlings vs. adult, i.e., 1 year vs. older) and breeding group size. In addition, they tested the two following interactions: class of relatedness by age and breeding group size by age. The analyses conducted on the restricted 'male helper' data set tested the effects of the relatedness to the breeding female and to the breeding male (each in two classes: $b \leqslant 0.125$; $b = 0.5$ because we add only one modality for $b = 0.25$) instead of the relatedness to the nestlings. The other factors included were the same as the ones included in the full data set, i.e., helper age, breeding group size, class of relatedness by age and breeding group size by age. In addition, in all models season and colony size were included in the analyses run, respectively, on the feeding rate and food size.

For significant factors, p values correspond to the values obtained when all the significant factors are in the final minimal model obtained after backward deletion. For non-significant factors, p values correspond to values of the factors before their exclusion from the model.

3. Results

3.1. Kinship relationships and relatedness between helpers and individuals helped

The assignment of pairs of individuals to specified categories of relationships as implemented in KINGROUP confirmed the previous results (Covas et al., 2006). It showed that 14 helpers were close relatives of both breeders, seven were close relatives of the breeding male only, eight were close relatives of the breeding female only, and five were more distant relatives or seemingly unrelated to the breeding pair. Over these 34 helpers, classes of relatedness to the nestlings were: 0.5 (41% of helpers: 12 yearlings + 2 adults), 0.25 (44%: 10 yearlings + 5 adults), 0.125 (6%: 2 adults) and 0.0 (9%: 1 yearling + 2 adults). The latter two classes were lumped together into a single class, distant relatives or unrelated ($b \leqslant 0.125$) for further analyses because with only four loci it is difficult to resolve accurately relatedness between 0.125 and 0.0 and because the low sample size would prevent us from testing interactions between age and relatedness.

3.2. Effect of age, relatedness and group size on helper's feeding behaviour

3.2.1. Feeding rate and relatedness to the nestlings

Although non-significant, in our GLMM there was a strong tendency for an effect the interaction between the helpers' age and their relatedness to nestlings on helpers' feeding rate ($p = 0.057$; Table 1, Figure 1). Post-hoc tests showed adult helpers fed more when unrelated than related to the nestlings (class $b \leqslant 0.125$ vs. $b = 0.5$: $p = 0.008$; class $b \leqslant 0.125$ vs. $b = 0.25$: $p = 0.046$; class $b = 0.50$ vs. $b = 0.25$, $p = 0.19$). In contrast yearling feeding rate was not significantly different between the different class of relatedness (class $b \leqslant 0.125$ vs. $b = 0.5$: $p = 0.40$; class $b \leqslant 0.125$ vs. $b = 0.25$: $p = 0.26$, class $b = 0.50$ vs. $b = 0.25$, $p = 0.75$). The feeding rate of the helpers was not significantly affected by the breeding group size alone ($p = 0.24$) or in interaction with age (age × group size: $p = 0.15$).

3.2.2. Feeding rate of male helpers and relatedness to the breeding male and female

Although not significant, in our GLMM, there was a strong tendency for an effect of the interaction between age and relatedness to the breeding

Table 1. Factors affecting the variation in helpers' feeding rate.

	df	*F*	*p*
Model with average helpers' relatedness to the nestlings			
Relatedness to the nestlings	2, 8	1.22	0.34
Age	1, 8	0.70	0.42
Age × relatedness to the nestlings	2, 8	4.19	0.057
Model with average male helpers' relatedness to the breeding male and female			
Relatedness to the nestlings	1, 4	1.97	0.23
Age	1, 4	0.06	0.81
Age × relatedness to the nestlings	1, 4	6.19	0.067

The first GLMM model is run on the whole data set, containing both male and female helpers and the second GLMM model is run on a restricted data set containing only the male helpers.

