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The effect of helpers on artificially increased brood size in sociable weavers (*Philetairus socius*)

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Abstract In cooperatively breeding birds, the presence of helpers is expected to increase the reproductive success of the breeding pair. However, some studies fail to find this effect. A positive effect of helpers may be restricted to cases in which a breeding pair has a poor likelihood of raising the entire brood on its own, as would be the case under stressful environmental conditions or with enlarged brood sizes. We conducted brood size manipulations in a cooperative breeder, the sociable weaver, *Philetairus socius*, to investigate the relationship between the difficulty of raising nestlings and the effort and impact of helpers. Overall, sociable weavers did not work harder to raise the enlarged broods. However, the presence of helpers significantly increased the feeding rates at enlarged nests, but not controls. This was insufficient to prevent generalised brood reduction in enlarged broods, whether attended by pairs alone or with helpers. Nonetheless, the presence of helpers was associated with decreased nestling mortality and an increase in the numbers of young fledged. Our results suggest that groups are better able to respond to the needs of enlarged broods than pairs alone and that the presence of helpers has a beneficial effect on overall reproductive success.

Keywords Breeding success · Brood size · Helpers · *Philetairus socius* · Sociable weavers

Introduction

In cooperatively breeding species, mature individuals known as ‘helpers’ provide parental care to young that are not their own progeny. Understanding why these non-breeders help has been a central issue in behavioural ecology for over two decades, leading to a long list of potential benefits for both helpers and parents (reviewed in Cockburn 1998). Since most helpers are related to the breeding pair that they help, enhanced production of non-descendant kin (i.e. the indirect component of inclusive fitness; Hamilton 1964) has been seen as a major selective force driving the evolution of helping behaviour. In addition, direct benefits to helpers could play an important role. For example, where survival is higher in larger groups helpers should benefit from helping others to breed if that leads to increased production of young and concomitant increase in group size (e.g. Clutton-Brock et al. 1999).

Most adaptive explanations of helping behaviour predict a positive effect of helper presence on reproductive output. Before proceeding with adaptive explanations for helping, we should therefore address the question of whether helpers increase the breeders’ fitness, and if so, how. This is not a trivial question, since the presence of helpers is not necessarily associated with increased group productivity: about one-third of the studies reviewed in Cockburn (1998) failed to find such an effect.

The tendency to find an effect of group size on reproductive success may depend upon breeder quality or environmental conditions (Magrath 2001). An example of dependence of helper effects upon breeder quality is demonstrated in white-browed scrubwrens (*Sericornis frontalis*). Preliminary analysis of reproductive success failed to detect any effect of group size on reproductive success (Magrath and Yezerinac 1997). However, in a larger sample of birds of known age and breeding experience, the presence of helpers more than doubled the reproductive success of yearling females, while it had no effect on reproductive output of older, experienced females (Magrath 2001). A similar pattern can be expected

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where adverse environmental conditions, such as poor territories or bad years, may depress breeding success and provide the opportunity for helping behaviour to improve reproductive output, while under good breeding conditions there may be no visible effect of helpers simply because there is no major factor that can be ameliorated (Magrath 2001; Covas et al., unpublished data). This discrepancy in the effect of helpers under good conditions could be mediated through feeding behaviour. Hatchwell (1999) found that, in species where nestling starvation is rare, parents may compensate for helper presence by decreasing their own feeding rate, whereas there might be no compensation where brood reduction is common. This 'adverse conditions' effect of helper presence on reproductive success may be widespread (reviewed in Magrath 2001), but has seldom been studied explicitly.

We conducted brood size manipulations on sociable weavers (*Philetairus socius*) to experimentally increase the difficulty of raising a brood and study the effect of helpers under these conditions. The sociable weaver is a colonial cooperatively breeding passerine that inhabits the semi-arid savannas of southern Africa (Maclean 1973b). Previous correlative analyses of reproductive success showed that helpers do not have a significant overall effect on most reproductive parameters, but have a positive effect under adverse conditions. The presence of helpers improved fledging mass when rainfall was low and decreased brood reduction in large colonies, where food seemed more limiting than in small colonies (Covas et al., unpublished data). Hence the role of helpers in this species seems particularly relevant under difficult conditions. Under this hypothesis, nests with helpers should be better able to respond to the needs of enlarged broods than nests attended by pairs alone. Hence we predicted that enlarged broods with helpers would: (1) receive higher provisioning rates; and experience: (2) decreased nestling mortality; (3) improved fledging success; and (4) improved nestling condition, or a combination of these.

