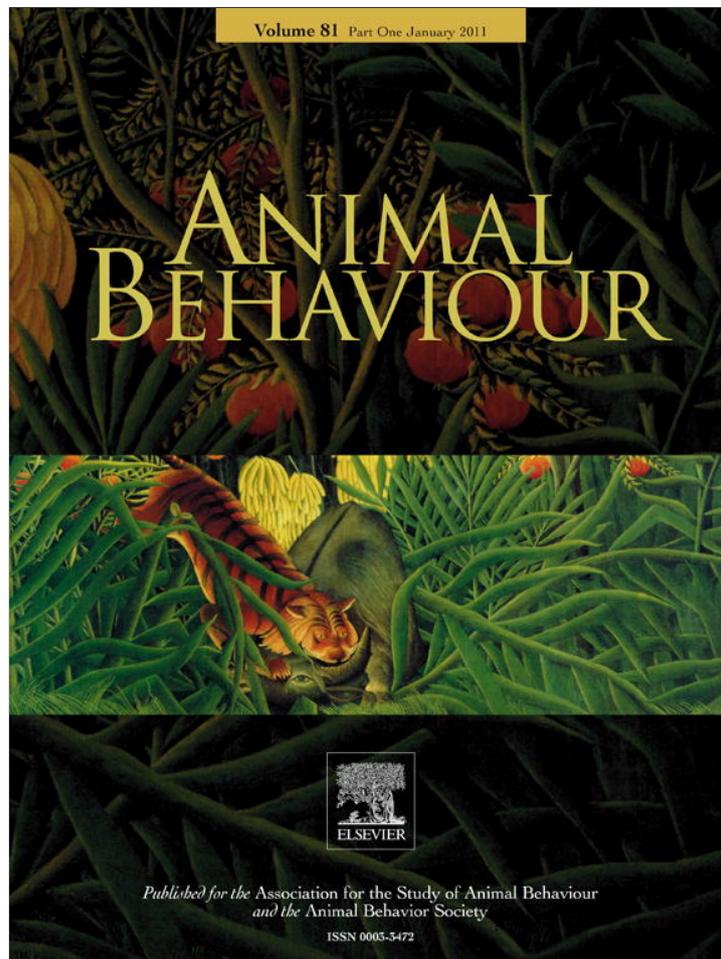


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## The effect of helpers on the postfledging period in a cooperatively breeding bird, the sociable weaver

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Understanding the evolution of cooperation requires determining the costs and benefits of cooperative behaviour. In cooperative breeders, where nonbreeding individuals assist in raising offspring, these 'helpers' are expected to increase the fitness of breeders and hence empirical research has focused on the effect they have on reproductive output and breeder survival. However, the effects of helpers during the postfledging period are poorly known because of the difficulty of tracking fledglings in the wild. Helper presence might be beneficial for fledglings, for example through continuous food delivery or increased predator vigilance, but potential competition between helpers and fledglings, or changes in investment of parents assisted by helpers, could counteract these positive effects and have a negative influence on postfledging survival probabilities or promote dispersal. We investigated the survival of juvenile sociable weavers, *Philetairus socius*, raised in pairs alone versus pairs with helpers by using capture–mark–recapture methods to control for individual detectability in survival estimation. We found that local survival in the first year was reduced in young raised by groups versus those raised by pairs. This may reflect either higher mortality or emigration of juveniles raised in groups. Hence, our study reveals significant postfledging effects of cooperative breeding that have not been reported previously and that need to be investigated in studies addressing the evolution of cooperative breeding.

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In cooperatively breeding vertebrates, where nonbreeding 'helpers' assist in raising young, research has largely focused on understanding the benefits of helping (Cockburn 1998; Dickinson & Hatchwell 2004). Since helping often takes place in family groups, kin selection is seen as a key factor in the evolution of cooperative breeding, and helpers are expected to improve reproductive output (Emlen 1982; Cockburn 1998; Griffin & West 2003; Dickinson & Hatchwell 2004). In addition, helpers are expected to affect offspring survival after the nestling period, but this has rarely been studied, presumably because of the logistical difficulties associated with tracking highly mobile young. After fledging or weaning, animals face important survival challenges as their foraging skills are developing and they are exposed to new predators. Hence, helpers can make a difference during this period, by continuing to provide

additional food and/or protection from predators (Langen 2000; but see Raihani & Ridley 2007). In addition, since early rearing conditions can have lasting effects (e.g. Verhulst et al. 2006; Alonso-Alvarez et al. 2007), the extra food provided by helpers at the nest could affect future condition and survival. For example, in meerkats, *Suricata suricatta*, the additional food provided by helpers decreased age at first reproduction and increased dispersal into dominant positions (Russell et al. 2007).

