



Helping has signalling characteristics in a cooperatively breeding bird

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In a communication network, individuals can observe and gain information from behaviours not directed at them. In this context, behaviours not primarily intended to be a signal might evolve a secondary signalling function if they contain reliable information used by others for fitness decisions. We examined whether this could be the case for helping behaviour, since it can take place in a communication network, be associated with increased fitness benefits and be costly. We investigated whether helping has signalling characteristics in a colonial cooperative bird, the sociable weaver, *Philetairus socius*. We found that the behaviour of helpers increased their chances of being seen by other individuals when feeding, and was influenced by the audience and by the value of the prey brought to the nest. Specifically, helpers (1) spent longer than parents holding the prey at the colony before feeding; (2) fed the nestlings when the number of birds in the audience had increased; (3) spent longer holding their prey at the colony before feeding when they brought larger prey and (4) when rain and thus food was less abundant. We discuss whether these results can be explained by alternative hypotheses such as lower willingness to undertake predation risk by helpers. However, we suggest that helping has characteristics compatible with signalling and thus, in addition to the primary function of feeding young, helping behaviour might be used to convey information.

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Animals need information to make important fitness decisions such as mate choice or habitat selection. This information can be obtained through cues or direct exchanges between individuals in a dyad. In addition, individuals standing by, or 'eavesdroppers', may also obtain this type of information by monitoring behaviours that are directed at other individuals in what is called a communication network (McGregor & Dabelsteen 1996; Naguib & Todt 1997; Oliveira et al. 1998; Otter et al. 1999; Doutrelant & McGregor 2000; Doutrelant et al. 2001; Peake et al. 2001; Danchin et al. 2004; McGregor 2005). In these communication networks, signalling theory allows us to take one step further to predict that some behaviours not primarily intended to be a signal can

evolve a signalling function if they contain reliable information used by an audience of eavesdroppers (see also Lotem et al. 1999; Borgia & Coleman 2000; Johnstone & Bshary 2004; Bshary & Grutter 2006). First, individuals are expected to 'eavesdrop' when observing the behaviour of others increases their fitness; then the individuals performing the behaviour relevant to the eavesdroppers are expected to perform it more frequently in the presence of an audience of eavesdropper(s) if the reaction elicited in this audience is beneficial to them (Bshary & Grutter 2006).

A signal is an easily detectable behaviour or trait, which should contain reliable information and have positive fitness consequences for the signaller and the receiver to evolve (Maynard Smith & Harper 1995; Johnstone 1998). In addition to these three major requirements (fitness value, reliability and detectability), a signal is expected to be displayed in a conspicuous manner to increase the probability of being transmitted to the receiver, and to

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be altered in relation to the expected payoffs, that is, in relation to the cost of the signal and the presence/absence of receivers (Endler 1993; Maynard Smith & Harper 1995, 2003; Bradbury & Vehrencamp 1998).

Helping behaviour in cooperatively breeding species, where mature nonbreeding individuals assist others in taking care of their offspring, mob predators and/or defend the territory, might have evolved such a secondary signalling function. Helping can be associated with direct fitness benefits for the helpers such as increased likelihood of reproducing (Reyer 1986; Whittingham et al. 1997; Richardson et al. 2002; Webster et al. 2004) or being accepted in a coalition (Heinsohn et al. 2000). These direct benefits suggest that helping contains information used for fitness related decisions by others (the individuals helped, the potential mates or the partners in coalition). In addition, helping involves costly behaviours such as parental care (Heinsohn & Cockburn 1994; Heinsohn & Legge 1999; Russell et al. 2003) or territorial defence (Maklakov 2002) and thus should contain reliable information on individual quality. Finally, feeding, mobbing or sentinel behaviour helpers takes place in a 'communication network' (the breeding group, the colony or the border of the territory) where the help performed by one individual can often be observed by others, and hence the information it contains can be easily transmitted. The prediction that helping can act as a signal has been formulated by two theoretical models (Gintis et al. 2001; Lotem et al. 2003), verbal argument (Zahavi 1995; Putland 2001) and could explain the occurrence of deceptive feeding in some cooperative breeders where helpers sometime consume the food brought to the nestlings once in the nest (Boland et al. 1997; but see Canestrari et al. 2004; Clutton-Brock et al. 2005).