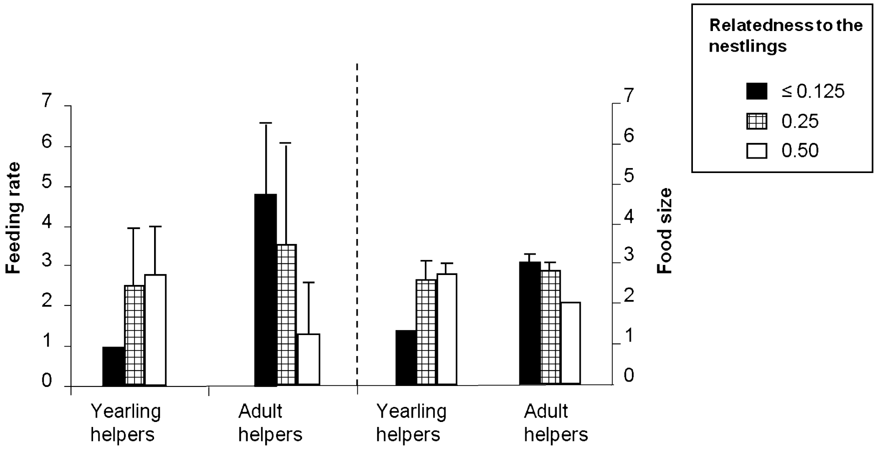

Figure 1. Mean ± standard feeding rate (number of visits per hour, left panel) and food size (right panel) brought by helpers in relation to their relatedness to the nestlings ($N = 34$, 11 adults helpers and 23 male and female yearling helpers). Helpers in relation to their relatedness to the nestlings of different age fed differently.

female on the variation in the feeding rate of male helpers ($p = 0.067$; Table 1, Figure 2). The post-hoc analyses revealed that adult helpers feed more the nestlings of unrelated females than the ones of related females ($p = 0.05$). By contrast the feeding rate of the yearlings helpers was not significantly related to their relatedness to the breeding females ($p = 0.53$). Finally, we found that the feeding rate of male helpers was not significantly

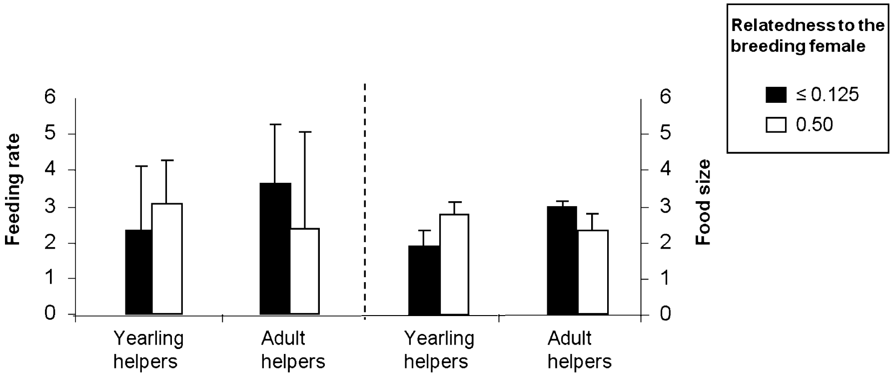

Figure 2. Mean ± standard feeding rate (number of visits per hour, left panel) and food size (right panel) brought by male helpers in relation to their relatedness to the breeding female ($N = 25$ males, 9 adults helpers and 15 yearling helpers). Age affected the relationship between the feeding behaviour and the relatedness the breeding female (see results section for details).

related to their relatedness to the breeding male either alone ($p = 0.44$) or in interaction with age (age × relatedness to the breeding male: $p = 0.31$).

3.2.3. Food size and relatedness to the nestlings

The interaction between age and relatedness to the nestlings significantly explained the variation in prey size (Table 2, Figure 1). Post-hoc analyses revealed that yearling helpers brought larger prey to related nestlings than unrelated ones (class $b \leqslant 0.125$ vs. $b = 0.5$: $p = 0.009$; class $b \leqslant 0.125$ vs. $b = 0.25$: $p = 0.017$; class $b = 0.50$ vs. $b = 0.25$, $p = 0.34$). Inversely, they showed that adult helpers brought smaller prey to related nestlings than unrelated ones (class $b \leqslant 0.125$ vs. $b = 0.5$: $p = 0.04$; class $b \leqslant 0.125$ vs. $b = 0.25$: $p = 0.51$; class $b = 0.50$ vs. $b = 0.25$, $p = 0.09$). The size of the food was not significantly affected by the breeding group size alone ($p = 0.49$) or in interaction with age (age × group size: $p = 0.74$).

