Benefits and costs of helpers: investigating the underlying mechanisms

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Abstract

In cooperatively breeding species, sexually mature individuals (“helpers”) forgo reproduction to help raise offspring that are not their own. Such assistance is expected to improve the reproductive output and survival of both parents and young. However in some situations, no effect of helpers has been detected or even negative effects have been reported. Exploring the underlying mechanisms of both benefits and cost of helpers is therefore crucial to the understanding of cooperation. Here I use a well-studied cooperative breeding passerine the sociable weaver, *Philetairus socius,* to explore several potential mechanisms that might explain both positive and negative effects reported on the survival and reproductive success in this species. I focus on a potential transfer of care from breeders to helpers and ask whether this alleviating of work load for breeders may represent a cost for nestlings by comparing the feeding quality of breeders and helpers. I also test if helpers induce a delayed fledging date and discuss the potential associated costs in this species. Finally I use Capture-Mark-Recapture methods to investigate a potential year effect of negative effect of helpers in juvenile post-fledging survival reported in a previous work. I found that helpers provide a compensatory rather than additive effect to the overall care provided to nestlings allowing breeders to decrease their work load. The helpers work load is more pronounced at the end of the nestling stage where demand for food is higher. However this may represent a cost as I also found that helpers bring smaller prey to the nest. Juveniles raised in larger groups take more time to fledge which may increase their exposure to nest predation. Finally no effect of helpers was detected on the post-fledging survival for this year suggesting that the influence of helpers on this parameter may vary between years or social contexts. The results from this study highlight the need to explore several possible mechanisms underlying the positive and negative effects of helpers in the study of cooperative breeding.

Keywords: Cooperative breeding, mechanisms, group size, reproductive success, survival.

Resumo

Em espécies que se reproduzem cooperativamente, indivíduos sexualmente maduros (“ajudantes”), abstêm-se da própria reprodução para auxiliar nos cuidados parentais de crias que não as suas. É esperado que esta ajuda tenha efeitos benéficos na reprodução e sobrevivência tanto para os pais como para as crias. No entanto, em algumas situações não é detectado nenhum efeito ou até mesmo efeitos negativos são constatados. De forma a compreender melhor a evolução da cooperação é assim necessário investigar os mecanismos subjacentes aos custos e benefícios associados a estes ajudantes. Neste estudo uso um passeriforme muito estudado no campo da reprodução cooperativa, o tecelão social, *Philetairus socius* para explorar os mecanismos subjacentes aos efeitos positivos e negativos na reprodução e sobrevivência que têm vindo a ser detectados nesta espécie. Foco-me numa potencial transferência de cuidados parentais dos pais para os ajudantes e questiono se o alívio da carga de trabalho para o casal reprodutor pode representar um custo para as crias, ao comparar a qualidade da alimentação fornecida pelos pais e pelos ajudantes. Neste trabalho também testo se os ajudantes induzem as crias a abandonar o ninho numa idade mais avançada e discuto os potenciais custos associados nesta espécie. Por fim, utilizo o método de Captura-Marcação-Recaptura para investigar potenciais diferenças de ano para ano no efeito negativo dos ajudantes na sobrevivência dos juvenis após abandonarem o ninho detectado num trabalho anterior. Os resultados deste trabalho revelam que os ajudantes providenciam um efeito compensatório e não adicional nos cuidados totais que as crias recebem, permitindo que o casal reprodutor alivie a sua carga de trabalho. Os ajudantes participam mais na alimentação das crias quando estas estão perto de estarem preparadas para abandonar o ninho aquando as necessidades nutricionais são mais elevadas. No entanto, isto pode representar um custo pois os resultados demonstram que os ajudantes trazem presas mais pequenas para alimentar as crias. Os juvenis criados com mais ajudantes demoram mais tempo a abandonar o ninho, o que pode amentar a sua exposição a predadores. Por fim, no ano do presente estudo não foi detectado um efeito pronunciado dos ajudantes na sobrevivência das crias depois de saírem do ninho, sugerindo que a influência dos ajudantes neste parâmetro pode variar de um ano para o outro ou entre contextos sociais. Estes resultados realçam a necessidade de explorar vários mecanismos subjacentes aos efeitos negativos e positivos dos ajudantes no estudo da cooperação.

Palavras-chaves: Reprodução cooperativa, mecanismos, ajudantes, sucesso reprodutivo, sobrevivência.

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Introduction

Cooperation comprises all costly behaviours performed by an individual that benefit another organism (West et al. 2007b). It is puzzling how cooperative behaviours can arise under the classical Darwinian view of evolution, as natural selection should favour selfish behaviours which are expected to increase the reproductive output of the actor (individual who performs the behaviour) and select against behaviours favouring other individuals. This problem has received much attention over the last decades, which has led to solid theoretical foundations for the fundamental processes underlying the evolution of cooperation (Gardner & Foster 2008). The major breakthrough on this subject was the work of Hamilton which developed the theory of inclusive fitness (Hamilton 1964) in which the fitness of the individual is not only linked to his reproductive success (direct fitness), but is also related to the reproductive success of its relatives (indirect fitness). Individuals can gain indirect fitness benefits by improving the reproductive output of closely relatives, as they share part of their genes. Cooperation towards kin is therefore, expected to increase with the degree of genetic relatedness as the indirect benefits to the actor are higher and decrease with the associated costs. Hamilton (1964) defined a rule stating that a cooperative behaviour will be selected if the costs for the actor (c) are outweighed by the benefits for the recipient (b), weighted by his genetic relatedness (r) to the actor ($rb-c>0$; reviewed in West et al., 2007b). Exploring the costs and benefits of cooperative behaviours is therefore crucial to understand the evolution of cooperation.

Cooperative breeding is a type of cooperation in which mature individuals (“helpers”) forgo their own reproduction to assist other breeding individual in raising their offspring. If this helping behaviour is directed towards kin, helpers gain indirect fitness (Hamilton 1964). Cooperative breeding is widespread among both invertebrates and vertebrates, including insects (Choe & Crespi 1997), birds (Cockburn 1998), fish (Wong & Balshine 2011) and mammals (Jennions & Macdonald 1994). Most studies on this subject have focused on the net fitness benefits that both breeders and offspring gain by having the aid of helpers (Bergmüller et al. 2007). These benefits can be translated in increased breeder reproductive output and/or in increasing survival to breeders and/or offspring (e.g. Khan & Walters 2002; Kingma et al. 2010; Hodge 2005; Paquet et al. 2015).

However in some cases no significant effect of helpers is detectable and even negative effects of helpers on breeders and their offspring have been reported (e.g.

Leonard et al. 1989; Magrath & Yezerinac 1997; Legge 2000; Covas et al. 2011). The reasons for such contradictory results demand explanation and can be better understood if the underlying mechanisms for the benefits and costs for both breeders and offspring are explored.

One mechanism, by which helpers can directly benefit offspring and thus, indirectly benefit breeders, include increasing the overall care that offspring receives, for example by increasing total food intake and protection (Brown 1987). When assisted by helpers, if breeders maintain the same level of effort, this is termed additive provision (Hatchwell 1999). For example in the banded mongoose, *Mungos mungo,* pups that are regularly escorted by helpers have higher survival probability, most likely because of greater protection from predators as this is the major cause of know death (Gilchrist 2004). In birds, some studies have reported an additive effect of helpers in the total food intake received per nestling (e.g. Hatchwell et al. 2004; Woxvold et al. 2006; Kingma et al. 2010) For instance in, the cooperative breeding bird apostlebird, *Struthidea cinerea,* the number of carers is positively related with the amount of food provided per chick and this additional provisioning may explain the higher fledging success in larger groups of helpers (Woxvold & Magrath 2005).

Another mechanism which might allow breeders to directly benefit from the presence of helpers is when the extra care provided by helpers allows breeders to lightening their work load, which is termed "load-lightening" (Crick 1992) or compensatory provision (Hatchwell 1999). Breeders can then save energy for next breeding attempts or invest the spare time in other activities that can improve their survival such as feeding, preening or grooming and resting (Crick 1992). In red-cockaded woodpeckers, *Picoides borealis,* for instance, breeders assisted by helpers have improved survival and this might be linked to a reduction in the time spent incubating and feeding the nestlings in the presence of helpers (Khan & Walters 2002). In some cases, as in pied babbler, *Turdoides bicolor,* the lightening of work that helpers provide to breeders is so pronounced that brood overlap may occur. Breeders completely transfer the care of the first brood to helpers and may start another brood before the previous one is independent (Ridley & Raihani 2008).