Methods

Study area and population

The sociable weaver is a small passerine (26–32 g) endemic to the semi-arid savannas of southern Africa. Sociable weavers feed predominantly on insects and seeds (Maclean 1973a, 1973d; Mendelsohn and Anderson 1997). They are colonial cooperative breeders that communally build a massive nest with separate chambers wherein breeding takes place and where the breeding pair, with their offspring and/or helpers, roost throughout the year. The helpers can be both males and females (although helpers older than 1 year are invariably males; (Doutrelant et al. 2004). Helpers are most commonly offspring, but unrelated birds may also help (Doutrelant, Dalecky, Caizergues, du Plessis and Covas, unpublished data).

The study was conducted at Benfontein Game Farm, situated ca. 6 km south-east of Kimberley, in the Northern Cape Province, South Africa (28°53'S, 24°89'E). The vegetation in the study area consists of open savannah and is dominated by *Stipagrostis* grasses and camelthorn trees (*Acacia erioloba*). The area is semi-arid, experiencing low and unpredictable rainfall (average 431±127 mm

per year, C.V.=35.4, $n=96$ years; Weather Bureau, Pretoria), with most of the precipitation falling during the summer months from September to April.

The study area contains ca. 26 sociable weaver colonies, of which 15–20 colonies were monitored for dispersal and survival since 1993 (Covas et al. 2002, 2004a). During 1998–2001, we conducted a detailed study of breeding characteristics which involved daily visits to nests of colour-ringed individuals (Covas 2002). The experiment was conducted over two breeding seasons, from September 1999 to April 2000 and from September 2000 to January 2001. These two seasons experienced contrasting rainfall conditions; the first year had 25% above average rainfall and the second year had 20% below average rainfall, resulting in conspicuous differences in both reproductive effort and success (Covas 2002; Covas et al., unpublished data). Rainfall was measured in the study site on a daily basis with a rain gauge.

Brood size manipulations

During the breeding season, all nest chambers in each colony were inspected every 4–7 days to detect initiation of new clutches. We used a small round mirror fitted with a torch lamp to inspect the contents of each nest chamber. Sociable weaver eggs usually hatch asynchronously at 1-day intervals. Nests were visited daily from just before hatching until hatching was complete. In the experiment, we used only nests where hatching started the same day. The day the first egg hatched was regarded as day 1. We created enlarged broods by removing two 1- to 3-day-old chicks from nests assigned to the "reduced" treatment and adding them to the "enlarged" treatment. Treatment was assigned to nests at random, but the choice of nests was constrained by hatching patterns. For example, when hatching occurred simultaneously at only two nests and one egg failed to hatch in one of these, this nest could no longer become an enlarged nest, although two chicks from that nest could be used to create an enlarged brood elsewhere. No enlarged brood ever exceeded the maximum natural brood size of six and no broods were ever depleted; i.e. 2-egg clutches were never used as donors of nestlings. Control broods were created by swapping two chicks (one first- and one last-hatched chick) between two broods without altering the size of those broods.

Because hatching is normally asynchronous, there is a natural size hierarchy in broods and it appears that smaller chicks experience higher mortality (Covas et al., unpublished data). It was therefore important to maintain the degree of asynchrony in enlarged broods in order to minimise the impact of differences in size hierarchy on survival probabilities of nestlings. We mimicked this size pattern by always adding a first-hatched and a last-hatched chick to create the enlarged broods. This approach might have affected mortality patterns or provisioning rates and these possible effects are taken into account in the interpretation of the results obtained.

To collect data on feeding rates and identify all the individuals feeding at a given nest we conducted observations from under a hide placed 3–5 m from the colony. The observations lasted 1–2 h and were conducted between 0700 and 1000 hours (GMT+2) for 4 days, when nestlings were 3–6 days old. During the observation period, the contents of the nest chambers were inspected daily to verify the number of chicks present. If more than one chick disappeared the nest was excluded from analysis of feeding rates. Nests were visited again on day 9, when the number of nestlings was recorded, and on day 17, when all nestlings were measured and ringed. Although the nestling period lasts 21–24 days, nestlings will usually fledge prematurely if disturbed after day 17, so we made the assumption that the number of nestlings present at day 17 represented the number fledged.