On the other hand, after fledging, juveniles and their former helpers become potential competitors, as they may contend for access to mating (see Cockburn 2004; Magrath et al. 2004). Additionally, remaining in the family group may bring other fitness benefits, such as increased survival or access to resources (Ekman et al. 2004; Covas & Griesser 2007) and thus established helpers might not favour the addition of new members to the group. For example, in noncooperatively breeding Siberian jays, *Perisoreus infaustus*, retained offspring force younger recruits to disperse by aggressively chasing them (Griesser et al. 2008). Young born into a group with helpers may thus face higher mortality or dispersal rates. The consequences of within-group competition have seldom been quantified in terms of life history parameters, but in Alpine marmots, *Marmota marmota*, where males compete for

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reproduction, overwinter juvenile survival decreased with the number of male helpers (Allaine & Theuriu 2004).

Offspring survival may also be influenced by changes in parental investment in the presence of helpers. Cooperatively breeding parents may reduce their investment in offspring in the presence of helpers (e.g. Hatchwell 1999; Canestrari et al. 2007; Covas et al. 2008; Russell et al. 2008). Furthermore, there is indication that in some multibrooded cooperative species, after fledging one brood the parents may initiate another brood, leaving most of the post-fledging care to the helpers (e.g. Raihani & Ridley 2008; see also discussion in Langen 2000). In this case, no increase in fledgling survival should be detected in groups versus pairs alone, despite a probable increase in group productivity.

Studying the fate of individuals after fledging is often problematic because detecting individuals in the wild and obtaining long-term data can be difficult. Although some species are highly philopatric and easily detected (e.g. superb fairy wrens, *Malurus splendens*: Cockburn et al. 2008), this is rarely the case. Ignoring the fact that individuals may not be detected at any given time may lead to flawed conclusions (Gimenez et al. 2008). This problem can be addressed by using capture–mark–recapture (CMR) analyses, which provide an explicit way to model the detection process reliably (Lebreton et al. 1992). CMR analyses, however, do not allow one to distinguish between true mortality from permanent emigration (i.e. dispersal) from the study area. Nevertheless, they are the only methods that provide robust estimates of local survival.

A survey of studies that analysed the effect of helpers on post-fledging survival reveals mixed results. Three different studies, on Arabian babblers, *Turdoides squamiceps*, puff-throated bulbuls, *Alophoixus pallidus*, and apostlebirds, *Struthidea cinerea*, found no effect of helpers (Woxvold & Magrath 2005; Ridley 2007; Sankamethawee et al. 2009;), while two studies on white-winged choughs, *Corcorax melanorhamphos*, and long-tailed tits, *Aegithalos caudatus*, revealed improved juvenile survival in the presence of helpers (Heinsohn 1991; McGowan et al. 2003). However, only two of these studies (on puff-throated bulbuls and long-tailed tits) have analysed survival beyond independence and were based on CMR methods. More studies on the postfledging period based on adequate statistical analyses are therefore needed.

Here we used CMR methods to analyse the postfledging survival of sociable weavers, *Philetairus socius*, raised in nests with and without helpers. We examined both short-term (fledging to 1 year) and long-term survival. In a previous study, sociable weaver helpers had a positive effect on nestling mass when rainfall was low (Covas et al. 2008) and on fledging success when breeding in large colonies or under brood size manipulation (Covas & du Plessis 2005; Covas et al. 2008). However, the presence of helpers alone was not associated with more young fledging per nesting attempt (Covas et al. 2008). Since fledging condition may affect survival, and since helpers continue providing care postfledging, helping in sociable weavers could lead to increased juvenile survival. However, in this species, parents reduce their feeding effort in the presence of helpers (Covas et al. 2008), which may counterbalance this possible benefit of helping in terms of postfledging survival. Finally, if there is competition between helpers and young or if the presence of helpers decreases the benefits of philopatry, this could lead to increased juvenile dispersal and/or mortality.