Individuals might be expected to use helping behaviour as a signal for three different reasons: (1) to signal individual quality or social status (Zahavi 1995; Putland 2001); (2) to show that they are 'paying the rent' (Gaston 1978) for being accepted in a group or territory (e.g. Stiver et al. 2005); and/or (3) to obtain direct or indirect reciprocity, as shown in humans (Trivers 1971; Nowak & Sigmund 1998, 2005; Wedekind & Milinski 2000). Hence, potential signalling functions of helping could be directed at individuals of the other sex to have future access to mating (Putland 2001), at parents to be kept in the territory (Stiver et al. 2005), at allies to form coalitions (Zahavi 1995; Putland 2001; Stiver et al. 2005) or at the individuals helped or observing the help to receive help later (direct and indirect reciprocity: Trivers 1971; Nowak & Sigmund 1998, 2005; Wedekind & Milinski 2000).

The possible signalling characteristics of the feeding behaviour of helpers have been researched empirically only once. Wright (1997) investigated whether helping behaviour could be used to signal social status in Arabian babblers, *Turdoides squamiceps*. He found no evidence to support this hypothesis i.e. he did not find any male-male competition in relation to help and found that variation in the individuals' provisioning behaviour was adjusted to the nestling's need. Sentinel behaviour has also been hypothesized to act as a signal of quality (Zahavi & Zahavi 1997; Arnold 2000), but empirical results were

more convincingly explained by state-dependent hypothesis and selfish antipredator strategies (e.g. Clutton-Brock et al. 1999; Wright et al. 2001). By contrast in humans, the performance of altruistic behaviours was convincingly related to indirect reciprocity (Nowak & Sigmund 1998, 2005; Wedekind & Milinski 2000). In fish, a recent experimental study on a cleaning mutualism system showed an increase in the level of cooperation by fish cleaners in the presence of an audience of image scoring clients (Bshary & Grutter 2006).

In spite of the theoretical expectations of a possible signalling function of helping behaviour, there are no data available on two important characteristics expected under the signalling hypotheses: conspicuousness and alteration of the behaviour in relation to the expected payoffs. First, helpers are expected to behave so that their chance of being seen helping is increased. Second, the presence of an audience (of eavesdroppers) and the value of helping are expected to modify the signalling behaviour. Here, we investigated these two possible characteristics of helping behaviour in a colonial cooperative breeder, the sociable weaver, *Philetairus socius*, in a first attempt to examine whether helping has signalling characteristics in this species.

Sociable weavers inhabit the semiarid savannahs of southern Africa. These weavers build communally a massive nest mass where the colony breeds and roosts throughout the year. Sociable weavers may move around independently or in groups, and as a consequence the number of birds at the colony changes continuously (being sometimes zero). When feeding nestlings, sociable weavers can either fly directly into the nest or they can perch at the colony with the prey in their beak, wait and then enter the nest to feed. Under the signalling hypothesis the behaviour of the signaller is expected to change according to the number and/or identity of the individuals in the audience (i.e. the receivers). More specifically, under the 'pay to stay' hypothesis, the potential receptor is the breeding pair. By contrast, under the 'individual quality' or reciprocity hypothesis, the potential audience is more diffuse and, in our colonial system, we could not individually pinpoint the potential receivers outside the breeding group. Hence, we investigate whether the helpers arrive and feed in the presence of the breeding pair and whether there is a general audience effect in the behaviour of helpers. If helping has signalling characteristics in this species, we predicted that helpers would behave to maximize the chances of being seen feeding. We thus expected that: (1) helpers would perch for longer than parents holding a prey in the beak before feeding; (2) helpers would usually enter the nest with food after an increase in the audience and (3) there should be a negative correlation between the time spent with prey before feeding and the number of birds in the audience (as the probability of transmitting the information to the receiver increases). In addition, we expected the behaviour of helpers to be influenced by the value of the signal, and thus (4) helpers should display their prey for longer when they bring more valuable prey and (5) when prey abundance is low and hence the cost of obtaining food is higher.

