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Helpers in colonial cooperatively breeding sociable weavers *Philetairus socius* contribute to buffer the effects of adverse breeding conditions

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Abstract Some studies on the effects of helpers in cooperatively breeding vertebrates show a positive effect of helper presence on reproductive output whereas others find no effect. One possibility for this discrepancy is that helpers may have a positive effect when breeding conditions are adverse, while their effect might go unnoticed under good conditions. We investigate this hypothesis on sociable weavers *Philetairus socius*, a colonial cooperatively breeding passerine that inhabits a semi-arid region where breeding conditions vary markedly. We used multivariate mixed models to analyse the effect of helpers on reproduction under contrasting environmental and social conditions while controlling for parental and colony identity. We found that reproductive success in sociable weavers was primarily influenced by nest predation and rainfall. In addition, colony size was negatively associated with hatching and fledging success and number of young fledged per season. Helpers had a less prominent but significant influence on feeding rates and reproductive outcome. In agreement with expectations, the presence of helpers counteracted some of the negative effects of breeding in periods of low rainfall or in large colonies and was also associated with an increased number of young fledged per season. Our results illustrate that the effect of helpers might be detectable mostly under unfavourable conditions, but can contribute to improve reproductive performance in those situations.

Keywords Colony size · Cooperative breeding · Environmental stochasticity · Group size · Reproductive success

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Introduction

The question of whether helper presence significantly affects reproductive output is central to understand the evolution and maintenance of helping behaviour. Most cooperatively breeding species live in family groups and this has led to the suggestion that kin selection plays an important role in the evolution of cooperative breeding through a positive effect of helpers on the production of young (Emlen 1991; Cockburn 1998; Griffin and West 2003). Other adaptive explanations of helping behaviour also predict a positive effect of helper presence on reproductive output. For example, if survival is higher in larger groups it would be advantageous for helpers to increase the reproductive success of others since that would increase group size (e.g. Clutton-Brock et al. 1999).

Helpers could improve reproductive output in different ways. The food brought to the nest by helpers could alleviate parental work loads leading to an increase in fecundity or parental survival, or it could improve condition and survival of young. A number of studies have provided support for some of these effects but the evidence is inconsistent and

some studies fail to find any positive effect of helpers' presence on reproductive success (e.g. Legge 2000a, b; Eguchi et al. 2002; see also review in Cockburn 1998).

Difficulties in detecting the effect of helpers may arise if parents reduce their own investment in the presence of helpers (Russell et al. 2007). Another non-exclusive hypothesis is that the presence of helpers might be significant under adverse circumstances, but go unnoticed under more favourable conditions (Cockburn 1998; Magrath 2001; Covas and du Plessis 2005). For example, previous studies have suggested that helpers could have a particularly important effect on reproduction when the breeding pair is inexperienced (Magrath 2001), brood reduction common (Hatchwell 1999) or under poor breeding conditions (Koenig and Mumme 1987; Curry and Grant 1990; Emlen 1990; Canário et al. 2004). This hypothesis is further supported by a recent comparative study which has found that cooperative breeding among African starlings (Sturnidae) is positively associated with living in temporally variable environments, particularly semi-arid savannahs, where breeding conditions are unpredictable (Rubenstein and Lovette 2007). The authors suggested that cooperative breeding in these species might be an adaptation that buffers the effects of unpredictable rainfall and food availability.

Selection is expected to exert stronger pressure during periods of unfavourable conditions, when competition should be strongest (e.g. Smith 1990). Hence, if the presence of helpers is particularly beneficial under adverse conditions, this could provide a somewhat cryptic but significant mechanism favouring the maintenance of helping-at-the-nest in cooperative breeders. It is therefore important that analyses of helper effects investigate not only overall reproductive success but also specifically the effects of helpers under contrasting breeding conditions. This requires analysing simultaneously environmental, individual and social factors and the interactions between these and the effects of helpers. Yet, few studies have specifically studied the interactions between helper effects and environmental conditions (but see Russell et al. 2002).

We used multivariate mixed models to analyse factors affecting fecundity, offspring growth and survival and seasonal reproductive output in sociable weavers *Philetairus socius*, a colonial cooperatively breeding passerine inhabiting the semi-arid savannahs of southern Africa. In these regions, rainfall, which is unpredictable in timing and quantity, is the main determinant of food availability through its effects on seed and insect production (Maclean 1973d; Harrison et al. 1997; Dean and Milton 2001). The sociable weavers' breeding activity is closely linked to rainfall in both timing and duration; individuals will make several breeding attempts for several months as long as conditions are suitable instead of being restricted to a specific season (Maclean 1973c). These elongated breeding periods, together with the broad variation in rainfall experienced within seasons and the variation in the degree of sociality (colony and breeding groups size), allow the study of the relative effects of environmental and social factors on reproduction under contrasting natural conditions. Here, we examine the importance of environmental (rainfall, predation, season duration) and social factors (presence of helpers, number of helpers, colony size) on several reproductive traits while accounting for breeding pair identity and colony site. In particular, we were interested in finding if the presence of helpers is especially relevant in situations where breeding conditions are adverse, such as when rainfall is low or when breeding in large colonies, and whether it has an overall positive effect on reproductive success.