3.2.4. Food size and relatedness to the breeding male and female

The interaction between age and relatedness to the nestlings significantly explained the variation in prey size (Table 2, Figure 2). Post-hoc analyses revealed that yearling helpers brought larger prey to related females than unrelated ones (class $b \leqslant 0.125$ vs. $b = 0.5$: $p = 0.01$). Inversely, there was a tendency for adult helpers to bring smaller prey to related nestlings

Table 2. Factors affecting the variation in the size of the prey brought by helpers.

	df	*F*	*p*
Model with average helpers' relatedness to the nestlings			
Relatedness to the nestlings	2, 7	2.66	0.14
Age	1, 7	3.53	0.10
Age × relatedness to the nestlings	2, 7	9.08	0.01
Model with average male helpers' relatedness to the breeding male and female			
Relatedness to the nestlings	1, 4	0.50	0.51
Age	1, 4	3.07	0.15
Age × relatedness to the nestlings	1, 4	19.52	0.01

The first GLMM model is run on the whole data set, containing both male and female helpers and the second GLMM model is run on a restricted data set containing only the male helpers.

than unrelated ones (class $b \leqslant 0.125$ vs. $b = 0.5$: $p = 0.08$). Lastly, the relatedness to the breeding male was not significant either alone ($p = 0.44$) or in interaction with age (age × relatedness to the breeding male: $p = 0.58$).

4. Discussion

In this study we analysed the potential effects of genetic relatedness, breeding group size and age on the feeding behaviour of helpers. These results were based on a relatively small sample and number of loci and, therefore, had limited power. Nonetheless, they did suggest an interacting effect of age and relatedness on feeding behaviour and suggest that yearling and older helpers help at the nest for different reasons. For adults, i.e., males older than one year old, we found that feeding rate and prey size decreased with relatedness to the nestlings and to the breeding female. For yearlings, i.e., one-year-old males and females, there was no significant effect of relatedness to the nestlings or to the breeding female on the feeding rate but we found that yearling helpers brought larger preys when more related to the nestlings or to breeding female. We did not detect any significant effects of helper sex, breeding group size and relatedness to the breeding male.

Sociable weaver yearlings may help to obtain indirect fitness benefits. As expected under the kin selection hypothesis, the size of the prey brought by yearling helpers increased with their relatedness to the nestlings and to the breeding females. Although we did not detect an association between yearling feeding rate and relatedness, this indicates that related yearling helpers bring larger food loads than unrelated ones. This adds to previous results from this population indicating that helping behaviour is not random in relation to relatedness by finding that helpers are more related to the nestlings they feed than to the other nestlings present in the colony (Covas et al., 2006). The absence of a relationship between relatedness and feeding rate could be due to our relatively low number of loci and sample size.

Yearling helpers might also help at the nest to increase their own parental skills. This has been reported in bird species where yearling helpers feed less than older birds (Heinsohn & Cockburn, 1994; Komdeur, 1996; Woxvold et al., 2006). However, in our study, no overall effect of age was found. Instead, yearlings that were closely related to the nestlings fed more than closely related adults. Together these results suggest that age alone, and associated feeding experience, are not the main determinants of the variation in feeding rates we observe in this species.

For helpers older than one year, the negative correlation between helping and relatedness suggests that factors other than kin selection can be important reasons for helping. To our knowledge, to date, only two other studies have found a significant negative correlation between the amount of help and relatedness (Magrath & Whittingham, 1997; Stiver et al., 2005). Stiver et al. (2005) interpreted these results as support for the pay to stay hypothesis. They found that unrelated helpers invested more into helping in a cooperative fish and suggested that unrelated helpers worked harder because they had to pay a higher rent to be accepted in the group and the territory, whereas the parents would be more tolerant towards closely related helpers due to their fitness interest in their close relatives. In the sociable weavers' colonial system, having access to a nest chamber has important advantages for individuals as it significantly decreases the cost of thermoregulation and allows important energetic savings (White et al., 1975; Williams & du Plessis, 1996). Hence, it could be important for unmated unrelated adult helpers to remain in a group if that improves access to roosting chambers or if helping increases the chances of subordinate individuals being accepted in a colony, since being solitary is not an option in this obligate colonial species (Maclean, 1973).