On the other hand, helpers can also have negative effects for breeders and offspring in certain situations. Mechanisms such as food (e.g. Woodroffe & Macdonald 2000) or breeding (review in Koenig & Dickinson 2004) competition between helpers and breeders or between helpers and offspring have been pointed out as possible explanation for such negative effects. For example, in the Seychelles warblers, *Acrocephalus sechellensis,* helpers increase the reproductive output of breeders in high quality territories, but have a negative effect in low quality territories, suggesting that there is competition between helpers and offspring and/or breeders when resources are scarce. Furthermore, the presence of more than one helper in medium quality territories also decreased the reproductive success, reinforcing the idea of competition (Komdeur 1994b). Breeding competition has been reported both between male helpers and dominant male breeders and female helpers and dominant female breeders. For instance, in the fairy-wrens, *Malurus cyaneus,* the dominant breeding female allows approximately one-quarter of young to be fathered by subordinate unrelated males (Cockburn et al. 2003). In the Southern pied babbler, *Turdoides bicolor,* competition between female helpers and female breeders for breeding opportunities is associated with loss of eggs, nest abandonment and lower fledging success (Nelson-Flower et al. 2013).

Exploring the mechanisms underlying the positive and negative aspects of family living is therefore crucial to understand the evolution of cooperative behaviour. The sociable weaver, *Philetairus socius,* a cooperatively breeding monogamous passerine, is a highly suited biological model to investigate this question. Helpers have been reported to have a positive effect on reproduction. In particular fledging mass and fledging success, but mostly under adverse environmental conditions (Covas et al. 2008). Additionally, breeders feed less in the presence of helpers (Covas et al. 2008) and females decreased their investment in eggs (Paquet et al. 2013). The latter appears to represent load-lightening by females that have improved survival when assisted by helpers (Paquet et al. 2015). On the other hand, and surprisingly, the presence of helpers has also a negative effect on juvenile's survival in the first year after fledging (Covas et al. 2011).

A recent study showed that this effect is especially important in the first 10 days after fledging (Broom 2013) and hence it is a real survival effect and not a confounding effect of dispersal (since dispersal does not take place in the first three months post-fledging; R. Covas unpublished data). These puzzling results raise the question of what are the mechanisms underlying this negative effect of helper presence, as well as whether there might be other direct benefits for parents. For example, besides feeding helpers can also participate in other important tasks such as building the chamber (where breeding takes place) that might be beneficial for breeders. Therefore, the aim of this study is to explore in detail some of the possible causes for the benefits and costs that helpers provide to both offspring and breeders in the sociable weaver.

In the sociable weaver, helper's alloparental care take mostly the form of building the chamber, cleaning the chamber (by removing faecal sacs and uneaten food), brooding the nestlings and feeding the offspring which is the most pronounced helper's contribution. In order to comprehend the positive and negative effects of helpers it is crucial to explore in detail their importance in such tasks. Here I focus on all mentioned tasks and I test which of two non-exclusive scenarios occurs in this species: helpers might have an addictive effect through increasing the total amount of care that nestlings receive and/or allowing breeders to load-lightening their work load (compensatory effect).

I expect that breeder's investment in all tasks should decrease in the presence of helpers because: 1) this species is relatively long live and should favour survival over reproduction when possible; 2) it has been shown that helpers have a positive effect on female's survival (Paquet et al. 2015) and 3) only marginally increased reproductive success (Covas et al. 2008). This same study also showed that there are no differences in the amount of food that the nestlings receive in the presence of helpers (Covas et al. 2008). Nevertheless it did not cover all the nestling period (i.e. it was mainly conducted when chicks were around 8 days old). As nestlings grow bigger their demand for food increases and hence the investment rules of the breeders and helpers may change. Thus, a study in which the full nestling period is completely recorded is especially relevant. Finally, no study has ever investigated the effect of presence of helpers on the other tasks mentioned before (chamber construction, sanitation and brooding)

Also I investigated whether this decrease in breeder's workload might represent a possible cost for offspring if breeders "neglect" their brood and transfer their feeding care to helpers. For instance, as helpers are usually younger and less experience than breeders, they may bring lower amounts or quality of food to the nest. Such a scenario might explain the puzzling result of nestling survival in presence of helpers (Covas et al. 2011; Broom 2013).

Helpers could also have a negative effect on juvenile survival by influencing fledging date and fledging condition. In species in which nest predation is common, there might a trade-off between staying more time in the nest to develop (increasing mass or wing length) with being more vulnerable to predators (Raihani & Ridley 2007). In the sociable weaver, the major cause of known death among nestlings is depredation by snakes (ca. 70% of breeding attempts Covas et al. 2008). Therefore it can be more advantageous to the offspring to leave the nest as soon as possible to avoid predation, than delaying fledging to increase mass or wing length. Helpers could promote a later fledging by keep feeding the chicks while breeders may cease provision to induce them to leave the nest. For example, in pied babblers, *Turdoides bicolor,* fledglings that are attacked by parents direct their begging towards helpers, which are less aggressive (Raihani & Ridley 2008).

To summarise, in this work I investigate several possible mechanisms underlying both benefits and costs that helpers provide to breeders and offspring. Concerning the benefits I first test whether the number of helpers is related to an increase in the total amount of care provided to nestlings (i.e. feeding, chamber building, cleaning and brooding the nestlings). Second I test if breeders transfer their care to helpers and specifically whether as the nestling period progresses breeders decrease their number of feeding visits while helpers increase it. In addition, I test whether this transfer of care may represent a decrease in feeding quality by comparing the size of prey that breeders and helpers bring to the nest, as a proxy of food quality. Third, I test whether helpers are associated with a delayed fledge date. Finally, I use Capture-Mark-Recapture (CMR) approach, following similar procedures to a previous work (Broom 2013), to test if helpers have a negative effect on the fledgling‘s survival in the first 10 days after leaving the nest. The previous work (Broom 2013) found a negative effect of helpers and since this effect might vary between contexts (e.g. between different social and environmental conditions), it is important to study helper’s influence across years.

Methods:

Study species and field methods:

The sociable weaver is a sexually monomorphic, colonial cooperatively breeding passerine, which is endemic to the semi-arid savannahs of southern Africa (Maclean 1973a) where it feeds mainly on insects and seeds (Maclean 1973c). This weaver species builds massive nests with several chambers, usually on trees, where birds roost throughout the year and where breeding takes place (Maclean 1973b). The size of the colony can range from few to several hundred individuals. The breeding pairs can either breed with or without helpers (30-80% of breeding attempts have 1-5 helpers; Covas et al. 2008). Helpers are usually the offspring (both males and females) from the previous years, but up to 20% of helpers are more distant relatives or unrelated and there is no evidence of extra-paternity (Covas et al. 2006; Paquet et al. 2015). Females usually lay 3-4 eggs (1 per day) and can have several broods per breeding season (Covas et al. 2008).

This study was conducted at the Benfontein Game Farm, situated ca. 6 km south-east of Kimberley, in the Northern Cape Province, South Africa, between September and December 2014. Most of the colonies in this area have been captured since 1993 to mark the birds with a numbered metal ring and a unique combination of colours rings that allows for visual identification of the birds. Blood has been also collected for genetic sexing and determination or parentage and relatedness among individuals.

Between late August and early September 2014 (i.e. before the usual onset of the breeding season), most of the birds from the study colonies were captured by the team (including myself) using mist nets, to ring and collected blood from birds that were new to the study colonies (i.e. immigrants) or had never been captured before. Additionally the number of individuals caught was used as a measure of colony size (all colonies were caught only once). This study was conducted in 13 colonies. Since nest predation in this species is very high (ca. 70% of the breeding attempts are depredated; Covas et al. 2008) in order to ensure enough data, we protected 6 colonies against snake predation (the main nest predator) by wrapping cling plastic around the tree trunk.

We then routinely inspected all colonies every 3 days, to identify initiation of new clutches. The incubation period lasts 15 days and the nestlings usually hatch asynchronously (1 per day) and the nestling period lasts 21-24 days (Maclean 1973a). When the nestlings were 9 days old (day 9) the chambers were visited to ring the chicks (with a uniquely numbered metal ring), collect a small blood sample for sexing and genotyping analyses and weigh them. When the chicks were 17 days old (day 17), the chambers were visited again to weigh and measure the wing and tarsus of the chicks and give them a unique combination of plastic colour rings to allow for future individual identification. After day 17 chambers could no longer be inspected as this would induce premature fledging.