Methods

Study area and species

The sociable weaver is a 26–32-g passerine endemic to the semi-arid savannahs of the southern Kalahari and Namib regions of Namibia and of South Africa's Northern Cape Province (Maclean 1973a; Mendelsohn and Anderson 1997). They feed on a wide variety of insects (constituting approximately 80% of their diet), but also on seed and other plant products (Maclean 1973d). In these arid regions, food availability is closely dependent on rainfall over the previous month (Dean and Milton 2001; see also Maclean 1973c; Lloyd 1999). Sociable weavers build a very large communal nest which is made mainly of *Stipagrostis* grasses and is built on a variety of sturdy structures, *Acacia* trees being the most common (Maclean 1973b; Mendelsohn and Anderson 1997). The communal nest mass has several independent nest chambers where breeding takes place and which are also used for roosting throughout the year. Sociable weavers are facultative cooperative breeders and can breed in pairs or with one to five helpers (average group size in our study site was 3.1; Covas et al. 2006). The helpers are most commonly offspring of the breeding pair, but siblings or unrelated birds may also help (Covas et al. 2006). Both males and females may help, although helpers older than 1 year are normally all males (Doutrelant et al. 2004).

This study was conducted at Benfontein Game Farm in the Northern Cape Province, South Africa (approx. 28°53′S, 24°89′E). The study area covers approximately 15 km^2 and contains an approximate total of 30 sociable weaver colonies. The vegetation is Kalahari sandveld, consisting of open savannah dominated by *Stipagrostis* grasses and the camelthorn tree *Acacia erioloba*. The area is semi-arid, experiencing low and unpredictable rainfall (average 431±

127 mm/year, C.V.=35.4; Weather Bureau, Pretoria). Most of the precipitation in the study area falls during the summer months, from September to April, when breeding usually takes place. The study was conducted over two breeding periods lasting 9 and 5 months (September 1999– May 2000 and September 2000–January 2001). These periods experienced contrasting rainfall conditions within and between seasons; the difference in the duration of the breeding periods resulted essentially of the first year receiving 25% more rainfall than average, whereas the second year received 20% less than average.

Field methods

During the study period, we monitored 19 colonies where we marked 1,598 individuals (comprising both adults and nestlings) with a uniquely numbered aluminium ring and a unique colour combination. A significant proportion of adults in the population was already ringed as a result of a mark-recapture study initiated in 1993 (Covas et al. 2002; Brown et al. 2003; Covas et al. 2004a). Colonies used in experiments in a given year (Covas et al. 2004b; Covas and du Plessis 2005) were excluded from the present study. The resident birds at the study colonies 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. A proportion of colony members sometimes failed to get caught (up to 30%), but these individuals were subsequently targeted at the nest using a hand net in an effort to mark the totality of residents.

During the two breeding seasons included in this study, we monitored unmanipulated individual nesting attempts of 240 pair-years and confidently determined group composition for 94 pairs. To identify the individuals feeding at a given nest and record feeding rates, we conducted observations from a hide placed 2–5 m from the colony. Sociable weavers seemed oblivious of the observer once under the hide. For each nesting attempt, we first conducted observations for 2–3 days to identify the individuals feeding at a given nest and habituate the birds to the hide. Subsequently, when the nestlings were 7–17 days old, we conducted additional observations for 3 h on three consecutive days to record the feeding rate of each individual attending the nest (the effect of age was controlled for statistically, see below). When we failed to identify the individual responsible for a specific feeding visit, we nonetheless included that visit in the total feeding rate. Groups were usually stable within seasons, but the proportion of nests attended by pairs with and without helpers varied between years. In the first year, only 30% of the breeding pairs had helpers (n=43 groups), while 82% of the breeding pairs were assisted by helpers in the second year (n=51 groups). The higher number of

helpers in the second year seemed to result of a higher reproductive success in the first year, since most of those helpers were offspring of the breeding pair (Covas et al. 2006). In addition, under harsher conditions, more individuals might have failed to breed and acted as helpers instead (see Covas et al. 2004b).

All nest chambers in each 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. The nest mass was reached from the roof of a pick-up truck or from a step ladder (or both). To inspect the contents of each nest chamber, we used a small round mirror fitted with a lamp. Sociable weaver eggs usually hatch asynchronously at 1-day intervals. Nests were visited daily near the hatching date until all nestlings had hatched. The nestling period is 21–24 days (Maclean 1973c) and if disturbed from the 18th day onwards the nestlings will usually fledge prematurely (R. Covas, personal observation). To avoid this, we visited the nests for the last time when the oldest nestling was 17 days old. On these occasions, we measured mass, tarsus and wing length and recorded the number of nestlings present; we assumed that the number of nestlings present on day 17 was the number of young fledged from that nest.

To assess loss of eggs and nestlings to predation, we recorded all encounters with snakes during visits to the colonies; other nest predators, such as pygmy falcons, seem to only have a marginal effect on our population (Covas et al. 2004c; R. Covas, personal observation). A nest in a given colony was considered depredated if it was found empty on a visit following a day when a snake was seen foraging at that colony. If no snake was seen at the colony on a previous visit but the contents of two or more adjacent nests suddenly disappeared, these were also considered to have been depredated.

To collect rainfall data in the study area, we used a rain gauge that was read by an observer on a daily basis.

Statistical methods

The aim of our analyses was to understand the causes of variation in reproductive traits and breeding success. We analysed variation in the following dependent variables: (1) clutch size, (2) hatching success, (3) overall feeding rates, (4) parental and (5) helper feeding rates, (6) fledging success per nest, (7) fledging condition, (8) interval between nesting attempts and (9) number of young fledged per season. Since nest predation in our system was very high (see "Results"), we also tested whether there was an effect of the presence of helpers, colony size or year on nest predation rate.