METHODS

The Study Species and Area

The sociable weaver is a 28 g, sexually monomorphic passerine living in southern African open savannahs. These weavers are colonial cooperative breeders that live year round in a large thatched structure containing multiple separate chambers where breeding and roosting take place. These communal nests, or colonies, vary in size between ca. 1 and 4 m across and are built communally, typically on Acacia trees standing several metres apart (Maclean 1973).

In our population, sociable weavers breed in pairs or with one to five helpers (average group size is 3.1; Covas et al. 2006). During our study, the helpers always remained with the same pair during the entire breeding season; in the following year they could remain as helpers or become breeders (C. Doutrelant & R. Covas, unpublished data). Sociable weavers can make up to nine breeding attempts in one season and thus both parents and helpers feed several consecutive broods in each season. Experimental and correlative studies show that helpers have a positive impact on reproductive output and that parents decrease their feeding rate in the presence of helpers (Covas & du Plessis 2005; R. Covas, M. du Plessis & C. Doutrelant, unpublished data).

Sociable weaver helpers are mostly males (Doutrelant et al. 2004). In a previous study of the genetic mating system using four highly polymorphic microsatellites, 66 adults and 61 nestlings coming from 20 nests, we obtained no convincing cases of paternity sharing among feeding males or of extrapair paternity (Covas et al. 2006). In this same study we found that 50% of the helpers were offspring of one breeder and 43% were offspring of both breeders, while 7% were seemingly unrelated individuals (Covas et al. 2006).

Sociable weavers feed on a mixture of invertebrates and seed, but the nestlings are almost exclusively fed on invertebrates (Maclean 1973). Rainfall is the main determinant of food availability in the arid regions inhabited by these weavers (Maclean 1973; Dean & Milton 2001). Consequently, rainfall is also one of the main determinants of clutch size, fledging success and the duration of the breeding season (Maclean 1973; Covas 2002; Covas et al., unpublished data).

Field Methods

In this study, we monitored 10 colonies of 20–70 birds. During the breeding season, the nests were monitored several times a week to detect new clutches and obtain information on the number of nestlings present in the focal nests. Since 1998, individuals in the study colonies received unique colour ring combination.

Rainfall data were collected in the study area throughout the season using a rain gauge. In this study 'rainfall' is the total of rain collected over the 30-day period before the nestlings were 17 days old (i.e. soon before the fledging date at 21–24 days), as this was significantly related to nestling condition and fledging success

(R. Covas, M. du Plessis & C. Doutrelant, unpublished data).

Behavioural Observations

Data were collected during two breeding seasons. We obtained data on the behaviour of 122 sociable weavers feeding at 40 nests. To identify the colour rings of the individuals feeding at a given nest, we conducted 1 or 2 h of daily observations for 2–3 consecutive days when the nestlings were around 6 days old. Subsequently, to record each individual's behaviour in relation to the audience, we conducted 1 h of daily observations for 3 additional consecutive days. We defined audience as the total number of sociable weavers present at the colony when the focal bird arrives at the colony with food ('audience at arrival') or enters a nest with prey in its beak ('audience at nest entrance'). The observations quantifying an individual's behaviour in relation to the audience were conducted by a team of two people. One person was in charge of quantifying the audience at the focal colony. This person, situated at 20–30 m from the colony in a hide, noted each time a bird entered and left the colony with a stopwatch and a tape recorder. Another person (CD) was situated also in a hide placed at 5 m from the colony. Using another stopwatch set at exactly the same time, this second observer noted: (1) the time at which the focal bird arrived at the colony, (2) the time at which the focal bird fed and (3) the number and size of prey brought to the nest. Food load was scored from 1 to 4 relative to the size of the beak (score 1 indicates the smaller prey size and number). We also examined whether there were any aggressive interactions between individuals feeding at a nest; however, we never detected any and hence this was no longer considered in the study. When conducting the observations in the field, the observers did not know the identity of the feeder (helper, mother or father). This was determined later in the lab through genetic paternity analyses with a likelihood-based approach using the CERVUS software version 2.0 (see Covas et al. 2006). Sex determination was done by molecular techniques (Doutrelant et al. 2004) using the P2 and P8 universal primers of Griffiths et al. (1998). Once the identity of the feeding individuals had been revealed by molecular work, we calculated the number of times the focal helpers arrived alone or with one of the breeders. We also calculated the number of times the helpers fed in the presence or absence of one of the member of the breeding pair.