The other study that found a negative relationship between relatedness and helping behaviour was on white-browed scrubwrens *Sericornis frontalis* (Magrath & Whittingham, 1997). The authors suggested that in this species, helpers fed nestlings in order to obtain EPCs. In our sample, none of the helpers had access to paternity and extra-pair paternity has not been detected (Covas et al., 2006). Hence in sociable weavers, the higher feeding rate of less related male helpers cannot be explained by access to current reproduction. However, helping could act as a signal of quality, which could increase access to breeding opportunities in the future (Zahavi, 1995; Putland, 2001; Griffin & West, 2002; Doutrelant & Covas, 2007). Under this hypothesis, unrelated helpers could pair to the breeding female in case of divorce or death of the male breeder and so a higher feeding rate of unrelated helper might be expected. Our results provide some support for this possibility, since when we included both relatedness to the breeding male and to the breeding female in the same statistical model, the feeding rate of male helpers tended to be affected by the interaction between relatedness to the breeding female and age, and not by the interaction between relatedness to the breeding male and age. In addition, in our sample, all the helpers older than 1 year were males, suggesting that males need to queue for longer in order to obtain breeding positions. Additional data are required to further assess this hypothesis in this species.

Finally, helping behaviour could be performed in order to increase group size (the group augmentation hypothesis; Clutton-Brock et al., 1999; Kokko et al., 2001). However, the variation in helper feeding behaviour in our data was not related to the breeding group size and, thus, might not be explained by the group augmentation hypothesis. In addition, in this colonial species the costs and benefits associated with group size are likely to relate also to the size of the colony, but in the present study we did not have enough data to test these possible interactions.

To conclude, our results showed that age and relatedness affect the feeding behaviour of sociable weaver helpers, producing different helping patterns for the two age groups considered here. These results are in agreement with the hypothesis that indirect benefits mostly explain the helping of yearling individuals and direct benefits may explain helping behaviour in older helpers. Additional work is now needed to investigate the possible direct benefits gained by helpers older than one year.

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References

Bergmüller, R., Bshary, R., Johnstone, R.A. & Russell, A.F. (2007). Integrating cooperative breeding into theoretical concepts of cooperation. — Behav. Proc. 76: 61-72.

Blouin, M.S. (2003). DNA-based methods for pedigree reconstruction and kinship analysis in natural populations. — Trends Ecol. Evol. 18: 503-511.

Bshary, R. & Grutter, A.S. (2006). Image scoring and cooperation in a cleaner fish mutualism. — Nature 441: 975-978.

Canestrari, D., Marcos, J.M. & Baglione, V. (2005). Effect of parentage and relatedness on the individual contribution to cooperative chick care in carrion crows *Corvus corone corone*. — Behav. Ecol. Sociobiol. 5: 422-428.

Clutton-Brock, T.H. (2002). Breeding together: kin selection and mutualism in cooperative vertebrates. — Science 296: 69-72.

Clutton-Brock, T.H., Brotherton, P.N.M., O'Riain, M.J., Griffin, A.S., Gaynor, D., Kansky, R., Sharpe, L. & McIlrath, G.M. (2001). Contributions to cooperative rearing in meerkats. — Anim. Behav. 61: 705-710.

Clutton-Brock, T.H., Gaynor, D., Kansky, R., MacColl, A.D.C., McIlrath, G., Chadwick, P., Brotherton, P.N.M., O'Riain, J.M., Manser, M. & Skinner, J.D. (1998). Costs of cooperative behaviour in suricates (*Suricata suricatta*). — Proc. R. Soc. Lond. B: Biol. 265: 185-190.

Clutton-Brock, T.H., Gaynor, D., McIlrath, G.M., Maccoll, A.D.C., Kansky, R., Chadwick, P., Manser, M., Skinner, J.D. & Brotherton, P.N.M. (1999). Predation, breeding group size and mortality in a cooperative mongoose, *Suricata suricatta*. — J. Anim. Ecol. 68: 672-683.

Cockburn, A. (1998). Evolution of helping behavior in cooperatively breeding birds. — Annu. Rev. Ecol. Syst. 29: 141-177.

Cornwallis, C.K., West, S.A. & Griffin, A.S. (2009). Routes to indirect fitness in cooperatively breeding vertebrates: kin discrimination and limited dispersal. — J. Evol. Biol. 22: 2445-2457.