## METHODS

### Study Species

The sociable weaver is a 26–32 g passerine endemic to the semiarid savannahs of the southern Kalahari and Namib regions of Namibia and of South Africa's Northern Cape Province

(Maclean 1973a; Mendelsohn & Anderson 1997). They feed on a wide variety of insects, seeds and other plant products (Maclean 1973c). These 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 & Anderson 1997). The communal nest masses vary from under 10 to several hundred independent nest chambers where breeding takes place and which are also used for roosting throughout the year. Sociable weavers are facultative cooperative breeders and usually breed in pairs or with one to three 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 their siblings or unrelated birds may occasionally help (Covas et al. 2006). Both males and females may help, although in a previous study helpers older than 1 year were all males (Doutrelant et al. 2004). The breeding group is stable during the breeding season, but group composition can change between years as older helpers leave, or young from the previous season become helpers. Breeding usually takes place during the summer months (from September to April), coinciding with the rainy season.

### Field Methods

The study was conducted at Benfontein Game Farm near Kimberley, Northern Cape Province, South Africa (approximately 28°53'S, 24°50'E). The study area covers approximately 15 km<sup>2</sup> of Kalahari sandveld, consisting of open savannah dominated by *Stipagrostis* grasses and the camelthorn tree, *Acacia erioloba*. The area is semiarid, experiencing low and unpredictable rainfall (average 431 ± 127 mm per year; Weather Bureau, Pretoria). The study area contains about 30 sociable weaver colonies. This study was conducted on 16 of those colonies, although the number of colonies caught each year varied between 10 and 16. Nest chambers in each colony were individually identified with a numbered plastic tag. During the 1999 and 2000 breeding seasons all nest chambers were inspected every 4 days to detect initiation of new clutches and obtain information on hatching and fledging numbers (Covas et al. 2008). The nestling period is 21–24 days (Maclean 1973c). To avoid premature fledging, 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 marked nestlings with a uniquely numbered aluminium ring and a unique colour combination. We assumed that the number of nestlings present on this date was the number of young that fledged from that nest. The average number of young fledged per nest was 2.2 ± 1.1 (Covas et al. 2008).

From 1999 to 2005, all the resident birds in the study colonies were annually captured with mist nets that were placed around the colony before dawn (i.e. when the birds were roosting inside; Covas et al. 2002, 2004a; Spottiswoode 2007). Individuals were processed and released on the site of capture. All individuals were given a uniquely numbered aluminium ring and colour combination. Colonies or nests used in experiments in a given year (Covas et al. 2004b; Covas & du Plessis 2005) were excluded from the present study. To identify the individuals feeding at each nest, we conducted observations from a hide placed 2–5 m from the colony for a minimum of 1 h a day over 3–5 days (see Doutrelant & Covas 2007; Covas et al. 2008). Sociable weavers seemed oblivious of the observer once under the hide.

The work was conducted under permission from the Northern Cape Department of Tourism, Environment and Conservation and under the approval of the Ethics Committee of the University of Cape Town.

Statistical Methods

We tested for differences in survival between juveniles raised by pairs alone versus pairs assisted by helpers using maximum likelihood statistics, following the general methods of Lebreton et al. (1992) and the program MARK (Cooch & White 1998; White & Burnham 1999). Individual capture histories were built for each fledgling known to be alive in the nest at day 17 of the nestling period. The study colonies were subsequently captured over 5–6 years and we recorded the presence/absence of a given individual in any of the colonies captured. By analysing individual capture histories, it is possible to distinguish a probability of survival ( $\Phi$ ) from a recapture probability ( $p$ ), which is not the case when simply studying return rates. We first verified that our data set met the expectations of the Cormack–Jolly–Seber assumptions (no trap dependence and no transient effect), using programme RELEASE GOF (Burnham & Anderson 1998) in the program MARK, confirming that this was so ( $\chi^2_7 = 5.29, P = 0.63$ ).