Pairs or groups often make multiple breeding attempts in a season (up to nine clutches laid per pair under sustained

rainfall; Maclean 1973c). In the present study, the weavers made up to eight breeding attempts in the first year (4.9± 1.9) and up to five in the second (2.4±1.1). In addition, pairs were often present in the study for more than 1 year and the nests were clumped in colonies. Hence, there was potential for non-independence within the data. Mixed models are necessary to analyse such data appropriately, since they incorporate random as well as fixed effects (Bennington and Thayne 1994). To control for pair and colony identity, we included the random factor 'pair identity' nested in 'colony' in all the analyses of individual breeding attempts (e.g. clutch size, hatching success). In case of divorce or replacement of one of the breeders, the identity of the remaining breeder was maintained, since it could still influence reproductive traits (two instances in this data set). In the analyses of fledging condition, we additionally included the random term 'brood identity' to control for non-independence within the brood. The random terms were never dropped from the models, even when they were non-significant, since this would inflate the degrees of freedom and hence would revert to pseudo-replication.

Nest predation in this species is normally an all or nothing event, and thus we could only include in the analyses of reproductive parameters nests that did not suffer predation up to that stage. For this reason, the sample sizes vary for the different analyses presented below.

The analyses were conducted in SAS v.8. Continuous data (e.g. fledgling mass) were analysed using Proc Mixed and the normality of residuals from the minimal model was verified. Proportional data (hatching and fledgling success) and data with Poisson distribution (total number of breeding attempts in a season) were analysed after respectively specifying a binomial or a Poisson distribution in GLIMMIX, which is a SAS macro for fitting generalised linear mixed models (GLMM). Modelling began with all factors and pertinent interactions. A final model was selected after sequentially dropping all non-significant terms or interactions, and we present the significance of each term when it was dropped from the model.

Explanatory variables

Helpers In all analyses, the potential effect of helpers was of particular interest. Sociable weavers bred in pairs or in groups of up to seven individuals. The effect of helpers on reproductive output may be additive (i.e. a linear relation-ship) or it can have a significant but non-additive effect (i.e. pairs with helpers do better than pairs alone, regardless of helpers' number). Alternatively, helpers could have a non-linear effect on reproduction, leading to a decline in breeding success in very large groups (e.g. Legge 2000a, b). We found no evidence of this latter possibility and hence it was

no longer considered in the analyses presented here. The effect of helpers on breeding parameters was therefore examined by running analyses treating helpers as a dichotomous factor (pair or group), and a linear variable ('group size'=2–7 individuals). The results obtained in both ways were similar in most analyses performed, with small changes in the values of the statistical tests. We chose to present the results based on 'group type' (pairs alone or pairs with helpers) because it facilitates the interpretation of interactions, but we present the results obtained with 'group size' where different.

Other explanatory variables In addition to group type, the following factors were considered in all models: rainfall (0–189 mm; we used the total amount of rain over the previous 30 days; see Dean and Milton 2001); colony size (12–180 individuals), brood number (1st–8th; to account for a possible decline in breeding effort) and year. In addition, the analyses of fledgling condition and feeding rates also took into consideration the number of nestlings. Finally, the analyses of feeding rate also tested the effect of nestling age. Interactions between 'group type' and the terms 'rainfall', 'colony size' and 'year' were of particular interest and were tested in all analyses.

In the analyses of overall breeding success (number of young fledged per pair per season), we included an additional term to account for variation in predation rates. We devised an 'individual predation index' by adding the total number of broods that had been depredated in a season for each pair and dividing it by the total number of breeding attempts made by that pair in that season.

Results

Of a total of 710 nesting attempts monitored, 546 (77%) failed, with ca. 70% being attributed to snake predation. We never found dead chicks in the nest and hence cannot confidently attribute the disappearance of the remaining 7% nestlings to starvation. We did, however, occasionally find dead or dying nestlings on the ground under the nest and these could have been evicted by the parents under unfavourable breeding conditions (see also Spottiswoode 2007). Boomslangs *Dyspholidus typus* and Cape cobras *Naja nivea* were the most important nest predators and could deplete all nest contents in a colony. We failed to identify any ecological or social factors associated with nest predation probability. A GLMM in Glimmix of the outcome (depredated or not) of individual breeding attempts with binomial distribution and the random term 'nest' nested in 'colony' found no significant relationships between a nest being depredated and colony size, rainfall, helper presence or year. There was, however, a significant

effect of colony identity, with some colonies having significantly higher chances of suffering nest predation than others ($F_{13, 121}=4.70$, $p<0.0001$).

Clutch size

Sociable weavers laid clutches of two to four eggs, rarely five (mean 3.3 ± 0.7, $N=216$ clutches). There was a significant interaction between group type and rainfall, indicating a steeper increase in clutch size in relation to rainfall for pairs breeding alone (Table 1). This suggests that under lower rainfall pairs are more constrained by food availability than pairs with helpers, but the effect was modest (see parameter estimates in Table 1). Clutch size was also higher in the first year (Table 1). The main terms colony size and brood number and the interaction of colony size with group type were not significant and were dropped from the model.

Hatching success

We analysed the proportion of eggs laid that hatched. Average hatching success was 0.86 ± 0.21 (SD) ($n=132$ non-depredated clutches). We found a negative effect of colony size on hatching success ($F_{1, 125}=5.49$, $p=0.021$; estimate$\pm$SE$=-0.01\pm0.004$). All other terms and interactions were not significant.