Covas, R., Dalecky, A., Caizergues, A. & Doutrelant, C. (2006). Kin associations and direct vs indirect fitness benefits in colonial cooperatively breeding sociable weavers Philetairus socius. — Behav. Ecol. Sociobiol. 60: 323-331.

Covas, R., du Plessis, M.A. & Doutrelant, C. (2008). Helpers in colonial cooperatively breeding sociable weavers *Philetairus socius* contribute to buffer the effects of adverse breeding conditions. — Behav. Ecol. Sociobiol. 63: 103-112.

Curry, R.L. (1988). Influence of kinship on helping behaviour in Galapagos mockingbirds. — Behav. Ecol. Sociobiol. 22: 141-152.

De Meeûs, T., Guégan, J.-F. & Teriokhin, A.T. (2009). MultiTest V.1.2, a program to binomially combine independent tests and performance comparison with other related methods on proportional data. — BMC Bioinformatics 10: 443-451.

Doutrelant, C. & Covas, R. (2007). Helping has signalling characteristics in a cooperatively breeding bird. — Anim. Behav. 74: 739-747.

Doutrelant, C., Covas, R., Caizergues, A. & du Plessis, M. (2004). Unexpected sex ratio adjustment in a colonial cooperative bird: pairs with helpers produce more of the helping sex whereas pairs without helpers do not. — Behav. Ecol. Sociobiol. 56: 149-154.

Emlen, S.T. (1991). The evolution of cooperative breeding in birds and mammals. — In: Behavioural ecology: an evolutionary approach (Krebs, J.R. & Davies, N.B., eds). Blackwell Scientific Publications, Oxford, p. 301-337.

Gardner, A., West, S.A. & Wild, G. (2011). The genetical theory of kin selection. — J. Evol. Biol. 24: 1020-1043.

Gaston, A.J. (1978). Evolution of group territorial behavior and cooperative breeding. — Am. Nat. 112: 1091-1100.

Goodnight, K.F. (2000). Relatedness 5.0. — Goodnight Software, Houston, TX.

Griffin, A.S. & West, S.A. (2002). Kin selection: fact and fiction. — Trends Ecol. Evol. 17: 15-21.

Griffin, A.S. & West, S.A. (2003). Kin discrimination and the benefit of helping in cooperatively breeding vertebrates. — Science 302: 634-636.

Griffiths, R., Double, M.C., Orr, K. & Dawson, R.J.G. (1998). A DNA test to sex most birds. — Mol. Ecol. 7: 1071-1075.

Hamilton, W.D. (1964). Genetical evolution of social behaviour. — J. Theor. Biol. 7: 1-52.

Hatchwell, B.J. (2009). The evolution of cooperative breeding in birds: kinship, dispersal and life history. — Philos. Trans. Roy. Soc. B: Biol. Sci. 364: 3217-3227.

Heinsohn, R. & Cockburn, A. (1994). Helping is costly to young birds in cooperatively breeding white-winged choughs. — Proc. Roy. Soc. Lond. B: Biol. 256: 293-298.

Heinsohn, R. & Legge, S. (1999). The cost of helping. — Trends Ecol. Evol. 14: 53-57.

Heinsohn, R.G. (1991). Slow learning of foraging skills and extended parental care in cooperatively breeding white-winged choughs. — Am. Nat. 137: 864-881.

Koenig, W.D. & Walters, E.L. (2011). Age-related provisioning behaviour in the cooperatively breeding acorn woodpecker: testing the skills and the pay-to-stay hypotheses. — Anim. Behav. 82: 437-444.

Kokko, H., Johnstone, R.A. & Clutton-Brock, T.H. (2001). The evolution of cooperative breeding through group augmentation. — Proc. Roy. Soc. Lond. B: Biol. 268: 187-196.

Kokko, H., Johnstone, R.A. & Wright, J. (2002). The evolution of parental and alloparental effort in cooperatively breeding groups: when should helpers pay to stay? — Behav. Ecol. 13: 291-300.

Komdeur, J. (1994). The effect of kinship on helping in the cooperative breeding Seychelles warbler, *Acrocephalus sechellensis*. — Proc. Roy. Soc. Lond. B: Biol. 256: 47-52.