We assumed that if at least one nestling was present in the nest during a given visit, the nest had not suffered predation. Predation is very high in this species (Maclean 1973c; Marsden 1999; Covas 2002), with over 70% of the broods in a season being taken by predators (Covas 2002). The main nest predators are snakes (boomslangs *Dispholidus typus* and Cape cobras *Naja nivea*; Ma-

clean 1973c; Marsden 1999; Covas 2002), which normally take the whole brood (R. Covas, personal observation).

Statistical methods

We manipulated a total of 63 broods. Due to high nest predation, the sample sizes decreased markedly during the nestling period and only 28 broods fledged young (12 controls, 11 enlarged and 5 reduced). Therefore the sample sizes vary for different analyses.

The sociable weavers made several breeding attempts in both seasons and most individuals were present in the area in both years of the study. To guarantee independence of data only one manipulation was conducted for any breeding pair. Yet, if the brood got depredated before day 6 that pair was randomly reassigned to a treatment; this happened in only two instances.

Statistical analyses were aimed at investigating what factors were associated with variation in: (1) feeding rates; (2) survival to day 9 (first stage of the nestling period); (3) survival from day 9 to day 17 (second stage); (4) nestling mass on day 17; and (5) number of young fledged per nest. The following explanatory variables were considered in all models: group size (i.e. number of birds attending the nest), treatment, year and the interaction group size \times treatment. Initially, rainfall over the 30-day period prior to the day when measuring and counting the chicks took place was also included, since this was found to be significantly associated with measures of reproductive success presented elsewhere (Covas et al., unpublished data). However, rainfall had no significant effect on this experiment and it was dropped from all models.

Sociable weavers are colonial and several manipulated nests can occur in the same colony. We used mixed models specifying 'colony' as a random factor to account for possible dependence of data. In addition, the analyses of fledging mass included several chicks from the same nest. To take this into account we included a random term 'nest identity' nested within 'colony'. However, non-significant random terms were dropped from the analyses because it is best to obtain the most parsimonious and powerful model possible.

Analyses of nestling survival (from manipulation to day 9 and from day 9 to day 17; binomial distribution) and number of young fledged (Poisson distribution) were initially analysed with Glimmix, a macro for fitting generalised linear mixed models in SAS v.8. However, the random term 'colony' was not significant, and these analyses were repeated, without the random term, in Proc Genmod, the SAS procedure to fit generalised linear models, which allows to control for over-dispersion by specifying the 'dscale' option.

Continuous variables (feeding rate and fledgling mass) were analysed using Proc Mixed in SAS v.8. Proc Mixed allows fitting a

variety of mixed linear models using the restricted maximum likelihood method. Feeding rate data were log-transformed to improve normality and reduce heterogeneity of variances. Analyses of nestling condition were performed using body mass as the dependent variable and both wing and tarsus as covariates to control for differences in age and body size between nestlings.

In all analyses modelling began with all factors in addition to the interaction. A final model was selected after sequentially dropping all non-significant terms, with the significance of terms being determined when the term was dropped from the model. A post-hoc *t*-test was conducted to analyse which levels of the treatment differed significantly. Only significant results are presented.

Results

Feeding rate

Overall, sociable weavers did not work harder to raise enlarged broods (Fig. 1). Although there was an effect of brood size treatment on feeding rates, only reduced broods differed significantly in receiving fewer feeding visits than controls and enlarged broods ($F=3.96$, $df=2,17$, $P=0.0387$; 'control' vs 'reduced': $t=2.34$, $df=17$, $P=0.0320$; 'enlarged' vs 'reduced': $t=2.65$, $df=17$, $P=0.0169$; Fig. 1). There was no significant difference between the feeding rates of control and enlarged broods ($t=-0.57$, $df=17$, $P=0.58$). However, there was a significant interaction between treatment and total number of individuals attending the nest, showing that the number of helpers significantly increased the feeding rates at enlarged nests ($F=3.85$, $df=2,14$, $P=0.0465$; Fig. 2). The effect of group size on feeding rates when considering all nests combined was in the predicted direction, but it was not statistically significant ($F=3.85$, $df=1,16$; $P=0.0674$; Fig. 2).