Feeding rates

The most important determinant of number of total feeding visits to the nest per hour was the number of nestlings being fed (Table 2). We also found a significant effect of the number of helpers feeding at the nest (Table 2). However, the feeding rate did not differ significantly in relation to group type (i.e. parents alone vs. parents with helpers). Closer inspection of the data suggested that this difference might arise from the relatively high feeding rates of a few groups larger than four (data not shown). Nestling age, rainfall, colony size, brood number and the interaction of rainfall and colony size with group type were not significant.

Parents from nests with helpers fed at a lower rate than parents in pairs ($F_{1, 62}=15.65$, $p<0.001$; Fig. 1). Parental feeding rates also increased with the number of young in the nest ($F_{1, 60}=24.95$, $p<0.0001$, estimate$\pm$SE$=1.49\pm0.32$), with rainfall ($F_{1, 60}=38.12$, $p<0.0001$, estimate$\pm$SE$=0.03\pm0.01$) and decreased in the second year ($F_{1, 60}=14.3$, $p<0.001$). Non-significant and dropped from the model were the terms colony size, brood number and the interaction of rainfall and colony size with group type.

The feeding rate of helpers increased with nestling age ($F_{1, 24}=6.0$, $p=0.02$, estimate$\pm$SE$=0.27\pm0.11$). The terms nestling number, rainfall and year were not significant.

Fledging success per nest

Fledging success was analysed as the proportion of hatched eggs that survived to fledging in 67 nests. Average nestling survival per nest from hatching to day 17 was 0.83 ± 0.3 (SD) and the average number of young fledged per nest was 2.23 ± 1.1.

The variation in fledging success was only significantly associated with an interaction between two social factors, colony size and group type ($F_{1, 14}=5.69$, $p=0.032$). This indicated a decrease in fledging success with increasing colony size for pairs alone (slope estimate$\pm$SE$=-0.112\pm0.07$) but not for pairs with helpers (slope estimate$\pm$SE$=0.06\pm0.07$; Fig. 2). In these analyses, we only included colonies ranging in size from 12 to 44 individuals (instead of 12–180) because we had only two data points for the larger colonies and the models were unlikely to fit adequately data that were distributed so scantily over such a wide range. There was also a significant effect of the random effect 'pair identity' nested in 'colony'. Other non-significant terms tested were rainfall, brood number, year and the interactions of group type with rainfall and year.

Fledging condition

The analyses of fledging condition were conducted on body mass using body size indicators (wing and tarsus) as covariates following García-Berthou (2001) and Green (2001). The results obtained were the same regardless of

Table 1 GLMM showing the terms associated with clutch size variation

Minimal model	Num. df	Den. df	F	P	Estimate	Standard error
Intercept					3.412	0.13
Year	1	140	23.81	<0.0001		
1st					3.412	0.13
2nd					2.899	0.24
Group type×rainfall	1	140	4.11	0.045		
Pairs					0.006	0.002
Groups					0.002	0.002

$N=216$ clutches

Table 2 Terms associated with variation in overall feeding rate per nest per hour obtained by GLMM

N=51 nests

Minimal model	Num. *df*	Den. *df*	*F*	*P*	Estimate	Standard error
Intercept					0.75	2.64
Number of nestlings	1	39	20.74	<0.0001	2.97	0.65
Group size	1	39	8.37	0.006	1.74	0.6

whether only one or both body size indicators were included in the model. The analyses were conducted on 169 fledglings from 77 broods.

Fledging condition was influenced by the interactions of group type with year ($F_{1, 87}$=5.39, *p*=0.023) and group type with rainfall ($F_{1, 87}$=4.33, *p*=0.04). The slope estimates indicated that the condition of young fledged increased with rainfall for pairs alone (slope estimate= 0.02±0.01) but not for groups (slope estimate=−0.0003± 0.01). Hence, there appears to be a positive effect of helpers when conditions are poorer, which is the most common situation in our study area (Fig. 3). The random term 'brood identity' was significant. Other non-significant terms tested were colony size, brood number and the interaction of group type with colony size.

Inter-nesting interval

The number of days between the end of a nesting attempt and the initiation of the next clutch in the same season depended on the fate of the previous brood, and varied between years. The intervals were generally shortest if the brood failed during incubation (9.2±5.3, *n*=13; mean±SD), intermediate when the brood failed during the nestling phase (13.5±10.7, *n*=15) and longest after a successful brood (32.0±16.2, *n*=25; $F_{2, 49}$=20.61, *p*<0.0001). The intervals were also generally longer during the second year (1st year, 19.3±14.8, *n*=27; 2nd year, 23.2±17.8, *n*=26; $F_{1, 47}$=3.89, *p*=0.054). There were no effects of helpers, rainfall, colony size or related interactions.

Seasonal breeding success

Seasonal breeding success (total number of young fledged per pair per season) was generally low (average 2.0±1.6; *n*=77). In both years, the number of young fledged increased significantly with group size ($F_{1, 56}$=8.34, *p*= 0.006; 0.27±0.09; Fig. 4a). This result was valid regardless of whether we analysed each year separately or included both years and a 'year' effect in the model. However, there was no significant effect of presence of helpers alone. This difference is probably due to the very high success of groups larger than three in the first year and larger than four in the second year (cf. Fig. 4a). In addition, breeding success was significantly higher in the first year, when the breeding season was longer ($F_{1, 56}$=51.49, *p*=<0.0001; 1st year [9 months]=1.64±0.33; 2nd year [5 months]=0.36± 0.18 [estimate±SE]) and declined with both nest predation ($F_{1, 56}$=23.5, *p*<0.001; −1.06±0.22) and colony size ($F_{1, 56}$=4.62, *p*=0.036; −0.017±0.01; Fig. 4b). As above, in these analyses, we only included colonies ranging in size from 12 to 44 individuals.