Genotyping analysis:

Genotyping analyses were conducted at the University of Sheffield (UK). Sex was determined by amplification of chromo-helicase-DNA-binding genes located on the W and Z sex chromosomes using the P2 and P8 universal primers (Griffiths et al. 1998). To distinguish between breeders and helpers 17 microsatellite loci were used to determinate parentage (PS1-GCSW15, GCSW47, INDIGO40, TG22- 001, PS2-GCSW35, INDIGO41, Ppi2-Gga, TG01-148, WBSW9, PS3 GCSW13, INDIGO29, CAM1, CAM15, PS4-Ase18, GCSW31, GCSW57, TG07-022; Martinez et al. 1999; McRae & Amos 1999; Richardson et al. 2000; Sefc et al. 2001; McRae et al. 2005; Dawson et al. 2010, 2013).

GenePop v.4.0.1 (Raymond & Rousset 1995) was used to test for conformity to Hardy–Weinberg equilibrium and to check for linkage disequilibrium for each locus and microsatellite GCSW57 was excluded since it was not in conformity to Hardy–Weinberg equilibrium. I used Colony v2.0.3.8 (Jones & Wang 2010) to assign each juvenile to a most likely father and mother by full-likelihood method. I used all the genotypes from all adult birds ever genotyped (1377 females and 1418 males) and 76 offspring genotypes from 31 chambers of interest (see below). Marker typing error was set to 1% and the proportion of candidate parents genotyped was set to 75% to include the possibility of an unknown bird being the parent (all other settings or set to default). I assigned parentage when parentage probability was 1. In four situations, one of the birds feeding the nestlings was not ringed or had lost most colour rings. Since there is no evidence for extra-group paternity in this species (Covas et al. 2006; Paquet et al. 2015) and none of the other birds from these groups had genotypes compatible with being one of the parents, I assigned parentage to the unidentified bird.

Video analysis and group size determination:

I used video camera recordings (Sony Handycam HD) to identify which birds were feeding at a given chamber and to determine the breeding group size.

To test whether parents transfer parental care to the helpers, I recorded the feeding behaviour of 31 chambers over the nestling period (21 days) by splitting it in 3 different stages: stage 1 - from 4 to 6 days old, stage 2 - 8 to 12 day old and stage 3 - from 16 to 21 days old. Each stage was recorded for at least 1 hour per day in 1 to 3 different days (155±55 SD minutes per day and 320±120 SD per stage). Recordings were conducted from early to mid-morning and mid to late-afternoon, avoiding the hottest parts of the day when birds are less active.

To test if the number of helpers is related to fledging date I conducted observations after the nestlings were 17 days old (see below) for 20 chambers: 13 of the 31 chambers mentioned above and another 7 chambers for which I had enough videos to estimate group size, but not enough to including in chamber attendance analyses (2 to 3 days of recordings only). For the post-fledging survival analysis I used the same mentioned chambers and an additional 4 (with 2 to 3 days recordings).

During video analyses I distinguished between feeding visits and visits for other purposes, specifically nest building and sanitation visits (i.e. when the birds bring grass to the nest and are seen weaving or when they remove faecal sacs, respectively). I also estimated the time a bird spent brooding the nestlings during the video analyses (see below). Videos in which I failed to identify more than 5% of the visits were excluded from the analyses (only in one video). In addition, it appears that not all the birds that feed the nestlings are actually part of the breeding group: some birds sporadically feed the juveniles, but are usually chased away by the group members (personal observation). To determine if a bird was part of the breeding group I used the following criterion: a bird had to feed on more than 1 one day and contribute more than 1% for the total feeding visits of the chamber. This criterion seemed to successfully exclude those birds (N= 14 males, 9 females and 8 unidentified)

1) Overall care:

To test if group size is related to the total amount of feeding, building, sanitation and brooding care that the nestlings received I used generalized linear mixed models (GLMMs) with number of feeding, building or sanitation visits that a nest receives per day as dependent variables and a linear mixed model with the time (min) that the nestlings spent being brooded by at least one adult as dependent variables. The explanatory variables were group size (number of adults feeding the nestlings), colony size (small or big), the interaction group size*colony size, age of the nestlings (in days), brood size, maximum day temperature (ºC), wind speed (m/s), the sum of rain fall (mm) in the previous 30 days before the observation, the recording midpoint time since sun rise (min; hereafter time since sun rise), recording length (min) to control for differences in recording effort. Nest and colony identity were introduced as random factors. Weather condition variables were collected at Kimberley Airport Station, 12 km from the centre of the study site and were included in the analysis since they probably affect all types of visits and the time spent inside the nest. Colony size as been reported to significantly interfere with helpers effects in previous studies in this species (e.g. fledging success; Covas et al. 2008; juvenile survival; Broom 2013), therefore I included in this analysis as well. Half of the nests used in this analysis were in colonies with less than 46 individuals (individuals captured at the beginning of the season) and the other half were in colonies with more than 86 individuals (the smallest colony had 7 and the biggest 104 individuals). Consequently I used colony size as a dichotomous variable, small when less than 46 versus large with more than 86, instead of number of individuals per colony.

For the analysis of feeding, building and sanitation visits I ran GLMMs with a negative binomial distribution, instead of poisson since models with a poisson distribution were overdispersed (c-hat; residual deviance/residual degrees of freedom>4.351, ideally 1). Overdispersed models can be a result of misspecification of the error term distribution and increase the type I error rates (Crawley 2012). In this case using a negative binomial distribution successfully account for overdisperison of the data (c-hat ca. 1 for all models). For the analysis of time spent brooding the dependent variable seemed to be normal distributed and the residuals of the model were visual inspected (QQ plots, fitted versus residuals plots and histograms) to verify assumption of the linear mixed model.

For the sanitation and building visits analysis I only used data obtained when the chicks were less than 8 days old and older than 12 days old, respectively, since most of these visits (96% and 89% respectively) only occurred within these time periods. Regarding brooding, since maintaining nestling warm while they are developing their feather might be one of the main functions. I only used data until the nestlings were 6 days old, i.e. when they have no feathers yet. I considered that an adult was brooding if it stayed for more than 20 seconds at the nest, visits shorter than that were excluded to clearly distinguish from feeding visits which usually last for less than 10 seconds.

From the 31 chambers used to analyse overall care, four chambers had only the breeding pair therefore were excluded from this analyses, as groups without helpers can have a very different care dynamics and I did not have enough data to conduct analyses of helpers *vs* no helpers. For this analysis I used 27 chambers with 2.44±1.47 helpers per nest.

For all analysis above model selection was based on the Akaike information criterion corrected for sample size (AICc). I had a group of variables which I was not particularly interested in, but could affect sociable weaver's behaviour (weather variables and time since sun rise). To avoid problems with over-parameterising the models (Burnham & Anderson 2002) I did a preliminary analysis to select for the most important variables within this group. I ran (G)LMMs with the respective dependent variable (feeding, building, sanitation visits or brooding time) and all possible combinations of the explanatory variables: time since sun rise, the weather variables, nestling's age, video length and brood size and calculated the relative importance for each variable (flowing Symonds & Moussalli 2011; see supplement material for more details) within the ΔAICc = 2 range. For all analyses the relative importance of all variables were either 1 or less than 0.66 (see supplement material), therefore time since sun rise and weather variables were kept for the main analysis if had a relative importance of 1.

For the main analysis I compared the AICc for all possible model combinations of the variables of interest and the ones considered important. The model with the lowest AICc is considered to be the best model, but models with less than 2 AICc from the best model are considered to be as good as the best one (Burnham and Anderson 2002). For most cases, there were more than one model within the ΔAICc = 2 range, which were a result of adding or removing variables which were not significant in any of the models. Since adding or removing them did not cause major changes on the estimates and p-values of the variables present in the best model, there was no need for a model averaging approach and I choose to present the results from model with the lowest AICc and show the AICc for all models within the ΔAICc = 2 range in the supplement material. The significance of the fixed effects was tested by comparing models with and without the predictor with likelihood ratio tests (LRT). Normality of the residuals and homoscedasticity were visually inspected using plots (QQ plots, fitted versus residuals plots and histograms) and for all GLMMs and I checked for overdispersion (c-hat=residual deviance/residual degrees of freedom) All analyses were conducted using R (v.2.15.3; R Core Team, 2012) and with the packages: “lme4” (Bates et al. 2012), “RVAideMemoire” (Hervé 2014) and “MuMIn” (Barton 2012).