Statistical Analyses

To test the signalling hypothesis and describe the feeding behaviour and efficiency of helpers versus breeders, we quantified the individual variation in the following five behavioural variables: (1) time spent holding a prey at the colony before feeding, (2) difference in the number of birds in the audience between the time an individual arrived at the colony with food and the time it entered the nest to feed, (3) feeding rate (number of

Table 1. Results of the GLMM including the random factor 'individual nested in nest' to detect which factors are associated with a change in the feeding behaviour of helpers (H) and parents (P)

Variables	N†	Minimal models	F	Estimate±SE	P	Nonsignificant factors
Time spent holding prey before entering the nest	114	Intercept		4.01±0.27		Sex; number and age of nestlings; year; number of helpers
		Identity‡ (H>P)	$F_{1,539}=7.0$	0.64±0.24	0.009	
		Audience at arrival	$F_{1,539}=51.3$	-0.060±0.017	1×10^{-4}	
		Rain	$F_{1,539}=4.7$	-0.0037±0.0017	0.03	
		Food load	$F_{1,539}=5.4$	0.15±0.068	0.02	
		Identity*audience at arrival	$F_{1,539}=6.8$	-0.07±0.026	0.01	
				(H=-0.13; P=-0.068)		
Change in audience	122	Intercept		0.26±0.049		Sex; year; number of helpers; nestlings' age and number; food load
		Identity‡ (H>P)	$F_{1,1420}=5.65$	0.24 ±0.10	0.018	
Time spent on the colony after feeding	67	Intercept		3.6±0.14		Audience at nest entrance; nestlings' age and number; rain; time before feeding; number of helpers; identity§
		Sex (females<males)	$F_{2,144}=5.65$	-0.58±0.24	0.02	

†N = number of individuals monitored. The sample size differs for the behavioural variables 'change in audience' and 'time spent holding prey before entering the nest' because the food load of eight individuals was not estimated. Degrees of freedom are higher than the number of individuals as several observations were taken for each individual. For the 'time spent on the colony after feeding' only 67 individuals are included because this behaviour was monitored only during the second year.

‡The factor identity is divided into two classes (parents and helpers) when the behaviour of the mothers and fathers of the same brood did not differ ($P > 0.60$).

§The factor identity is divided into three classes otherwise (mother, father and helper).

feedings per individual and per hour), (4) food load and (5) time spent at the colony after feeding.

The details on the statistical tests performed for each variable, the explanatory variables included in each model and the results obtained are given in Tables 1 and 2. We always ran general linear mixed models (GLMMs) including the random covariable 'Individual identity' nested in 'nest' to account for the fact that more than one observation has been taken for each individual. This random factor was always significant, indicating that the feeding behaviour varied significantly between individuals. Backward selection procedures were used in SAS version 8 (SAS Institute Inc., Cary, NC, U.S.A.). Only the *F* values, model estimates and *P* values of the significant factors are detailed in Table 1.

RESULTS

All the five predictions formulated in the introduction were verified. Helpers spent significantly longer time holding their prey before feeding than parents (Fig. 1a, Table 1). The increase in the number of birds in the audience between the time an individual arrived at the colony with food and the time it entered the nest to feed was significantly higher for helpers than parents (Fig. 2, Table 1). The time spent holding the prey before feeding decreased significantly with the increasing number of birds in the audience (Fig. 1b, Table 1). Conversely, the time spent on the colony after feeding did not differ between parents and helpers (Table 1) and so the helpers were not spending longer at the colony than parents unless they had prey.