Discussion

We found that reproductive output in sociable weavers was primarily influenced by nest predation. Nest predators were
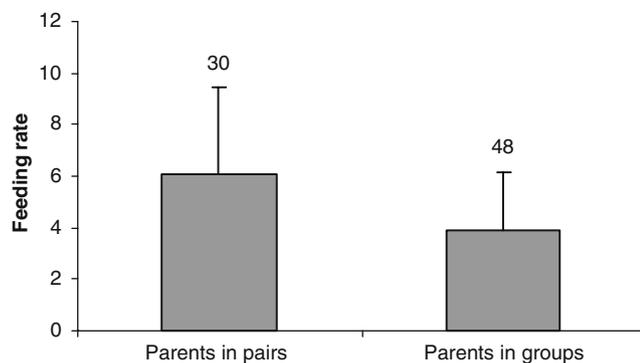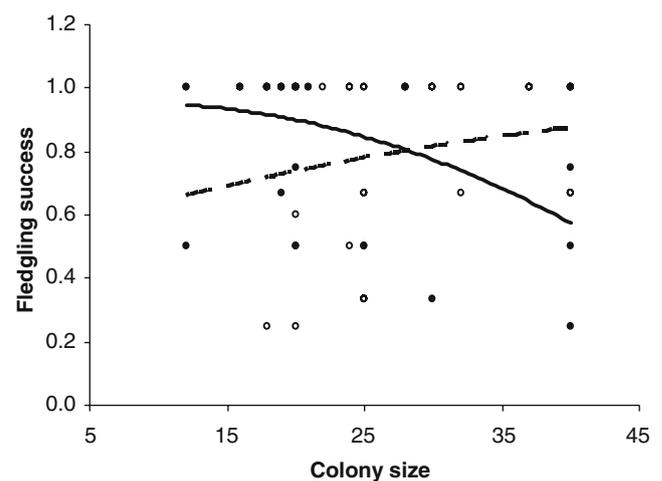

Fig. 1 Parents assisted by helpers fed at a lower rate than pairs breeding alone. *Bars* represent means and SD of data. Sample sizes are given *above the bars* and refer to the number of individuals observed in each category

Fig. 2 Fledging success decreased in relation to colony size for pairs (*black circles*, *solid line*) but not for pairs with helpers (*open circles*, *dashed line*). *Lines* indicate the predicted values. See text for parameter estimates
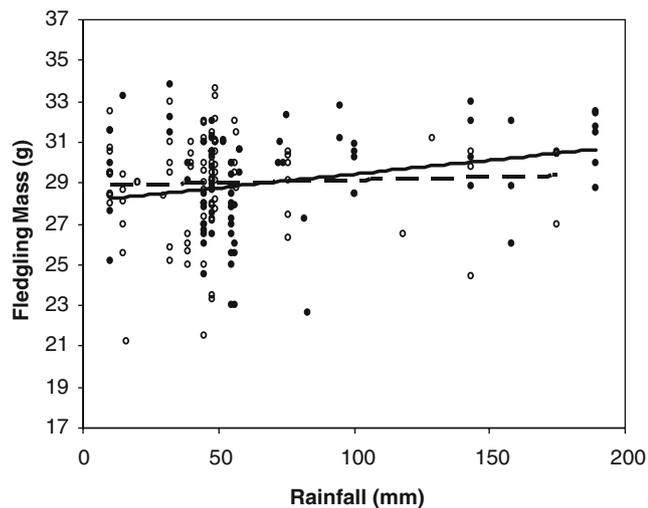
Fig. 3 Fledging mass increased in relation to rainfall for pairs nesting on their own (*black circles*, *solid line*) whereas it remained essentially constant for pairs with helpers (*open circles*, *dashed line*). See text for parameter estimates. The analyses were conducted with wing and tarsus as covariates to control for body size

the main reason for nesting failure, taking approximately 70% of the broods laid. The nests that avoided predation were significantly affected by rainfall, colony size and the presence of helpers. Rainfall, which is one of the main determinants of food availability, had a positive effect on fecundity and fledging condition, while colony size was in general negatively associated with breeding performance. The presence of helpers influenced feeding rates and had a positive effect on reproductive outcome. However, the effect of helpers was usually only detectable under adverse breeding conditions. When rainfall was low, pairs with helpers laid slightly larger clutches than pairs alone and fledged young in better condition. In addition, fledging success was higher for pairs with helpers than for pairs alone when breeding in large colonies, where breeding success was lower. Finally, in both years studied, the overall number of young fledged increased with group size.