2) Transfer of care:

To test if breeders transfer their care over time to helpers I did a similar analysis to the ones above, with feeding, building, sanitation visits or time spent brooding per adult per day as dependent variables (instead of number of each visit and time spent brooding per chamber per day). The explanatory variables were status (breeder male, breeder female or helper), group size, colony size, age of the nestlings, brood size, maximum day temperature, wind speed, the sum of rainfall in the previous 30 days, the recording midpoint time since sun rise and recording length, and the interactions: nestling’s age*status, nestling’s age*group size, status*group size and nestling’s age*status*group size. The random factors were bird identity, chamber and colony identities. Even though female and male helpers can behave differently I did not distinguished between female and male helpers since the genetic analysis failed to identify the sex of 15% of the helpers and removing these helpers from the analysis would decrease the statistical power.

In order to understand whether helpers provide poorer feeding care to nestlings than breeders, I compared the feeding quality of helpers with breeders based on the size of the prey brought to the nest. I collected prey size from the video analysis every time that the prey length was clearly visible. Prey size was assigned in 2 categories:

small prey- smaller than twice the beak length, and large prey if bigger. I collected prey sizes from 330 feeding events from 63 identified birds (37 breeders and 26 helpers). I analysed this data with a GLMM with a binomial distribution, prey size (small or big) as dependent variable, weather variables, time since sun rise, brood size, group size, colony size, nestling's age and status as fixed factor and bird, nest and colony identities as random factors.

In addition to the four pair only chamber mentioned above (in the overall care analysis), in another two chambers genetic analysis failed to identify the breeders as a result of more than one bird were completely unrigged or lost most of the colour ring. I successfully identified 25 breeding pairs and 60 helpers (2.4±1.5 per group), which were used in all analysis of this section.

For all analysis above model selection was done following similar procedures as in the overall care section. With the exception of prey size analysis, there was no need for a preliminary analyses on the weather variables and time since sun rise as the data is the same as in the overall care. I included weather variables and time since sun rise if they were considered important in the overall care analyses.

3) Fledging date and juvenile survival:

I tested if the number of helper would decrease the nestling period and influence juvenile survival using a Capture-Mark-Recapture (CMR) approach. Capture life histories are usually used to estimate survival parameters through maximum likelihood methods (Lebreton et al. 1992), which can take into consideration the probability of surviving and the probability of recapture.

For fledging date I built capture life histories by observing each chamber every day after day 17 of the oldest chick in the chamber until day 25. Day 17 is the last day that we can safely check inside the chamber (inspecting nest-chambers after can induce a premature fledge by the juveniles) to confirm how many nestlings are inside the chamber. After day 25 I assumed that at least the oldest juvenile in the nest was able to fly (usually nestlings are 0-1 day older than the following as a result of 0-1 day hatching asynchrony). Once juveniles are over 15 days old, they usually stay at the chamber entrance begging for food (Fig. 1), and it is possible to count how many chicks are inside the chamber. Juveniles were not visually marked and it was not possible to see their colour rings, therefore I had to see simultaneously all the juveniles from one chamber to confirm that none of them had fledge. I observed each chamber with a hide 2-3m away for 15min; this is enough to see one feeding event, which induces juveniles to beg at the entrance. Observations for each chamber were always done at the same time of the day (early morning or late afternoon). Whenever I saw all the juveniles from one chamber I scored 1 and if one or more juveniles were missing the score was 0, therefore the “statistical unit” is the brood and not the juveniles themselves. In this case probability of survival corresponds to the inverse of the fledging probability, i.e. the probability of staying in the nest (φ; hereafter delayed fledging probability), and the probability of recapture corresponds to probability of seeing all nestlings inside the nest (P). I did a similar analysis but focusing on the last chick to leave the nest instead of the first one. In this analysis I score 0 for a totally empty nest and 1 if I saw at least one juvenile. As the results were the same (not presented) I chose to present only the analysis focusing on the first juvenile to leave the nest.

I could be certain that the absence of a juvenile was due to fledging and not due to predation since most of the chambers (19 out of 23) were in colonies protected from snakes and in the ones that were not, all juveniles except one were seen after they have fledge (and predators usually take the whole brood). Even though I cannot exclude the absence of nestling as a result of starvation, all the juveniles had their mass within the normal range at day 17, suggesting that starvation was unlikely.

Figure 1. Two, 17 day old juveniles visible at the chamber entrance

I was mainly interested in the effect of the group size on delayed fledging probability; nevertheless other factors could influence this probability: number of nestlings, mass and nestling development (for which I used as a proxy wing length at day 17). As the “statistical unit” was chamber identity, I used the mass of the nestling with the largest wing in the nest since I expect that the most developed juvenile will be first to leave the nest

Although it is improbable that a juvenile would fledge before day 21, I started the observations at day 18 to obtain better estimates of the recapture probability which was set to be constant over time (P(.)). In addition, the best model was highly likely to be age-dependent, since older chicks will have higher probability of leaving the nest and also because juveniles are unlikely to fledge before day 21. Therefore, before introducing the variables of interest, I first started by running an age-dependent model for survival (Φ(Age)P(.)), which showed as expected a clear decreasing trend on survival estimates (in this case delayed fledging estimates) from 0.99±0.01 at day 18 to 0.22±0.13 at day 25. Second, since it was easier to miss one juvenile from a nest of 3 than from a nest of 1, I added to the recapture probability brood size (Φ(Age)P(Brood)) which was better than the Φ(Age)P(.) model (ΔAICc=10.01). Finally I added one by one the variables of interest to the delayed fledging probability (Φ). I compared the AICc values of the different models and used LRT tests to determine variables significance. This analysis was conducted using Mark software (Cooch & White 1998; White & Burnham 1999). Besides wing length, mass, brood size and group size, other factors could influence fledging date (e.g. colony size and weather conditions). However the final sample size was small (20 chambers) and large model sets are not reliable with small sample sizes (Burnham and Anderson 2002), therefore I tested only the most relevant ones which I was most interested in.

To analyse post-fledging survival, regular observations after the juveniles had reached 30 days of age were conducted by the team and I with the aim of building recapture histories. Observations were conducted every week or every two weeks before sun set when the entire colony comes to the colony to roost. Each colony was visited 4 times. Data from 95 juveniles from 38 chambers was used and followed the similar procedures as in previous analysis. I tested if juvenile survival and recapture probability were time dependent, constant or age dependent by comparing the AICc values from these models. Contrary to the previous work (Broom 2013) the model with constant and time dependent recapture (Φ(Age)P(t)) was the model with the lowest AICc. However the AICc of this best model is not low enough to distinguished from the model with 2 age classes (before and after day 30; ΔAICc=1.90) used as a starting model in the previous work (Broom 2013), which used a larger sample size (156 juveniles) and six more visual recaptures. Taking this into consideration and since I was particularly interest in helpers effect on juveniles survival right after fledging, I decided to also use the Φ(2Age)P(t) as a starting model. After this, I added colony size (small or big), and as covariate to the recapture probability of the Φ(2Age)P(t), (as in Broom 2013). Contrary to the previous work, this model had significantly low support (ΔAICc=2.63) and therefore I decided not use colony size as covariant for recapture probability. Finally I added to the survival probability several variables to the first age interval (day 17 to day 30), that could influence juvenile survival: rainfall in the 30 days before day 17, colony size, mass and wing length at day 17 as proxy of juvenile development, group size and the interaction group size*colony size. I did not use snake protection as covariant to avoid possible confounding effect with colony size as all small colonies (expect one) were unprotected and all big colonies were protected. Model combinations were compared using AICc and LRT to determine variable significances.