In these analyses we were mainly interested in the effect of helpers on juvenile survival. We were interested in the effect of helpers on short-term (from fledging to the following breeding season) and long-term (across all years) survival. However, a number of other factors could have affected survival and also had to be tested. Both survival and recapture probability models tested the following explanatory variables (see Table 1 for details): (1) the presence of helpers, (2) the sex of birds, (3) whether the effect was short term or long term, (4) year, (5) body mass and body mass<sup>2</sup> and (6) metal colour rings. In addition, we were interested in whether the effect of helper presence could interact with other factors, which we included only if they were considered biologically relevant a priori (Burnham & Anderson 1998). For example, the presence of helpers could have an effect on short-term, but not long-term survival (see McGowan et al. 2003) or could affect only one of the sexes (Table 1). To limit the number of parameters to estimate simultaneously (Grégoire et al. 2004), we first evaluated whether both survival and recapture were time dependent or constant. Second, we added the explanatory variables on recapture probability and selected the best model, and finally explanatory variables were added on survival probability. We tested hypotheses by comparing different models using the Akaike information criterion corrected for sample size (AICc). This method considers both the deviance and number of parameters (Akaike 1973). The model with the lowest AICc is the best, whereas models that differ by  $\Delta AICc < 2$  are considered to have equivalent support (Burnham & Anderson

1998). In our case, to evaluate the significance of specific effects, likelihood ratio tests (LRT) were performed between nested models with a  $\Delta AICc < 2$  (Lebreton et al. 1992).

RESULTS

The results presented here are based on 113 young (from 47 broods), of which 62 were raised by pairs and 51 by groups (with one to three helpers).

The 10 best survival models are listed in Table 2. The final model, which includes all significant factors, is Model 1 ( $\Phi(\text{help}^*\text{first-sub})p(\text{help} + \text{ring} + t)$ ). This model incorporates recapture probabilities, which varied between years ('t' effect, from  $0.51 \pm 0.077$  to  $1.00 \pm 0.33 \times 10^{-4}$ ) and were significantly negatively affected by the presence of helpers ('help' factor; Fig. 1). There was also a significant positive effect on recapture of the metal colour rings used in some colonies where individuals were captured more frequently during specific years, since these were central study colonies over a specific period ('ring' effect, Tables 1, 2;  $p_{\text{with ring}} = 0.87 \pm 0.042$  and  $p_{\text{without ring}} = 0.50 \pm 0.075$ ).

The estimated juvenile survival over the first year was very high (above 0.92; see Fig. 2). Juvenile survival probabilities were significantly affected by an interaction between the presence of helpers ('helper' factor) and a short- versus long-term effect ('first-subsequent' factor; first three models in Table 2). This indicates a negative effect of helpers on first-year survival, with fledglings raised in groups having an estimated first-year survival 7% lower than fledglings raised in pairs, although there is no effect on longer-term survival (Fig. 2).

Model 2 was similar to the above, but in addition supported a positive effect of mass on survival. However, a likelihood ratio test between Models 1 and 2 showed no significant difference between the models (LRT:  $p = 0.19$ ). A positive effect of mass is therefore possible, although Model 1 (without mass) has fewer parameters and is therefore considered more parsimonious than Model 2. Model 3 suggested an interaction between helpers' presence and mass indicating no relationship between mass and survival for juveniles raised by pairs, whereas there was a positive relationship between mass and survival for juveniles raised by groups (figure not shown). However, the  $\Delta AICc$  between Model 3 and Model 1 was 2.03. Hence, although of note, the effect of mass in interaction with group type does not seem to have a strong influence on the results presented here.