Colony size effects

The negative effect of colony size on hatching and fledging success and seasonal breeding success found in this study may be related to greater levels of food depletion and parasite loads at larger colonies (see Brown and Brown 2001; Spottiswoode 2007). Longer foraging trips could lead to longer periods off the nest, deficient incubation and ultimately to increased hatching failure. Increased extent of food depletion around the colony may also cause a decline in nestling condition (Marsden 1999; Tella et al. 2001), which may eventually lead to the death of nestlings causing the lowered fledging success observed in the present study for pairs breeding alone. However, we did not detect a

decrease in feeding rates in relation to colony size. Still, our measure of feeding effort might have been incomplete; the additional inclusion of food load and/or prey type could have been more revealing. In addition, nestlings from large sociable weaver colonies experience higher parasite levels (Spottiswoode 2007). This might explain the lower success per brood and overall lower numbers of young fledged found here for larger colonies. In addition, the decrease in production of fledglings in larger colonies could be related to larger colonies attracting more predators, as was found in other studies on sociable weavers (Marsden 1999; Spottiswoode 2007). However, although in this present study we found that some colonies suffered significantly
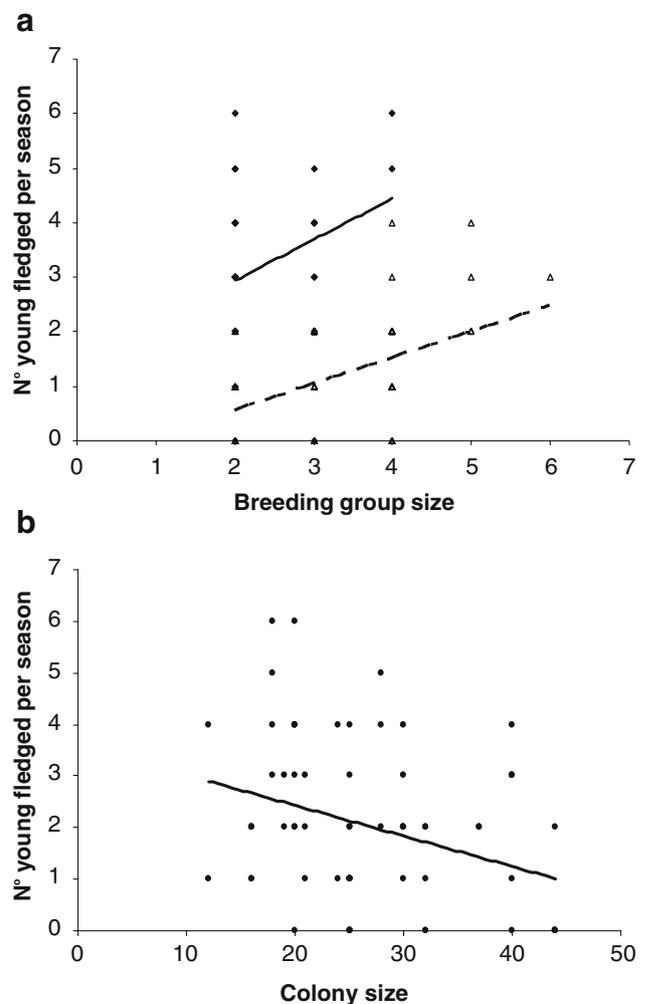

Fig. 4 a The overall number of young fledged per season increased with number of helpers attending the brood. See text for parameter estimates. This result was valid in both years of the study although the duration of the breeding season varied: 1999 (*black dots*, *solid line*) breeding continued for nine months; in 2000 (*open triangles*, *dashed line*) the breeding season lasted 5 months. **b** The number of young fledged per season declined in relation to increasing colony size (i.e. number of birds in the colony)

higher predation than others, there was no relationship between predation rates and colony size.

Helper effects

Understanding the effects of helpers on reproductive success is central for understanding the adaptive nature of cooperative breeding. However, this task can be difficult for several reasons. First, in analyses of reproductive success in cooperative breeders true positive effects of helpers can be difficult to separate from parental or territory quality (see Legge 2000a, b; Doerr and Doerr 2007). 'Good quality' parents or parents inhabiting good territories could produce more offspring that might become helpers at subsequent broods, creating an artificial relationship between the number of helpers and reproductive output (Cockburn 1998; Magrath 2001). This problem is unlikely to confound our results for two reasons. First, sociable weavers are non-territorial. The whole colony normally forages communally, and birds from different colonies may sometimes forage together (R. Covas, personal observation). Thus, individuals in a colony experience similar conditions and there are no strict boundaries with the feeding areas of other colonies; the effects of territory quality are therefore unlikely to be as important as in socially territorial species. Second, parental and colony identities were controlled for statistically in all models, thus accounting for the variation associated with these factors, and these terms had no effect on the majority of the breeding parameters tested. However, our power to detect parental effects was sometimes low, since not all pairs reached the nestling stage several times. Nonetheless, there was an effect of the random term 'pair identity' nested in 'colony' on the analyses of fledging success. This result is unlikely to be explained by the particularly high predation rates at some colonies because these analyses were based on non-depredated broods. It might be related to other unidentified colony effects or to parental and/or helper effects, for example, if some individuals or groups are more experienced than others. Unfortunately, at this stage, we cannot distinguish between these possibilities. Longer term data with a larger number of observations per individual should allow a better understanding of the role of individual and colony characteristics in this system.

Another difficulty in detecting helper effects on reproductive output is that parents might reduce their investment in the presence of helpers. Additionally, helpers might provide significant assistance only under unfavourable conditions, their effects going unnoticed otherwise. Hence, helper effects might be very subtle (see also Russel et al. 2007). We investigated these two issues by analysing overall and parental feeding rates in the presence and absence of helpers, and the effect of helpers on reproductive output under variable environmental conditions. First, we found that the breeding pairs generally reduced their feeding rate in the presence of helpers. This implies that helpers are effective in lightening the work loads of parents. Lower work loads during the nestling stages might allow parents to invest more into reproduction, for example, by reducing the interval between nesting attempts or increasing fecundity. We found no evidence in favour of the former possibility. We did, however, find evidence suggesting that pairs with helpers lay slightly larger clutches when rainfall was low, although the effect was small. In addition, load lightening in this species might contribute towards improved survival, but this hypothesis remains to be tested.