Nestling mortality

Sociable weavers never raised a fully enlarged brood and in only three out of eleven nests did one extra chick fledge

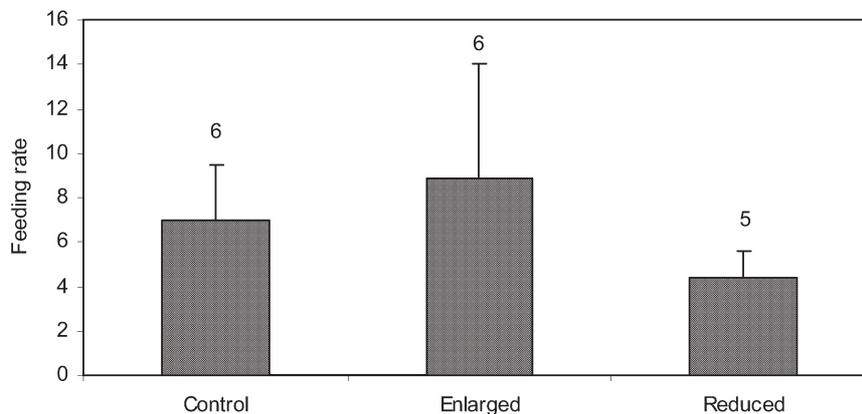


Fig. 1 Overall feeding rates (number of visits to the nest per hour) in enlarged, reduced and control broods of sociable weavers (*Philetairus socius*). There were no significant differences between

enlarged and control broods, but reduced broods differed significantly from the two other treatments. Bars represent mean and SD of data. Sample sizes are shown above the bars

Fig. 2 Feeding rates (feeding trips h^{-1}) increased significantly in relation to group size at enlarged nests (\square ; large dashed line), but not at control (\blacklozenge ; solid line) and reduced ----; small dashed line) ones. ($n=17$)

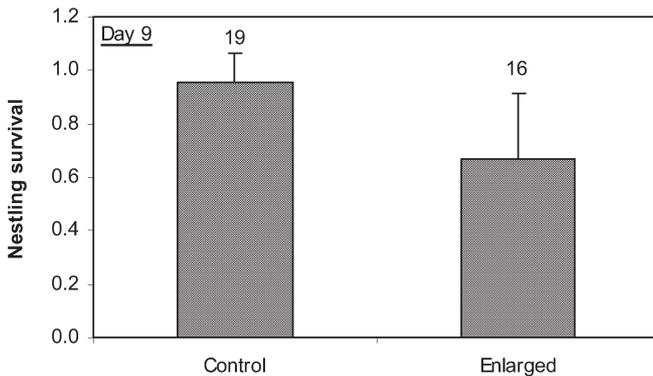
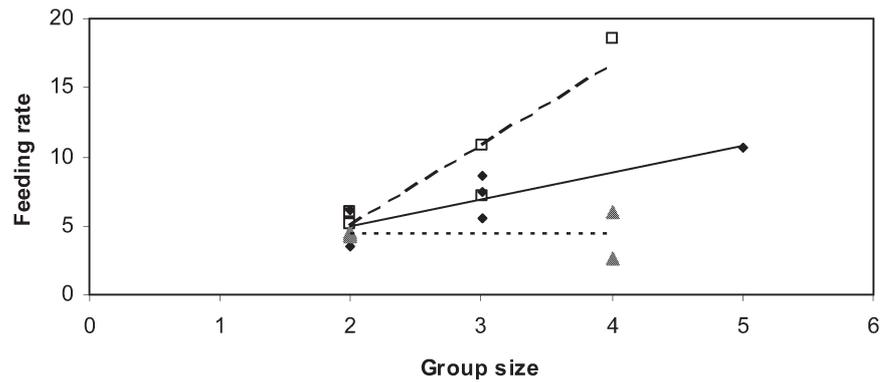
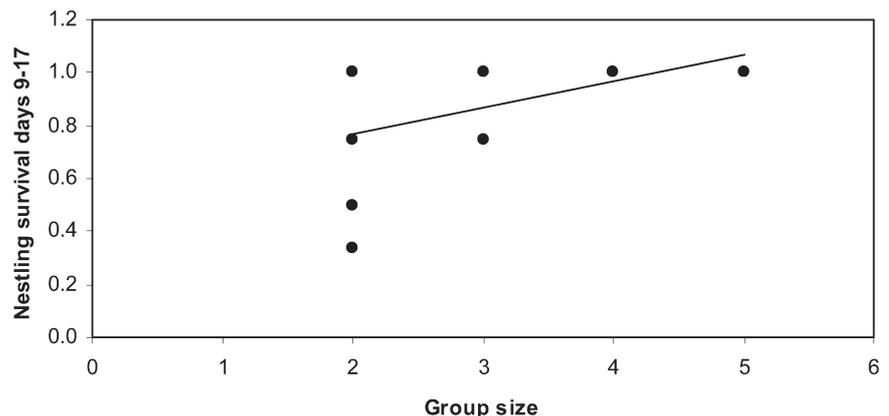