Table 2. Results of the GLMM including the random factor 'individual nested in nest' to detect whether fathers (F), helpers (H) and mothers (M) differ in their feeding rate (number of feeding events per hour) and in the food load they bring to the nest

Variables	N*	Minimal models	F	Estimate±SE	P<0.10	Nonsignificant factors†
Feeding rate	91	Intercept		0.05±0.0099		Nestlings' age; time before feeding; year; food load
		Identity (M>H=F)	$F_{2,220}=5.73$	M=0.053 versus H=-0.032, F=0.031	0.0038	
		Nestlings' number	$F_{1,220}=7.33$	0.009±0.003	0.0073	
		Rain	$F_{1,220}=2.8$	0.00009±0.00005	0.09	
Food load	114	Intercept		0.098±0.0014		Identity; nestlings' number; year
		Nestling's age	$F_{1,592}=4.5$	0.011±0.0053	0.03	
		Rain	$F_{1,592}=3.6$	0.0004±0.00022	0.076	

*N = number of individuals monitored. Degrees of freedom are higher than the number of individuals as several observations were taken for each individual. The sample size differs for the two behavioural variables because the feeding rate of the parents decreased in the presence of helpers and so the parents of the nests without helpers were excluded from the analyses on feeding rate (but are included in the analyses on the food load).

† $P > 0.10$.

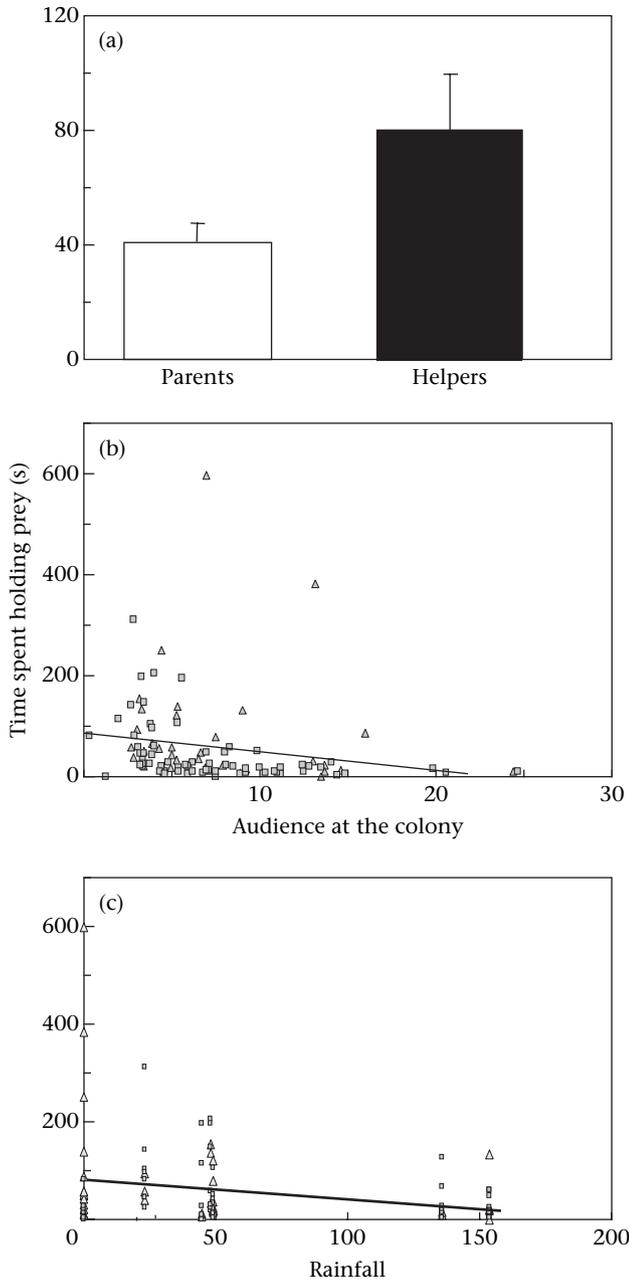


Figure 1. Three factors affecting significantly the time spent at the colony holding prey before feeding (in seconds) for both helpers (represented by triangles) and parents (represented by squares). (a) Identity: helpers spent significantly longer at the colony before feeding than did parents; (b) audience: the time spent with prey before feeding decreased with the number of birds present when the focal bird arrived at the colony; and (c) rainfall: individuals perched for longer when rainfall (and thus prey availability) was lower.