Second, the effect of helpers on reproductive parameters was mainly detectable under unfavourable conditions such as under low rainfall and when breeding in large colonies. This result is particularly interesting because it suggests a specific positive effect of helpers where needed. It is also consistent with the results of a brood size manipulation in sociable weavers (Covas and du Plessis 2005), which suggested a positive effect of helpers specifically in situations of greater demand. In that study, the number of helpers was associated with increased feeding rates at enlarged, but not control nests and helpers were associated with decreased mortality and improved fledging success. A similar result was also obtained by a correlative study on a cooperatively breeding mammal, the meerkat *Suricata suricatta*. Russell et al. (2002) found that interactions between environmental and social factors had a strong influence in reproductive parameters, even replacing to some extent the maternal factors that are typically important in mammals. Like sociable weavers, meerkats inhabit the highly variable semi-arid Kalahari regions. In this species, larger groups helped buffer the effects of extreme temperatures, which resulted in pups losing less weight during cold nights and influenced weight at independence. In birds, the effects of helpers are usually related to the extra food brought to the nest by helpers (e.g. Hatchwell 1999; Legge 2000a, b; Canestrari et al. 2008; see also Russell et al. 2007). In a study based on a comparative analysis of cooperative breeders, Hatchwell (1999) suggested a mechanism for the effects of helpers under adverse conditions, by showing that helpers' effects on provisioning are additive when brood reduction is high, but when it is not, parents may reduce their workloads in the presence of helpers. In sociable weavers, the mechanism through which helpers improve reproductive success is still unclear. Unlike what was expected, we did not find a specific effect of helpers on overall feeding rates under low rainfall or in larger colonies. We did, however, find an increase in helpers' feeding rate with nestling age, showing that helpers contribute more towards the needs of the brood in a situation when its demands are higher. As mentioned above, a limitation of

this study might have been an incomplete assessment of food provisioning behaviour, since we did not analyse variation in feeding loads and types of prey brought to the nest, which might be a more adequate measure than feeding rate. More study is needed to understand the exact mechanisms of investment by parents and helpers under different conditions to produce the results observed here. This means studying feeding behaviour in more detail but also investigating other factors affecting variation in reproductive outcome, such as maternal investment in eggs (see Russell et al. 2007) under varying environmental and social conditions.

In addition to the effects of helpers under lower rainfall and in larger colonies, we found an overall effect of the number of helpers on seasonal reproductive output. This result is interesting because it was significant even though it was based on data for the entire season, which includes a large number of depredated clutches. However, it should also be seen with caution since this result was not detected simply based on presence–absence of helpers, as for analyses of single nesting attempts, but only when we analysed our data in relation to breeding group size. This implies the effect might only be valid for large groups. In addition, this result was based on two seasons, but that is a relatively small sample compared to the within-season analyses presented. Ideally, breeding data should be obtained for sociable weavers over several breeding periods to allow a better testing of the effects of helpers on seasonal reproductive output as well as on the interaction of season quality and helper presence.

It has been proposed that cooperative breeding could be an important adaptation under variable breeding conditions, since it might help to buffer the effect of adverse conditions, while it may go unnoticed under good conditions (Cockburn 1998; Hatchwell 1999; Magrath 2001; Rubenstein and Lovette 2007). We took advantage of high social and inter-seasonal variation in breeding conditions to test these effects in sociable weavers. The results obtained in this study provide support to the suggestion that the positive effects of helpers might be mostly detected under adverse conditions. Hence, future studies on the effects of helpers on reproductive success should not overlook this possibility. Given that selection is likely to exert stronger pressure under unfavourable conditions, such effects of helpers could be an important mechanism promoting the maintenance of helping behaviour.

References

Bennington CC, Thayne WV (1994) Use and misuse of mixed model analysis of variance in ecological studies. Ecology 75:717–722

Brown CR, Brown MB (2001) Avian coloniality: progress and problems. Curr Ornithol 16:1–81

Brown CR, Covas R, Anderson MD, Brown MB (2003) Multistate estimates of survival and movement in relation to colony size in the sociable weaver. Behav Ecol 14:463–471

Canário F, Matos S, Soler M (2004) Environmental constraints and cooperative breeding in the Azure-winged Magpie. Condor 106:608–617

Canestrari D, Marcos JM, Baglioni V (2008) Reproductive success increases with group size in cooperative carrion crows, *Corvus corone corone*. Anim Behav 75:403–416

Clutton-Brock TH, Gaynor D, McIlrath GM, MacColl ADC, Kansky R, Chadwick C, Manser M, Skinner JD, Brotherton PNM (1999) Predation, group size and mortality in a cooperative mongoose, *Suricata suricatta*. J Animal Ecol 68:672–683

Cockburn A (1998) Evolution of helping behaviour in cooperatively breeding birds. Ann Rev Ecol Syst 29:141–177

Covas R, du Plessis MA (2005) The effect of helpers on artificially increased brood size in sociable weavers (*Philetairus socius*). Behav Ecol Sociobiol 57:631–636

Covas R, Brown CR, Anderson MD, Brown MB (2002) Stabilizing selection on body mass in the sociable weaver *Philetairus socius*. Proc R Soc Lond B 269:1905–1909

Covas R, Brown CR, Anderson MD, Brown MB (2004a) Juvenile and adult survival in the sociable weaver (*Philetairus socius*), a southern-temperate colonial cooperative breeder in Africa. Auk 121:1199–1207