Fig. 3 Nestlings survival to day 9 was significantly lower in enlarged broods. Bars represent mean and SD of data and sample sizes are shown above the bars

(i.e. in 27% of the enlarged nests). Deaths in enlarged broods occurred early in the nestling period. By day 9, less than halfway through the nestling period, there was already a significant effect of treatment on nestling survival ($F=17.91$, $df=1,33$, $P=0.0002$; Fig. 3a). On day 9, enlarged broods did not have significantly more nestlings than did control broods ($F=3.79$, $df=1,25$, $P=0.063$), because enlarged broods suffered a disproportionately high frequency of early brood reduction.

The factors affecting nestling mortality changed in the second half of the nestling period. The effect of treatment was no longer significant, while the presence of helpers

Fig. 4 During the second half of the nestling period, nestling survival in both control and enlarged broods increased in relation to the number of helpers attending the brood. Nestling survival in this analysis was calculated as the proportion of nestlings in manipulated broods that survived from day 9 to day 17. ($n=13$)



resulted in increased nestling survival ($F=7.63$, $df=1,11$, $P=0.0185$; Fig. 4).

Considering all nests combined, more young fledged from nests with helpers than from nests attended by pairs alone ($F=5.43$, $df=1,10$, $P=0.042$; Fig. 5). Production of fledglings was also higher in the first year of the study, when conditions were generally better ($F=4.86$, $df=1,10$, $P=0.052$; number of fledglings per nest in 1999: 2.71 ± 0.95 , $n=8$; in 2000: 2.20 ± 1.10 , $n=5$).

Fledgling condition

Brood enlargement had a negative effect on fledgling condition ($F=4.62$, $df=2,18$, $P=0.0241$; Fig. 6). Only enlarged broods differed significantly from controls ($t=2.86$, $df=14$, $P=0.0125$). There were no significant differences between control and reduced nests ($t=-0.37$, $df=14$, $P=0.72$) or between enlarged and reduced nests ($t=-1.76$, $df=14$, $P=0.10$). The number of helpers had no significant effect on fledgling condition.

Discussion

Our results show a significant positive effect of helpers' presence on provisioning rates, nestling survival in the second stage of the nestling period and overall number of young fledged. According to predictions, there was a positive interaction between group size and treatment

Fig. 5 The overall number of young fledged increased in relation to group size (control and enlarged broods combined; $n=13$). There was also an effect of 'year' on this parameter (see text)