Lastly, sociable weavers spent significantly more time perching at the colony with their prey before entering the nest when they brought higher food load to the nest and when rainfall was lower (Fig. 1c, Table 1).

In these analyses, we found that the interaction between ‘identity’ (parents versus helpers) and ‘audience at arrival’ had a significant effect on time spent holding prey before feeding. This interaction and the values of the

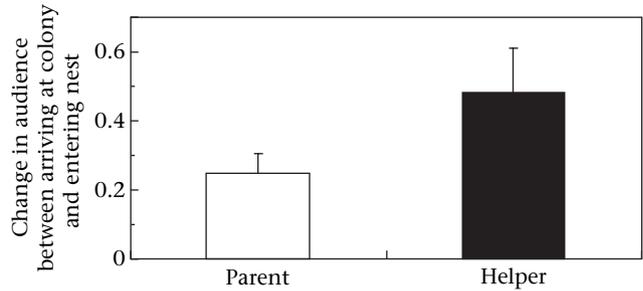


Figure 2. There was a significant increase in the average number of birds in the audience (mean ± SE) between the time an individual arrived at the colony with food and the time it entered the nest to feed. This increase was significantly more pronounced for helpers than parents.

estimates obtained for parents and helpers (Table 1) showed that the effect of the audience was more pronounced for helpers than parents. By contrast, the two-way interactions between rainfall, prey size and the term ‘identity’ (helpers versus parents) had no significant effect on the time spent holding prey. This suggests that rain and prey size influenced the behaviour of both parents and helpers in a similar way, although the helpers’ behaviour was consistently more responsive than the parents’ behaviour (Fig. 1b, c, Table 1).

Helpers provided as much food as the breeding females and both helpers and females fed less than the breeding males (Table 2, Fig. 3). The food load brought to the nest was not significantly different for helpers and parents (Table 2, Fig. 3).

The count of the numbers of simultaneous arrivals showed that in 83% of cases (298 cases out of 357), the helpers arrived alone at the colony (i.e. they arrived more than 30 s before or after one of the breeders). The count of feeding observations showed that in 82% of cases (156 cases out of 190), the helpers fed in the absence of breeders. In the instances where the helpers fed in the presence of one of the parents, 56% were in the presence of the breeding female ($N = 34$).

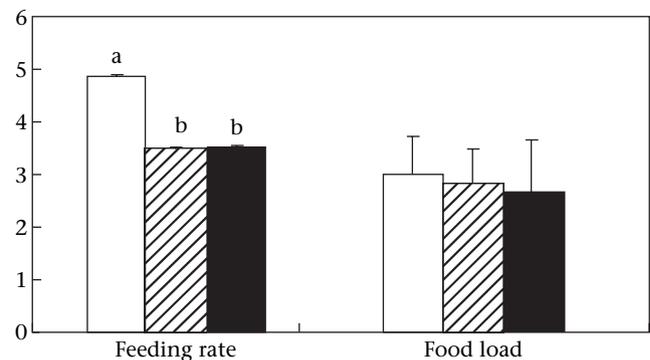


Figure 3. Mean ± SE feeding rate (number of visit per hour) and food load for fathers (□), mothers (▨) and helpers (■). The ‘a’ indicates a significantly higher feeding rate for fathers than mothers and helpers, the ‘b’ indicates a similar feeding rate for mothers and helpers. Mothers, fathers and helpers brought similar load.

DISCUSSION

All results are in agreement with the hypothesis that helping behaviour has signalling characteristics. First, the feeding behaviour of helpers can be more detectable by conspecifics than the feeding behaviour of parents, as helpers spent longer at the colony holding their prey before entering the nest to feed. Second, two results show an audience effect and suggest that the helpers may behave to increase the likelihood of being seen feeding: helpers, more than parents, waited for an increase in the number of birds in the audience before going into the nest; and individuals spent less time with prey in their beak before feeding if the number of birds present at the colony when they arrived was larger. Finally, two other findings suggest that individuals show their feeding behaviour more noticeably when the value and cost of feeding is higher: the individuals perched for longer at the colony with their prey when rainfall (and thus food) was less abundant and when they brought larger food load to the nest. In addition, we found that the helpers usually arrived and fed in the absence of the breeding pair.