Results:

1) Overall care:

Group size was not present in any of the best models for the analysed tasks: feeding, brooding, sanitation and building (see supplement Table S3). Group size was present within the ∆2AICc for overall feeding and building, however it was not significant in both cases (P>0.05) and the relative importance was less than 0.34 (see supplement material for information on relative importance), which gives very low support for an effect of group size. Colony size was significantly related with overall feedings with more visits in smaller colonies (estimate =0.27±0.07SE, LRT=7.86, P=0.006; Table 1). Nestling's age was positively related with feeding, sanitation and building visits, (estimate=0.03±0.01SE, LRT=20.57, P<0.001; estimate=0.11±0.02SE, LRT=18.12, P<0.001; estimate=0.11±0.02, LRT=10.26, P<0.001; Table 1) and negatively related with time that the nestlings spent being brooded (estimate=-12.68±4.50SE LRT=7.83, P=0.005; Table 1). Maximum day temperature and time since sun rise were negatively related with overall brooding (estimate=-2.94±0.84SE, LRT=11.76, P<0.001; estimate=-0.08±0.02SE, LRT=20.37, P<0.001) and wind speed was also negatively related with building visits (estimate=-0.18±0.06SE, LRT=7.34, P=0.007). As expected all tasks were positively related with video length (P<0.001 for all models; Table 1).

Table 1. Results from the GLMMs for the overall feeding, building and sanitation visits and from the LMM for the overall brooding time per nest.

Task	Predictors	Estimate	SE	LRT	P
Feeding	intercept	1.46	0.22		
	video length	0.01	0.001	97.31	<0.001
	nestling's age	0.03	0.01	20.57	<0.001
	brood size	0.20	0.06	10.51	<0.001
	colony size			7.86	0.006
	small colony	0.27	0.07		
Brooding	intercept	198.70	38.58		
	video length	0.54	0.07	39.35	<0.001
	nestling's age	-12.68	4.50	7.83	0.005
	temperature	-2.94	0.84	11.76	<0.001
	time since sun rise	-0.08	0.02	20.37	<0.001
Sanitation	intercept	-0.80	0.32		
	video length	0.01	0.001	15.93	<0.001
	nestling's age	0.11	0.02	18.12	<0.001
Building	intercept	-1.32	0.88		
	video length	0.01	0.003	17.87	<0.001
	nestling's age	0.13	0.04	10.26	<0.001
	wind speed	-0.18	0.06	7.34	0.007

2) Transfer of care:

Regarding feeding care, the results from the GLMM shows a significant effect of the interaction nestling’s age*status (LRT=11.89, P=0.003; Table 2). Although helpers fed on average less than male and female breeder, they increase more their feeding visits over time than male and female breeders (Figure 2). This means that although all status classes increase their feeding visits with the increasing demand for food (as the chicks grow older) helpers compensate more for this increasing demand than breeders. The interaction nestlings’ age*group size was also negatively significant (estimate=-0.01±0.003SE, LRT=6.18, P=0.01; Table 2), which means that over time each group member has to feed less in bigger groups than in smaller groups.

Table 2. Results from the GLMMs, for transfer of care regarding feeding visits and from the LMM for the time spent brooding

Task	Predictors	Estimate	SE	LRT	P
Feeding	intercept	1.62	0.30		
	video length	0.01	0.001	134.10	<0.001
	nestling's age	0.05	0.02		
	group size	-0.09	0.05		
	status				
	male breeder	0.11	0.21		
	helper	-1.28	0.18		
	nestling's age*group size	-0.01	0.003	6.18	0.01
	nestling's age*status			11.89	0.003
	male breeder	-0.0002	0.01		
	helper	0.03	0.01		
Brooding	intercept	115.98	24.43		
	video length	0.16	0.03	21.85	<0.001
	nestling's age	-11.08	3.74		
	status				
	male breeder	-24.66	24.56		
	helper	-112.66	22.21		
	temperature	-1.12	0.43	6.71	0.009
	time since sun rise	-0.02	0.01	7.57	0.005
	nestling's age*status			14.51	<0.001
	male breeder	5.41	4.98		
	helper	16.65	4.55		

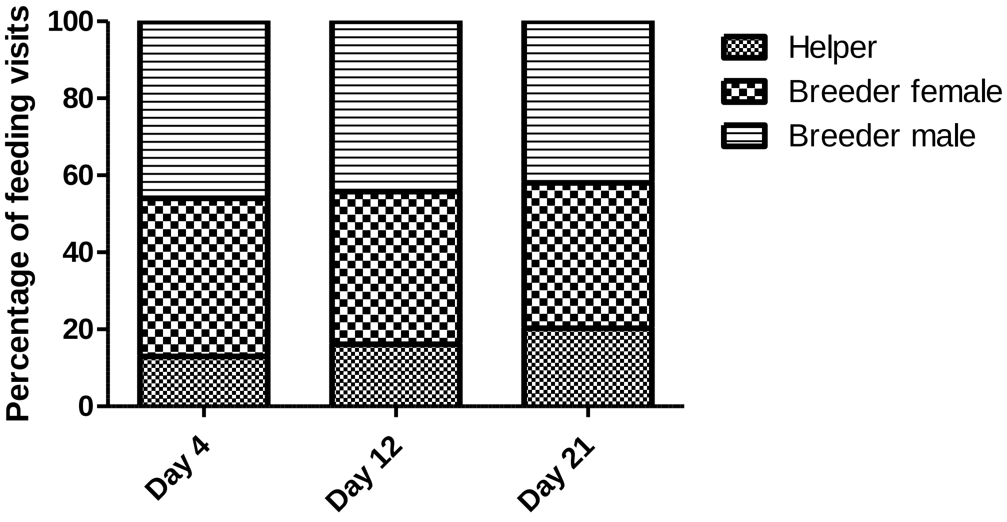

Figure 2. Percentage of feeding visits per status and nestling's age. Values used to compute the percentages were predicted from the best model (Table 2). Other parameters set to their mean values. Helper represents the feeding share of all helpers attending the nest.

A similar pattern is also observed for the time that adults spent brooding the nestlings, with a significant interactions of nestling's age*status (LRT=14.51, P<0.001;

Table 2). In this case breeders decrease over time the amount of time spent with the nestlings while helpers increase it (Figure 3). Temperature and time since sunrise have also a negative and on brooding as reported in the overall care (estimate=-1.12±0.43, LRT=6.71, P=0.009; estimate=-0.02±0.01SE, LRT=7.57, P=0.005, respectively; Table 2).

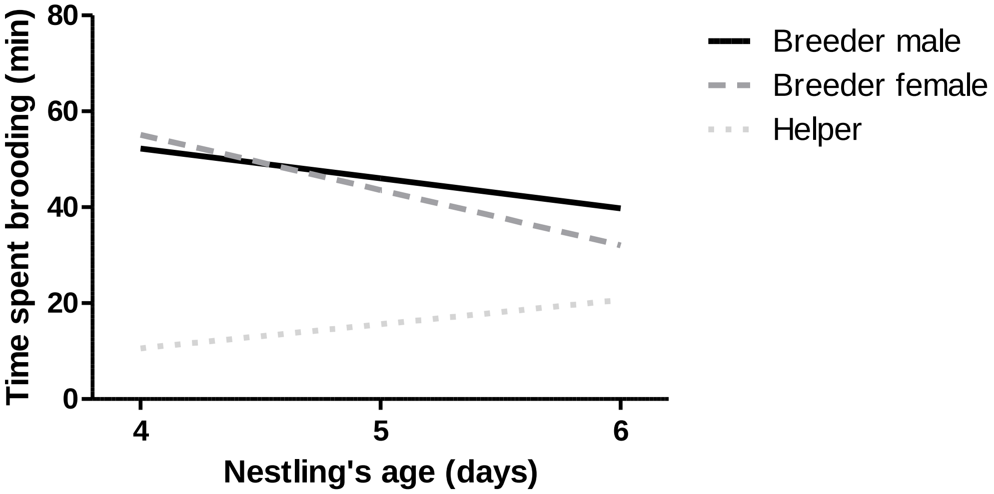

Figure 3. Time spent brooding per status and nestling's age. Values were predicted from the best model (Table 2). Other parameters set to their mean values.

There is a significant increase in the sanitation visits over time (estimate=0.07±0.03SE, LRT=10.82, P=0.001; Table 3), but all status increased in the same magnitude (nestling's age*status was not within 2ΔAIC). Male breeders were responsible for most of this type of visits (estimate=0.58±0.19SE; LRT= 37.269, P<0.001; Table 3).

Table 3. Results from the GLMMs, for the transfer of care regarding sanitation and building visits.