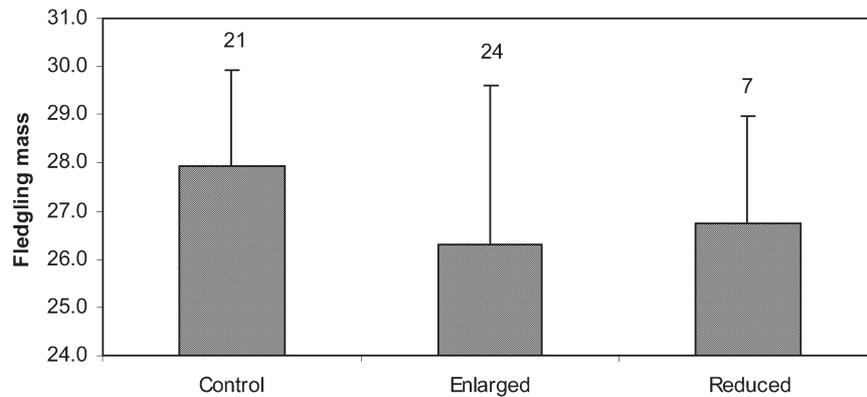
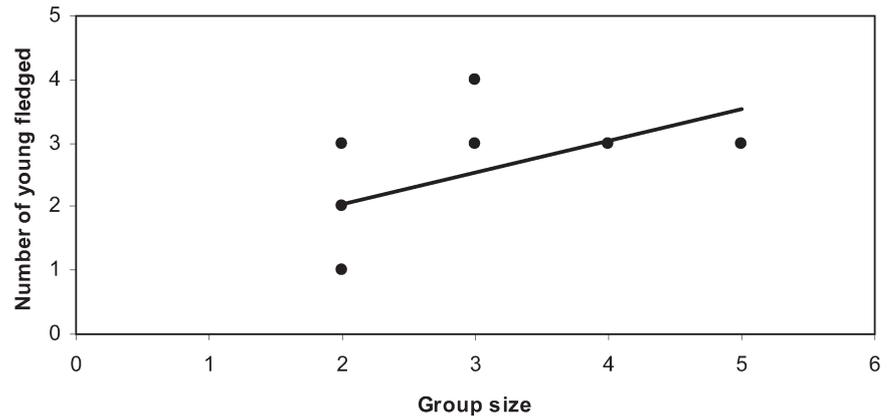


Fig. 6 Fledgling body mass was significantly lower in enlarged (E) than in control (C), and reduced (R) broods. Bars represent mean and SD of data; Sample sizes are shown above the bars. Nestlings of different ages were present in the nest AT day 17 as a conse-

quence of hatching asynchrony. This was controlled for in the analyses by including wing and tarsus as covariates (see Statistical Methods)

showing that the presence of helpers improved the feeding rates at enlarged nests more than at control nests. The latter result should be interpreted with caution; while it is based on data obtained from a controlled and randomised experiment, the sample size is small.

The brood enlargement had a significant effect on nestling survival to day 9, to such an extent that on this day the difference in number of chicks present in control and enlarged broods was no longer significant. This high mortality could, to some extent, have been affected by our manipulation which increased the degree of asynchrony within the broods. This, in turn, would have reduced the chances of survival of smaller nestlings. While we cannot rule out this possibility, it can also be argued that increasing the number of small, weaker, chicks increases the potential for helpers to help (but see below). Moreover, brood reduction occurs naturally in our population (in another study, 34% of broods lost 1–3 nestlings; Covas et al., unpublished data) and hence our experiment did not introduce an unnatural cause of nestling mortality. The results indicate low success of sociable weavers in raising the enlarged broods and this is expressed early in the nestling phase. As helpers appeared to increase their feeding investment when broods were enlarged, failure to raise enlarged broods could be due either to a strong

environmental constraint on the number of nestlings raised, or to the unwillingness of parents to increase their effort, perhaps to avoid future fecundity or survival costs (see also Covas et al. 2004b).

In spite of the fact that our brood enlargements caused a specific increase in feeding rates at nests with helpers, our results were not in agreement with the hypothesis that helpers have a prominent role in species that experience brood reduction (Hatchwell 1999), since brood reduction in enlarged broods remained prevalent. This could have happened for two non-exclusive reasons. First, if helping bears a cost to helpers (Heinsohn and Legge 1999; Russell et al. 2003), they may exhibit restraint in responding to the increased demands of enlarged broods. Second, it is possible that our adding two nestlings adjusted the natural size distribution of broods enough that helpers could not compensate for the greater asynchrony in enlarged broods. Nonetheless, after this initial brood reduction, the number of helpers had a significant effect on nestling survival.

In summary, we show a beneficial effect of helpers' presence on provisioning rates when broods were enlarged, which is consistent with the hypothesis that the presence of helpers might be particularly beneficial when the demands of the brood are higher and provides support

to correlative results presented elsewhere (Covas et al., unpublished data). However, this was insufficient to prevent dramatic brood reduction in broods enlarged by two chicks. Still, the presence of helpers significantly and positively affected nestling survival (during the latter stage of the nestling period), and the overall number of young fledged. Hence, helpers appear to have a moderate positive effect on reproductive success in sociable weavers, but this effect might be of little consequence during the early nestling period when brood reduction is most likely to occur.

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