DISCUSSION

In this study we found that fledglings raised in groups had lower local survival in their first year and had lower recapture rates than

Table 1 Description of the factors included in the model set

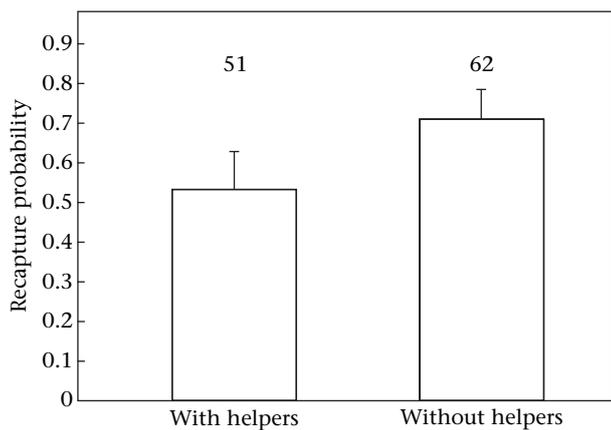
Factor	Factor explanation
Help	This effect was tested as a binary variable: juvenile fed by the pair versus pair + helpers. A continuous variable could not be used here as the number of helpers had a non-Gaussian, zero-inflated distribution
Sex	Juvenile sex was considered as previous studies suggested female-biased dispersal (Doutrelant et al. 2004), which could lead to sex differences in recapture or survival rates
First-sub	We evaluated whether helper effects were present only during the first year or persisted in subsequent years
t	We considered a potential effect of year
m+m <sup>2</sup>	A quadratic function of body mass was considered, following previous studies which detected a significant effect of this function on survival (Covas et al. 2002; Gimenez et al. 2006)
Metal colour ring	In 2000, we tried a new type of metal ring on some colonies, which caused moderate to severe injuries in several birds. Many of these rings were subsequently removed, but the potential effect of these rings on both survival and recapture probabilities was accounted for here

Interactions tested: help\*sex; help\*first-sub; help\*(m + m<sup>2</sup>); help\*sex\*first-sub.

Table 2 First 10 best models including factors affecting survival ( $\Phi$ ) and recapture ( $p$ ) probabilities

Model	AICc	$\Delta AICc$	K	Deviance	AICc (%) weights
<b>1. <math>\Phi(\text{help}^*\text{first-sub})p(\text{help} + \text{ring} + t)</math></b>	<b>397.11</b>	<b>0.00</b>	<b>16</b>	<b>362.09</b>	<b>0.29</b>
2. $\Phi(\text{help}^*\text{first-sub}+m+m^2)p(\text{help}+\text{ring}+t)$	398.71	1.59	18	358.86	0.13
3. $\Phi(\text{help}^*\text{first-sub}+\text{help}^*(m+m^2))p(\text{help}+\text{ring}+t)$	399.14	2.03	20	354.37	0.11
4. $\Phi(m+m^2)p(\text{help}+\text{ring}+t)$	399.76	2.65	13	371.77	0.08
5. $\Phi(\text{help})p(\text{help}+\text{ring}+t)$	400.33	3.22	13	372.34	0.06
6. $\Phi(\cdot)p(\text{help}+\text{ring}+t)$	400.74	3.62	12	375.04	0.05
7. $\Phi(\text{help}+m+m^2)p(\text{help}+\text{ring}+t)$	401.12	4.01	15	368.47	0.04
8. $\Phi(\text{help}^*\text{first-sub}+\text{ring})p(\text{help}+\text{ring}+t)$	401.61	4.49	18	361.77	0.03
9. $\Phi(\text{help}^*\text{first-sub}+\text{sex})p(\text{help}+\text{ring}+t)$	401.67	4.56	18	361.83	0.03
10. $\Phi(\text{help}^*(m+m^2))p(\text{help}+\text{ring}+t)$	402.57	5.45	17	365.15	0.02

The best model, including all significant factors is indicated in bold. K corresponds to the number of parameters.



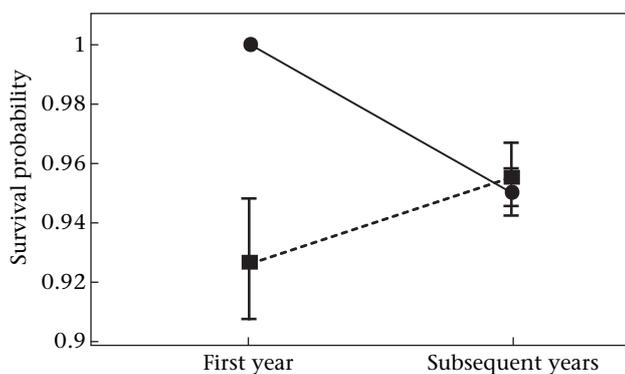
**Figure 1.** Juvenile recapture probability in relation to the presence of helpers at the nest. The bars represent mean  $\pm$  SD. Sample sizes are given above the bars.