Task	Predictors	Estimate	SE	LRT	P
Sanitation	intercept	-1.97	0.63		
	video length	0.01	0.001	19.86	<0.01
	nestling's age	0.07	0.03	10.82	0.001
	status			37.27	<0.001
	male breeder	0.58	0.19		
	helper	-0.80	0.21		
	group size	-0.12	0.06	2.82	0.09
	brood size	0.28	0.14	2.42	0.12
Building	intercept	-4.27	1.26		
	video length	0.01	0.00	9.86	<0.001
	nestling's age	0.26	0.06		
	status				
	male breeder	5.59	1.24		
	helper	0.96	1.27		
	group size	-0.17	0.09	2.88	0.09
	wind speed	-0.14	0.05	5.95	0.01
	nestling's age*status			10.65	0.005
	male breeder	-0.29	0.07		
	helper	-0.12	0.08		

Regarding building, breeding males build more than helpers and breeding females, but tend to decrease their building visits over time while female breeders and helpers increase it (LRT=10.65, P=0.005; Table 3; Figure 4).

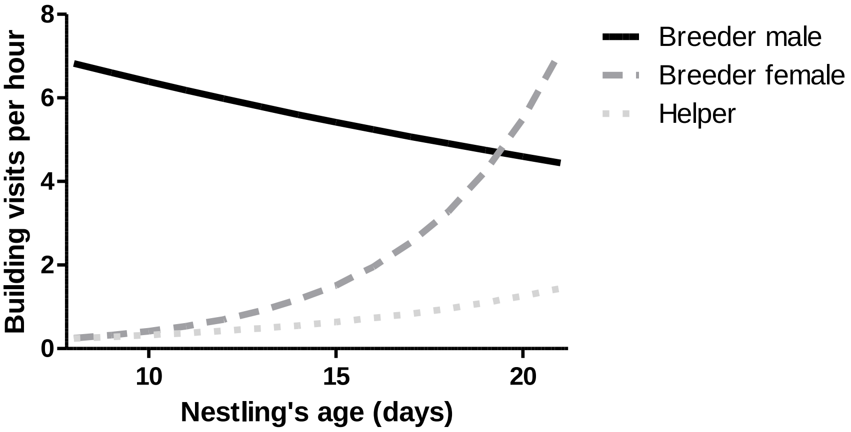

Figure 4. Building visits for per status and nestling's age. Values were predicted from the best model (Table 3). Other parameters set to their mean values.

Concerning prey size female breeders have a significant higher probability of bringing larger prey to the nest than male breeders and helpers (LRT=7.95, P=0.02,

Table 4; Figure 5). Rainfall in the previous 30 days to the observation was also positively related with prey size (estimate=0.05±0.02SE, LRT=6.10, P=0.01).

Table 4. The results from GLMM with binomial distribution relating prey size with rainfall and status.

Predictors	Estimate	SE	LRT	P
Intercept	-0.21	0.51		
Status			7.95	0.02
Male breeder	-0.73	0.34		
Helper	-1.33	0.48		
Rainfall	0.05	0.02	6.10	0.01

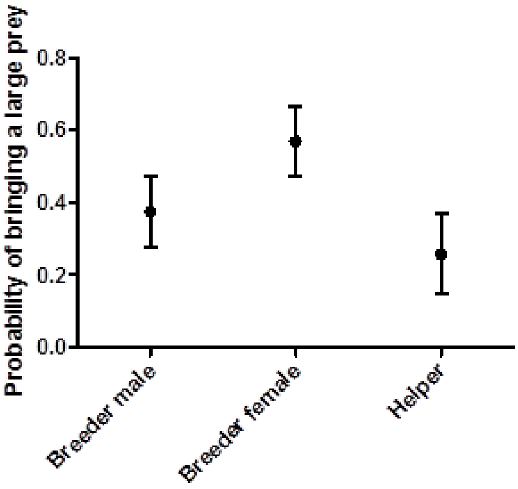

Figure 5. Estimated probability of feeding a larger prey to the nestlings. Means are shown ± SD

3) Fledging date and juvenile survival

Helper effect on fledgling date:

For fledge date the two models within 2ΔAICc range, had group size as covariant (Table 5). The best model show a positive effect of group size on the probability of a juvenile staying longer in the nest, i.e. juveniles raised in smaller groups have a higher probability of fledging earlier than juveniles in larger groups (Figure 6). LRT shows that this model is significantly better than the model without number of helpers (Φ(Age)P(Brood) vs Φ(Age+Group size)P(Brood)) LRT=4.36, P=0.04). Brood size was also in the second best model but LRT shows no significant effect of this variable (LRT=1.13, P=0.29). Models with other covariates (mass, wing length) had little support and we can consider group size as the most important factor to influence fledging date.

Table 5. The best models (lowest AICc) and predictors affecting delayed fledge (φ) and recapture (P) probabilities.

Model	AICc	Delta AICc	AICc Weights
φ(age, group size).P(brood size)	157.44	0	0.53
φ(age, brood size, group size).P(brood size)	158.64	1.20	0.29
φ(age).P(brood size)	159.52	2.08	0.18

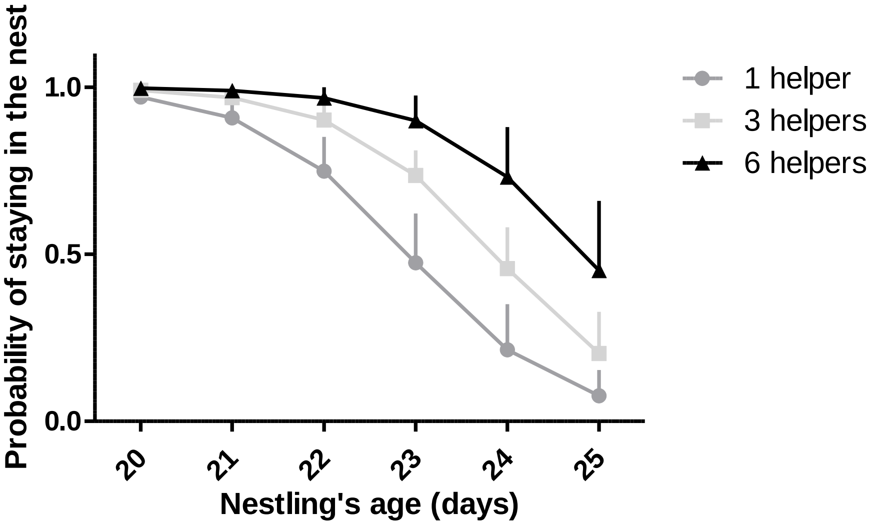

Figure 6. Estimated probability of leaving the nest in relation to nestling’s age for three types of groups: groups with 1, 3 and 6 helpers (maximum number of helpers in this data set). Means are shown ± SD

Regarding post-fledging survival, the model without any of the variables of interest had the lowest AICc, which means that none of the variables had significantly improved fit compared to the model with just age. Nevertheless all variables were present in models within the 2ΔAICc range, and therefore there is also not enough evidence to consider these variables as non-important to explain the variation in survival. Within the variables of interest wing length was the most important one with a relative importance of 0.55 (see model selection section in the supplement material for details on relative importance), followed by mass (relative importance=0.33), group size (relative importance=0.18), colony size (relative importance=0.12) and finally, rainfall (relative importance=0.06). Group size seemed to show a negative trend in juveniles survival (estimate from the best model in which the variable is present: estimate=-0.150±0.211). For the remaining variables, wing length and brood size seem to show a positive effect on survival (estimate= 0.171±0.115SE; estimate= -0.22±0.168SE; respectively), while, colony size, mass and rainfall seem to have a negative effect (β= -0.009±0.01SE; estimate=-0.223±0.168SE; estimate=-0.040±0.036SE; respectively). However since there is high model uncertainty and the model with just age is the best one I don’t draw strong inferences on these results.