Komdeur, J. (1996). Influence of helping and breeding experience on reproductive performance in the Seychelles warbler: a translocation experiment. — Behav. Ecol. 7: 326-333.

Konovalov, D.A., Manning, C. & Henshaw, M.T. (2004). KINGROUP: a program for pedigree relationship reconstruction and kin group assignments using genetic markers. — Mol. Ecol. Notes 4: 779-782.

Le Vin, A.L., Mable, B.K., Taborsky, M., Heg, D. & Arnold, K.E. (2011). Individual variation in helping in a cooperative breeder: relatedness versus behavioural type. — Anim. Behav. 82: 467-477.

Legge, S. (2000). Helper contributions in the cooperatively breeding laughing kookaburra: feeding young is no laughing matter. — Anim. Behav. 59: 1009-1018.

Maclean, G.L. (1973). The sociable weaver, part 1-5. — Ostrich 44: 176-261.

Magrath, R.D. & Whittingham, L.A. (1997). Subordinate males are more likely to help if unrelated to the breeding female in cooperatively breeding white-browed scrubwrens. — Behav. Ecol. Sociobiol. 41: 185-192.

McDonald, P.G., Te Marvelde, L., Kazem, A.J.N. & Wright, J. (2008). Helping as a signal and the effect of a potential audience during provisioning visits in a cooperative bird. — Anim. Behav. 75: 1319-1330.

Nam, K.B., Simeoni, M., Sharp, S.P. & Hatchwell, B.J. (2010). Kinship affects investment by helpers in a cooperatively breeding bird. — Proc. Roy. Soc. Lond. B: Biol. 277: 3299-3306.

Owens, D.D. & Owens, M.J. (1984). Helping behaviour in brown hyenas. — Nature 308: 843-845.

Putland, D. (2001). Has sexual selection been overlooked in the study of avian helping behaviour? — Anim. Behav. 62: 811-814.

Queller, D.C. & Goodnight, K.F. (1989). Estimation of genetic relatedness using allozyme data. — Evolution 43: 258-275.

Reyer, H.U. (1984). Investment and relatedness — a cost–benefit-analysis of breeding and helping in the pied kingfisher (*Ceryle rudis*). — Anim. Behav. 32: 1163-1178.

Rutte, C. & Taborsky, M. (2007). Generalized reciprocity in rats. — Plos Biol. 5: 1421-1425.

Sokal, R.R. & Rohlf, F.J. (1981). Biometry. — Freeman, New York, NY.

Stiver, K.A., Dierkes, P., Taborsky, M., Gibbs, H.L. & Balshine, S. (2005). Relatedness and helping in fish: examining the theoretical predictions. — Proc. Roy. Soc. Lond. B: Biol. 272: 1593-1599.

White, F.N., Bartholomew, G.A. & Howell, T.R. (1975). The thermal significance of the nest of the sociable weaver Philetairus socius: winter observations. — Ibis 117: 171-179.

Whitlock, M.C. (2005). Combining probability from independent tests: the weight Z-method is superior to Fisher's approach. — J. Evol. Biol. 18: 1368-1373.

Williams, J.B. & du Plessis, M.A. (1996). Field metabolism and water influx of the sociable weaver *Philetairus socius* in the Kalahari desert. — Ibis 138: 168-171.

Woxvold, I.A., Mulder, R.A. & Magrath, M.J.L. (2006). Contributions to care vary with age, sex, breeding status and group size in the cooperatively breeding apostlebird. — Anim. Behav. 72: 63-73.

Wright, J., McDonald, P.G., Te Marvelde, L., Kazem, A.J.N. & Bishop, C.M. (2009). Helping effort increases with relatedness in bell miners, but unrelated helpers of both sexes still provide substantial care. — Proc. Roy. Soc. Lond. B: Biol. 277: 437-445.

Wright, J., Parker, P.G. & Lundy, K.J. (1999). Relatedness and chick-feeding effort in the cooperatively breeding Arabian babbler. — Anim. Behav. 58: 779-785.

Zahavi, A. (1995). Altruism as an handicap — the limitations of kin selection and reciprocity. — J. Avian Biol. 26: 1-3.