fledglings raised by pairs. Differences in survival were no longer detectable after the first year, indicating that these effects do not persist through life. To our knowledge, this is the first study documenting a negative effect of helper presence on the local survival rates of the juveniles after fledging. However, lower first-year survival of juveniles raised in nests with helpers indicates either a true decrease in survival or increased dispersal from the colonies studied. These different scenarios are discussed below.

The absence of long-term survival benefits of helpers, despite an increase in fledgling condition (Covas et al. 2008) might appear surprising. However, the effect of helpers on fledging mass was restricted to conditions of poor rainfall (Covas et al. 2008). Although these are common conditions in our study area, this effect might be too weak to persist through life and be detected on the totality of individuals that were brought up with helpers under different rainfall conditions.

The negative effect of helpers on first-year survival may represent a true decrease in survival or an increase in dispersal. One way of distinguishing between the two hypotheses would be to conduct multistate analyses, which take into account dispersal probabilities. However, dispersal in this system is very low. Based on CMR data from 15–20 colonies that go back to 1993 (see Covas et al. 2002, 2004a) less than 10% of the juveniles recaptured as yearlings had moved between colonies. Hence we currently do not have enough data to distinguish between the two explanations.

The possibility of a true increase in mortality seems puzzling from an evolutionary point of view, since in this species helpers are well tolerated by parents and have a positive effect on body mass



**Figure 2.** Survival probability in the first and subsequent years of young raised in groups (squares) versus young raised in pairs (circles). Means are shown  $\pm$  SD.

and fledging success, at least under adverse breeding conditions (Covas et al. 2008). However, a previous study showed that parents decrease their feeding rate in the presence of helpers, suggesting that parents use the presence of helpers to improve their own survival rather than boosting offspring production or condition (Covas et al. 2008). A decreased investment in offspring in the presence of helpers could have negative effects on the survival of young after fledging. For example, in pied babblers, *Turdoides bicolor*, fledglings from a first brood come under the exclusive care of helpers when a second brood hatches (Raihani & Ridley 2008), and this pattern might occur in other cooperative breeders (Langen 2000). If helpers are less efficient carers this may negatively affect the fledglings' survival, although this hypothesis has not been investigated in sociable weavers or other systems.

Alternatively, young raised in groups could have higher propensity for dispersal. Our study should have been able to detect some of this movement since we monitored several colonies in the study area. However, for our first-year survival estimates we were only able to sample ca. 30–50% of all colonies known in the area (i.e. 10–15 colonies out of 28 colonies). Hence, some 1-year-old birds might have moved to colonies that were not sampled in that period, or might have moved away from the study area and would go undetected. Dispersal is therefore a possibility that requires further attention.

Dispersal is usually thought to be a costly process during which individuals face several risks, such as deteriorating physiological condition and mortality (e.g. Yoder et al. 2004; Griesser et al. 2008; Ridley et al. 2008), in which case both scenarios (i.e. reduced survival or increased dispersal) suggest a cost for nestlings of being raised in nests with helpers. However, the results found here could indicate a benefit of helping if offspring assisted by helpers are in better condition and disperse earlier in life to occupy breeding positions (e.g. Russell et al. 2007). This possibility might not be very likely in our system, since reproduction by 1-year-olds appears to be rare in sociable weavers under natural conditions, having so far been detected on only one occasion (see also Covas et al. 2004b). However, helpers have a positive effect on fledging mass under adverse conditions (Covas et al. 2008) and hence this hypothesis requires further investigation.