Covas R, Doutrelant C, du Plessis MA (2004b) Experimental evidence of a link between breeding conditions and the decision to breed or to help in a colonial cooperative breeder. Proc R Soc Lond B 271:827–832

Covas R, Huyser O, Doutrelant C (2004c) Pygmy Falcon predation of nestlings of their obligate host, the Sociable Weaver. Ostrich 75:325–326

Covas R, Dalecky A, Caizergues A, Doutrelant C (2006) Kin associations and direct vs. indirect genetic benefits in sociable weavers *Philetairus socius*. Behav Ecol Sociobiol 60:323–331

Curry RL, Grant PR (1990) Galápagos mockingbirds: territorial cooperative breeding in a climatically variable environment. In: Stacey PB, Koenig WD (eds) Cooperative breeding in birds. Cambridge University Press, Cambridge, pp 291–331

Dean WRJ, Milton SJ (2001) Responses of birds to rainfall and seed abundance in the southern Karoo, South Africa. J Arid Environ 47:101–121

Doerr ED, Doerr VAJ (2007) Positive effects of helpers on reproductive success in the brown treecreeper and the general importance of future benefits. J Anim Ecol 76:966–76

Doutrelant C, Covas R, Caizergues A, duPlessis MA (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

Eguchi K, Yamagishi S, Asai S, Nagata H, Hino T (2002) Helping does not enhance reproductive success of cooperatively breeding rufous vanga in Madagascar. J Animal Ecol 71:123–130

Emlen ST (1990) White-fronted bee-eaters: helping in a colonially nesting species. In: Stacey PB, Koenig WD (eds) Cooperative breeding in birds. Cambridge University Press, Cambridge

Emlen ST (1991) The evolution of cooperative breeding in birds and mammals. In: Krebs JR, Davies NB (eds) Behavioural ecology: an evolutionary approach. 3rd edn. Blackwell Scientific, Oxford, pp 301–337

García-Berthou E (2001) On the misuse of residuals in ecology: testing regression residuals vs. the analysis of covariance. J Animal Ecol 70:708–711

Green AJ (2001) Mass/length residuals: measures of body condition or generator of spurious results. Ecology 82:1473–1483

Griffin AS, West SA (2003) Kin discrimination and the benefit of helping in cooperatively breeding vertebrates. Science 302:634–636

Harrison JA, Allan DG, Underhill LG, Herremans M, Tree AJ, Parker V, Brown CJ (1997) The atlas of Southern African birds, 1st edn. Birdlife South Africa, Johannesburg

Hatchwell BJ (1999) Investment strategies of breeders in avian cooperative breeding systems. Am Nat 154:205–219

Koenig WD, Mumme RL (1987) Population ecology of the cooperatively breeding acorn woodpecker. Princeton University Press, Princeton

Legge S (2000a) Helper contributions in the cooperatively breeding laughing kookaburra: feeding young is no laughing matter. Animal Behaviour 59:1009–1018

Legge S (2000b) The effect of helpers on reproductive success in the laughing kookaburra. J Animal Ecol 69:714–724

Lloyd P (1999) Rainfall as a breeding stimulus and clutch size determinant in South African arid-zone birds. Ibis 141:637–643

Maclean GL (1973a) The sociable weaver, part 1: description, distribution, dispersion and populations. Ostrich 44:176–190

Maclean GL (1973b) The sociable weaver, part 2: nest architecture and social organisation. Ostrich 44:191–218

Maclean GL (1973c) The sociable weaver, part 3: breeding biology and moult. Ostrich 44:219–240

Maclean GL (1973d) The sociable weaver, part 5: food, feeding and general behaviour. Ostrich 44:254–261

Magrath RD (2001) Group breeding dramatically increases reproductive success of yearling but not older female scrubwrens: a model for cooperatively breeding birds. J Animal Ecol 70:370–385

Marsden RM (1999) Coloniality in the sociable weaver *Philetairus socius*. In: Animal and plant sciences. Sheffield University, Sheffield, pp 104

Mendelsohn JM, Anderson MD (1997) Sociable weaver *Philetairus socius*. In: Harrison JA, Allan DG, Underhill LG, Herremans M, Tree AJ, Parker V, Brown CJ (eds) The atlas of Southern African birds. Birdlife South Africa, Johannesburg, pp 534–535

Rubenstein DR, Lovette IJ (2007) Temporal environmental variability drives the evolution of cooperative breeding in birds. Curr Biol 17:1414–1419

Russell AF, Clutton-Brock TH, Brotherton PNM, Sharpe LL, McIlrath GM, Dalerum FA, Cameron EZ, Barnard JA (2002) Factors affecting pup growth and survival in co-operatively breeding meerkats *Suricata suricatta*. J Animal Ecol 71:700–709

Russell AF, Langmore NE, Cockburn A, Astheimer LB, Kilner RM (2007) Reduced egg investment can conceal helper effects in cooperatively breeding birds. Science 317:941–944

Smith TB (1990) Resource used by bill morphs of an African finch: evidence for intra-specific competition. Ecology 71:1246–1257

Spottiswoode CN (2007) Phenotypic sorting in morphology and reproductive investment among sociable weaver colonies. Oecologia 154(3):589–600

Tella JL, Forero MG, Bertellotti M, Donázar JA, Blanco G, Ceballos O (2001) Offspring body condition and immunocompetence are negatively affected by high breeding densities in a colonial seabird: a multiscale approach. Proc R Soc Lond B 268:1455–1461