Before proceeding with discussion of the signalling hypothesis and its implications for the evolution of cooperative breeding, we will consider the possible alternative explanations to these findings.

Individuals could wait before feeding because they are reluctant to go into the nest chamber to avoid revealing where the nest is located. This possibility can most likely be rejected for sociable weavers since their nests chambers are located in very large and conspicuous colonies. The main nest predators are snakes (Macleane 1973; Marsden 1999; Covas 2002), which forage by systematically searching all nest chambers (Macleane 1973; Covas 2002) and hence are likely to detect any nestlings there. In addition, this alternative does not explain why helpers should be more reluctant than parents to give away the nest location.

Helpers could have waited longer than parents before going into the nest because they were more reluctant than breeders to take risks at the nest in case there was a predator in the nest chamber. While we cannot dismiss this possibility, we believe it is not the most likely. The sociable weaver colonies seem to be the safest place for adults. Their main predator, the Gabar goshawk, *Micronisus gabar*, seizes weavers in flight when they move between trees in the open savannah (Macleane 1973; Marsden 1999) and, in the presence of a goshawk, individuals seek refuge in trees, often hiding in the colony's nest chambers (R. Covas, personal observation). Snakes, the main nest predator, have only been observed taking nestlings (personal observation). In addition, both breeders and helpers often fly directly into the nest when returning to the colony to feed the young, a behaviour that should be infrequent if the weavers need to assess the situation at the colony before flying into the nest. A higher reluctance in incurring predation risk on the part of helpers also does not explain the negative relationship found between the time spent with prey at the colony and rainfall (a surrogate of food availability). This relationship could be linked to predation if snakes visited the colony at higher rates

when rainfall is low, but these two parameters are not significantly correlated in our data set (R. Covas & C. Doutrelant, unpublished data). Finally, the longer waiting times when bringing larger prey loads could be related to lower flight manoeuvrability under those conditions. While we have no indication that this is the case, we cannot at this stage refute this possibility.

Another possible explanation for our results could be that helpers were waiting longer than parents before going into the nest because they were either less motivated to feed or less efficient than parents. However, the lack of significant differences between helpers and parents in the time spent at the colony after feeding shows that helpers did not stay at the colony for longer than parents unless they had prey. A lower motivation or efficiency, would also predict that helpers would feed less than parents, which was not the case. Helpers' feeding rates and the size of prey brought to the nest were similar to those of the breeding females. A lower motivation, would also not explain why helpers would choose to go into the nest to feed when the number of birds present at the colony increased.

Importantly, none of the above alternative hypotheses makes any clear predictions about two other important findings of this study: the time spent with food at the colony before feeding increased with the value of the prey brought to the nest and increased with decreasing rainfall (i.e. when food availability was lower and the cost of allofeeding was higher). By contrast, all the results found here fall into the predictions formulated if helping has signalling characteristics. At this stage, we conclude that both reluctance in undertaking predation risk and signalling hypotheses could explain our results but that the signalling hypothesis seems more parsimonious.

The information contained in helping behaviour might be used by different types of receivers. It might serve as an indication that the helper is 'paying the rent', it can serve to advertise individual quality with the purpose of obtaining reproductive benefits (i.e. to favour mate choice by either members of the breeding group, if the helper is unrelated to the breeding pair, or by other potential mates outside the breeding group if the helper is related), or to elicit direct or indirect reciprocity.

Sociable weavers are a nonterritorial colonial species and individuals may be less likely to have to pay a rent than in territorial species. None the less, in this colonial system, having access to a nest chamber and communal roosting seems to present important advantages for individuals, as it significantly decreases the cost of thermoregulation allowing important energetic savings (White et al. 1975; Williams & du Plessis 1996). Hence, it could be important for helpers to remain in a group if that improves access to roosting chambers.