Table 6. The best models (lowest AICc) and predictors affecting post-fledging survival (φ) and recapture (P) probabilities**.**

Model	AICc	ΔAICc	AICc Weights
φ(age).P(time)	356.9695	0	0.15313
φ(age, wing length).P(time)	356.972	0.0025	0.15294
φ(age, mass, wing length	357.148	0.1785	0.14006
φ(age, mass, wing length, rainfall).P(time)	358.4903	1.5208	0.07159
φ(age, group size, mass, wing).P(time)	358.6175	1.648	0.06718
φ(age, group, wing length).P(time)	358.6942	1.7247	0.06465
φ(age, brood size).P(time)	358.789	1.8195	0.06166
φ(age, rainfall).P(time)	358.8633	1.8938	0.05941
φ(age brood size, wing length).P(time)	358.9042	1.9347	0.0582
φ(age, mass, wing length, colony size).P(time)	358.9139	1.9444	0.05792
φ(age, mass).P(time)	358.9523	1.9828	0.05682
φ(age, group size).P(time)	358.9659	1.9964	0.05644

Discussion

The aim of this study was to identify some of the possible mechanisms that might underlie the costs and benefits associated with the presence of helpers-at-the-nest to both breeders and offspring. The results obtained suggest a transfer of work load from breeders to helpers - specifically for feeding and brooding care. This can be beneficial to breeders, but negative for nestlings as the feeding care of helpers seems to be of lower quality (smaller prey size) than female breeders. Furthermore, the presence of helpers was related to a delayed fledging date which may be disadvantageous in this species where nest predation is high. Moreover, there was no obvious effect of helpers on post-fledging survival compared to other variables, contrasting with results from previous years and suggesting a potential year effect. I discuss these results in turn.

The results showed no significant effect of group size on the overall effort for all studied tasks (feeding, building, brooding and sanitation). While all adults attending the chamber increased their feeding visits over time, male and female breeders increased it at a lower rate than helpers, which meant that at the end of the nestling period helpers provided approximately 20% of the feeding care. This share of care did not change with group size. These results suggest a compensatory rather than an additive effect of helpers. This is expected in species where nestling starvation is not the major cause of death (Hatchwell 1999), which is the case of the sociable weaver, as starvation is not frequent and predation is instead the main cause of nest failure (Covas et al. 2008). Similar results were found in other long-lived bird species. For example, in the purple-crowned fairy-wren, *Malurus coronatus,* breeders transfer 20%-30% of their care to helpers (Kingma et al. 2010). These results suggest that in bigger groups all members have the opportunity to work less, instead of improving the overall investment in the present brood. In long-lived and multi brood species, such as the sociable weaver or the purple-crowned fairy-wren example, breeders might benefit by minimizing their effort whenever possible in order to save energy for the next breeding attempt as this may result in a higher lifetime reproductive success (Trivers 1972; Ghalambor & Martin 2001; Kingma et al. 2010).

As nestlings grow older their feeding demand increases and, in this study, helpers seemed to compensate more than breeders for this growing demand. Even though breeders from day 4 to day 21 only transferred care to helpers by 8%, this represents a significant amount of feeding visits since nestlings receive 70% more food at day 21 than at day 4, which represents an average increase of 8 feeding visits per hour (as estimated from the best model in Table 1). Helpers may therefore, play an important role during the most demanding part of the nestling period. This result also brings awareness to the possible underestimation of helper’s contribution if the whole nestling period is not covered.

While the transfer of feeding care might be advantageous for the parents this can represent a cost for the offspring as helpers seem to bring smaller food items to the nest. Breeders may therefore be exchanging quality nestling care for the apparently lower quality care of the helpers, which may amount to trading off improving their own condition or survival prospects against that of their offspring. In some species, younger individuals have lower quality parental care than older individuals (Boland et al. 1997a). Therefore this trade-off should be expected in most species where helpers are younger and less experienced than breeders. Even though this is not the first work to report differences in prey size along with feeding visits between helpers and breeders in birds (e.g. du Plessis 1991; Wright 1998; Browning et al. 2012), this is to my knowledge the first to point it out as possible trade-off to breeders transfer of care.

I am aware that prey size may be a poor proxy of feeding quality and adding other traits such as prey type to the analysis could better reflect the nutritional content of the food (e.g. Naef-Daenzer et al. 2000), unfortunately it was not possible to successfully identify enough prey types to include in the analysis. Nevertheless prey size increased with rainfall, which is positively linked to sociable weaver’s breeding activity (Maclean 1973c). These results suggest that the reproductive success might be dependent on the size of the prey brought to the nest and therefore this analysis may have captured significant biological variance. Additionally, there was also evidence for a transfer of care regarding brooding behaviour, as breeders, especially females, decreased their brooding time with increasing brooding by helpers. Regarding building visits, there was also a significant interaction between nestling’s age and status, but this was mostly due to the increasing building rate of female breeders with the decreasing rate of building visits by the male breeders. Nevertheless, helpers also increased their building over time, but to a lesser extent than female breeders. Together these results suggest that breeders partially transfer their care to helpers, with a gradual task partitioning overtime in this species. Although this is correlative and not necessarily a causal relation, helpers investment in feeding and building tasks were higher at the end of the nestlings period when females start to invest more in building the chamber, perhaps to prepare another breeding attempt. If this is indeed a case of tasks partitioning this might positively affect the reproductive output of the parents. For example, in the pied babbler, *Turdoides bicolor,* there is an extreme case of task partitioning where helpers assume the majority of the care of the first brood while the breeding pair start to raise another one (Ridley & Raihani 2008). As a result breeders benefit from this reproductive tasks partitioning by successfully raise more young per breeding season than pairs that are not assisted by helpers (Ridley & Raihani 2008). .

Besides improving reproductive success, this lightening of workload provided by helpers may also give breeders more time to invest in other activities that can increase survival (Crick et al. 1992). Furthermore, as parental care is costly (Bryant 1988; Heinsohn & Legge 1999), breeders are likely to directly improve survival by reducing parental effort. For example in the purple-crowned fairy-wren, *Malurus coronatus,* both male and female breeders feeding rates are negatively related with their own survival (Kingma et al. 2010), which suggests that breeders may live longer by reducing feeding care. In the sociable weaver, the suggestion for a lightening of workload fits well with the findings of a previous work that showed that females reduce their investment in reproduction in the presence of helpers (by laying smaller eggs; Paquet et al. 2013) and have higher survival in the presence of helpers (Paquet et al. 2015). However, for males, helpers have a negative effect and the mechanisms underlying such effect might to be rather complex (discussed in Paquet et al. 2015). Even though in this work I showed that female and male breeders alleviate feeding care in the same magnitude in the presence of helpers, the same was not true for brooding care. Females apparently benefit more than males regarding this task. Hence, my work reveal different ways in which helpers contribute to lightening the workload for male and female breeders, which in turn might lead to different influences on their survival.

Similar results were found in the other bird species, for example in the red-cockaded woodpecker, *Picoides boreali,* both male and female breeders increased their survival probability with the presence of helpers and both tended to decrease their feeding and brooding care (Khan & Walters 2002). However there was a stronger decline in male than female mortality probability. Other similar studies (reviewed in Khan & Walters 2002) including the present one, showed that the association between work lightening and survival benefits is far from being straightforward. This might be due to breeders spending their spare time in other costly activities (Khan & Walters 2002). For example as suggested in this work, female invested the potential spare time provided by helpers in building the chamber. Nevertheless helpers may still benefit female breeder if nest building is less costly then feeding nestlings and/or if investing in a better chamber leads to improved future reproductive success. Such findings highlight the importance of similar works which explore several potential benefits to avoid underestimating helper’s contribution.

The number of helpers was positively related with the probability of delayed fledging, suggesting that in the presence of helpers, juveniles take longer to leave the nest. Similar results were found in another species, the pied babbler, *Turdoides bicolor,* in which fledging date was negatively related to group size and positively related to predation risk (Raihani & Ridley 2007). However that work also showed that predation is higher in smaller groups, suggesting that larger groups can dilute the cost of a delayed fledging date (Raihani & Ridley 2007). In the sociable weaver, while I cannot rule out the possibility of an effect of group size in the predation risk, nestling's predation by snakes is very high (Covas et al. 2008) and colonies protected from snakes have been growing compared to unprotected. Therefore a delayed fledging date may also explain the higher mortality during the first days of the fledging period. A previous study showed higher post-fledging juvenile mortality between 17 and 30 days old (Broom 2013). However, typically, between days 18 and 25 the chick can still remain in the chambers (although the chambers are inspected for the last time on day 17, since inspecting them after this date can induce premature fledging; R. Covas personal observation). Hence, there will be usually be 2-7 days during which juveniles are still unable to fly properly and are vulnerable to snake predation.