Another possible mechanism for higher dispersal propensity of juveniles raised in groups is competition between the newly fledged young and their older siblings, for example, if staying in the natal colony and remaining in a family group is an important asset for survival or future access to mating, and there is an optimal group size. Competition between group members over different resources has been reported for several cooperative societies (e.g. Cockburn 2004; Magrath et al. 2004; McGowan et al. 2006; Griesser et al. 2008; Dickinson et al. 2009). Sociable weavers are an obligate colonial species and are entirely dependent on a communal nest mass to roost and breed. Communal roosting results in significant energy savings (White et al. 1975; Williams & du Plessis 1996), and weavers may compete for roosting chambers (R. Covas & C. Doutrelant, personal observations). Additionally, several cooperative breeders appear to experience competition for breeding or helping positions (e.g. Cockburn et al. 2008; Chiarati et al. 2010; see also Kokko & Johnstone 1999). Hence, older and presumably dominant helpers might actively lead younger siblings to leave the colony as reported in the family-living (but noncooperatively breeding) Siberian jay (Griesser et al. 2008).

Juveniles may also choose to disperse freely when helpers are present. If there is a reproductive queue and older subordinates are dominant to juveniles, it may pay juveniles to seek reproductive opportunities elsewhere. In group-living species, individuals in large groups are more likely to disperse, since the per capita benefits of membership decrease (VanderWaal et al. 2009 and references therein). For example, kin-selected benefits of staying may be lower,

since additional helpers may not significantly improve the production of siblings (Covas et al. 2008). Under this scenario, the effect of helpers should be a function of helper numbers, and this would ideally have been examined by analysing helper number as a continuous variable rather than a binary category. However, this was not possible since the number of helpers had a non-Gaussian, zero-inflated distribution and hence a continuous variable could not be used with the methodology available currently. Additional behavioural data are therefore needed to test this hypothesis.

Finally, differential dispersal rates could arise from a parental strategy. Parents without helpers are more likely to benefit from delayed dispersal of their offspring since these offspring would act as helpers for future breeding attempts. A striking example of this is the Seychelles warbler, *Acrocephalus sechellensis*, study where parents were shown to bias offspring sex ratio in relation to helper presence and territory quality to produce more of the helping sex in the absence of helpers (i.e. females) and more of the dispersing males when they already had helpers or were in poor-quality territories (Komdeur et al. 1997). However, sociable weaver parents with helpers show the opposite pattern of producing more males (i.e. the main helping sex; Doutrelant et al. 2004).

If our results on first-year survival are explained by dispersal, the lack of a sex effect appears surprising since sociable weavers show female-biased dispersal (Doutrelant et al. 2004; Covas et al. 2006), and hence females could have lower 'local survival'. Similarly, under the competition scenario, we could have obtained an interaction between group type and sex, with lower male survival in the presence of helpers since helpers in this species are predominantly males (Doutrelant et al. 2004; Covas et al. 2006). However, both sexes have similar strategies in their first year, with over 90% of yearlings remaining at home and helping their parents (R. Covas, M. D. Anderson, C. Doutrelant & C. N. Spottiswoode, unpublished data), and female-biased dispersal taking place subsequently (Doutrelant et al. 2004; Covas et al. 2006). Hence, first-year survival of males and females is probably influenced by similar factors.

### Conclusions

This study shows a significant effect of sociable weaver helpers on the postfledging stage, which can be explained by increased mortality or dispersal of first-year birds. It appears puzzling that these results might be caused by increased mortality. However, given that the presence of helpers improves reproductive outcome under some conditions, allows parents to reduce their feeding effort (Covas et al. 2008) and improves female survival (R. Covas, A.-S. Deville, C. Doutrelant, C. Spottiswoode & A. Grégoire, unpublished data), helper presence could still be beneficial overall. Specifically, in our system very high predation rates (on average 70%; Covas et al. 2008) require breeders to put a great effort into reproduction for a proportionally small output; hence maximizing the length of reproductive life should be critical. Such benefits for breeders might compensate for the cost of reduced offspring survival. However, additional studies are needed to distinguish between mortality and dispersal, to understand what might favour dispersal of young raised in groups and to track the fate of dispersers. This requires hard-to-obtain data based on long-term monitoring of numerous groups (e.g. Clutton-Brock & Sheldon 2010), but is a necessary step to model the demographic and fitness consequences of helping behaviour. The evolution of cooperation involves a fine balance of costs and benefits for individuals and it is crucial to understand how possible survival or competition costs between helpers and fledged young might come about and whether, or to what extent, this may hamper the benefits of cooperation.

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