However, our data showed that helpers do not feed preferentially in front of the breeders. This suggests that the receiver is not one of the breeders and thus that helpers that are waiting with their prey at the colony before feeding are not signalling that they are paying their rent or displaying their quality to the breeding female. In sociable weavers, the level of extrapair paternity appears insignificant (Covas et al. 2006), which advocates against

any signalling benefits related to EPP. The sexual benefits of signalling for sociable weaver helpers might instead be linked to enhanced chances of pairing with females outside the breeding group since male sociable weavers, including some of the helpers observed in this study, normally become breeders at the colony. In addition to potential mating benefits, displaying helping behaviour to others could be an indicator of individual quality used to establish coalitions (Boland et al. 1997; Heinsohn et al. 2000) or encourage altruistic responses from others (Nowak & Sigmund 1998; Wedekind & Milinski 2000). Helping could also increase the chances of subordinate individuals being accepted in the colony. No data are currently available to test the importance of these hypotheses on sociable weavers.

The signal contained in helping might be unreliable if the helpers bring prey to the nest but eat it themselves instead of feeding it to the nestlings. This deceptive behaviour (Boland et al. 1997) has been observed most notably in white-winged choughs, *Corcorax melanorhamphos* (Boland et al. 1997) but not confirmed in carrion crows, *Corvus corone corone*, and meerkats, *Suricata suricatta*, where it was instead suggested that helpers ate the prey when the nestling showed satiation (Canestrari et al. 2004; Clutton-Brock et al. 2005). Such a possibility of cheating might advocate against the hypothesis of helping evolving a signalling function, since reliability is a major requirement of any signal (Maynard Smith & Harper 1995; Johnstone 1998). However, the other individuals in the feeding group should be able to evaluate the nestlings' satiety or condition. Receivers outside the breeding group might be able to evaluate whether the food was or was not delivered through the vocalizations produced by the nestlings during the visit to the nest and after the helper's departure, and hence those birds might use helping as a reliable signal. In addition, cheating could be prevented by parents if they did not tolerate nonworking helpers. The importance of such factors that are external to the signalling interactions in preventing the spread of deceit have been shown in other systems (Johnstone 1998). If cheating cannot be prevented, then the capacity to find food, bring it back and display it instead of consuming it may be a signal of foraging ability. At present, our data do not allow us to distinguish whether it could be the help that is potentially displayed or the feeding capacity.

A signalling component in the feeding behaviour might explain our findings that the parents' behaviour also seems to be influenced by rainfall and prey size in this study. Individuals may continuously update their evaluation of their partner in relation to other potential mates for extrapair copulations (EPCs) or the following reproductive season (cf. the hidden lek hypothesis; Danchin & Wagner 1997). EPCs do not appear to be an important strategy for sociable weavers (Marsden 1999; Covas et al. 2006). However, we know that divorces do take place in our population, although apparently at a low rate (R. Covas & C. Doutrelant, unpublished data).

In conclusion, this study suggests that helping in sociable weavers has characteristics compatible with signalling. These results need to be confirmed by further

studies and experimental tests as they are correlative, and some of the effect sizes are modest. However, a small effect size could be expected if helpers waited for one or a few particular individuals to see them feeding. In addition, possible effects of reluctance in incurring predation risk by feeders when going into the nest need also to be ruled out. Further studies should also investigate the target audience of receivers and experimental studies are needed to manipulate signalling behaviour and establish whether signalling has a direct fitness payoff. None the less, correlative studies, such as this one, constitute a first step to test predictions, reveal patterns and propose new explanations.

Recent studies of cooperative breeders suggest that these systems might often be maintained by a combination of direct and indirect benefits (e.g. Clutton-Brock 2002; Double & Cockburn 2003; Richardson et al. 2003). Investigating the evolution of altruism in a network context allows accounting for different types of receivers and hence for the possibility of a signalling function evolving from behaviours that are also intended to perform other tasks. Such a network context has thus the benefit of considering the coexistence of direct and indirect benefits for helpers and the mutual reinforcing of both types of benefits. We suggest that signalling is an overlooked strategy that deserves further attention in studies addressing the evolution of cooperative breeding and other seemingly altruistic behaviours.

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