The association between longer nestling periods and group size raises the question of the mechanism involved in this delay. I propose two explanations for the latter fledgling date of the nestlings. First, a previous study showed a marginally significant negative relation between the concentration of cortcosterone in the eggs laid by the female and the presence of helpers (Paquet et al. 2013). A study (Chin et al. 2009) in the European starlings, *Sturnus vulgaris,* showed that high concentration of corticosterone during the embryotic stage promoted an acceleration of muscle development and an improved flight performance. Suggesting that high concentration of this hormone in the eggs can influence future development and flying performance. It has been also suggested a link between this hormone and fledging behaviour, because in some species, juveniles have high concentrations of corticosterone prior to fledging (e.g. white stork, *Ciconia ciconia*; Corbel & Groscolas 2008). However, in the sociable weaver, there are no evidences for an effect of group size in the cortcosterone concentration prior to fledge (Paquet et al. unpublished results) and therefore other possible explanation should be explored.

Another possibility would be that breeders might decrease their feeding visits in order to induce the juveniles to leave the nest, but if helpers keep feeding them that may decrease their willingness to leave the nest. In pied babblers, *Turdoides bicolor,* adults cease feeding their young after they fledge and repress begging behaviours by attacking them. Young redirect their begging towards helpers, which assume the majority of the parental behaviour (Raihani & Ridley 2008). An analogous situation may occur at end of the nestling period in the sociable weaver. Breeders may have a strategy to induce chicks to leave the nest, but helpers may interfere with this. However I did not record the feeding behaviour after the juveniles were more than 21 days old and therefore this suggestion remains speculative.

In altricial bird species, fledging represents a dramatic change from a sedentary to a more active and mobile form of life-style. Therefore any interference during this critical transition is likely to be reflected on juvenile's survival. However, studies on the helper's role in patterns of fledging are scarce. The result reported in this work supports the need for further research on the association between helpers and fledging behaviour, either on the mechanism (e.g. interaction between helpers and offspring) and consequences (e.g. juvenile survival)

Contrary to a previous study (Broom 2013) I found no clear support to distinguish between the effect of several variables, including group size, on the post-fledging survival of the juveniles between day 17 and day 30. Group size still showed a negative trend with juvenile survival. Nevertheless such high model uncertainty was unexpected and inferences on such results should be taken carefully. Four possible explanations may underlie these different results. First, here I tested helper's effect as a continuous variable. An approach comparing groups with and without helpers (as in Broom 2013) might have wielded different results. However, during this breeding season there were not enough juveniles raised by pairs alone to tests this dichotomous effect (only 4 broods were raised by pairs alone). Second, colony size generally increased since the last study and there is a reproductive bias with more data coming from larger colonies. In the previous study only 26% of the juveniles were raised in colonies larger than 45 individuals, while in the present study 88% of the juveniles were raised in colonies larger than 45 individuals. If the negative influence of helpers is only detected in small colonies, as previously suggested (Broom 2013), then such effect could be unnoticed for this year. Third, there might be a year effect for post-fledge mortality, as a previous study reported different effects of helpers on reproduction under different conditions (Covas et al. 2008). Lastly the lower sampling effort used in the present study compared to the previous one (less 59 juveniles and six visual recaptures than the previous study) may also explain the lack of statistical power in these results.

Growing evidence (including this work) has been suggesting that in sociable weavers the effect of helpers is not always detected, but the positive effects are often noticed when help is most needed. A previous work (Covas & Plessis 2005) showed that helpers increased significantly the overall feeding rates in artificially increased broods, when demand for feeding is higher, leading to a decreased nestling's mortality (Covas & Plessis 2005). Another work showed that helpers have a positive effect in fledging mass and fledging success, but only under adverse conditions (Covas et al. 2008). In this present work I showed that helper's share of feeding care is higher, at the end of the nestling period, when demand for food is also higher. These results suggest that helpers respond to the demands of the brood, raising interesting questions about the mechanisms underlying helpers' investment decisions. Furthermore, they show that both the social and environmental context should be taken into account when accessing helper's benefits.

In the same way helper's costs may only be detected in certain situations. In this work I showed that helpers bring smaller prey to the nest. This might be either due to helpers being less motivated to share high quality food with the offspring as breeders, or because they are less experienced foragers. Breeders and offspring may pay a high cost if breeders transfer too much feeding care to helpers when food is scarce as helpers might not be able to attend the nestling's nutrition needs. Finally, I showed that helpers have a positive influence on the duration of the nestling period, but this delayed fledging date may increase vulnerability to nest predation. This possible negative effect may also only be detected in years or areas were snakes are more abundant.

In order to understand the evolution and maintenance of cooperation the mechanisms underlying the fine balance of costs and benefits for the individuals need to be revealed. This study showed suggestion for several positive and negative aspects of helpers that can balance breeders and offspring fitness. Studies focusing on broader approaches, such as this one, that consider the interactions and trade-off between several mechanisms as well as the social and environmental context, should give insight on the selective pressures underlying the evolution of cooperative breeding.

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Supplement material

Model selection procedures:

For the analyses of the overall care and transfer of care (section 1 and 2 of the methods), I had several explanatory variables. For some of them I was not particularly interested in their effect, namely weather condition variables and the time since sun rise, but they could significantly affect sociable weaver's behaviour. To avoid having a large number of possible variable combinations which can lead to over-parameterisation of the models (Burnham and Anderson 2002) I did a preliminary model selection to choose the most important variables within this group of variables, including the null model (intercept-only model). For each dependent variable I computed the AICc for all possible combination of explanatory variables: sum of rainfall in the previous 30 days to the observation, maximum day temperature, wind speed and the recording midpoint time since sun rise. Weather condition variables were not correlated (Spearman's rank correlations $P>0.48$). The random factors were included in all models - colony identity and nest identity. Brood size, nestling's age and video recording were also included in this preliminary model selection to control for obvious influence of these variables in the total amount of care.

I computed the differences in AICc values (ΔAICc) from the best model (with the lowest AICc value) and considered models within the ΔAICc=2 range to estimate the relative importance of each variable. ΔAICc values can be used to calculate the Akaike weights that can be interpreted as the probability that a given model is the best approximating model (Symonds & Moussalli 2011). Akaike weights can then be used to estimate the relative importance of each variable by summing the Akaike weights of all model in which a given variable is present. This sum can be interpreted as the probability of the variable to be a component of the best model (Symonds & Moussalli 2011). For all analysis, variables had either a relative importance value of 1 or less than 0.65 (Table S1).For the main model selection analysis (with the variables of interest; e.g. group size) I used only the variables with an importance of 1 as they likely to be part of the best model.

For the main model selection analysis I included variables that were considered to be important and compared the AICc values of all possible combinations of variables (described in the methods section 1 and 2). Data for overall care and transfer of care has the same origin, just changes the way of analysing the data. In the overall care the "statistical unit" is chamber per day and in the transfer of care is individual per day. As a result I did not do a preliminary model selection analysis for the transfer of care; instead I included in the main model selection the variables that were considered important in the overall care model section preliminary analysis.

Table S1. Results from the preliminary model selection analyses. All models and respective AICc weights within the ΔAICc=2 range are listed.

Task	Predictors	AICc	ΔAICc	AICc weights
Feeding	video length, brood size, nestling's age, rainfall	1294.7	0.00	0.2
	video length, nestling's age, brood size, rainfall, wind speed	1295.06	0.36	0.17
	video length, nestling's age, brood size	1295.47	0.76	0.14
	video length, nestling's age, brood size, rainfall, temperature	1295.79	1.08	0.12
	video length, nestling's age, brood size, temperature	1295.99	1.29	0.11
	video length, nestling's age, brood size, wind speed	1295.99	1.29	0.11
	video length, nestling's age, brood size, rainfall, temperature, wind speed	1296.46	1.76	0.08
	video length, nestling's age, brood size, time since sun rise, rainfall	1296.67	1.97	0.08
Brooding	video lentgh, neslting's age, temperature, time since sun rise	507.19	0.00	1
Sanitation	video lentgh, neslting's age	395.36	0.00	0.49
	video length, nestling's age, brood size	396.24	0.88	0.32
	video lentgh, neslting's age, temperature	397.21	1.85	0.19
Building	video lentgh, neslting's age, rainfall, wind	508.23	0.00	0.31
	video lentgh, neslting's age, temperature, wind	508.93	0.69	0.22
	video lentgh, neslting's age, wind	509.29	1.06	0.18
	video lentgh, neslting's age, rainfall, wind, time since sun rise	509.82	1.59	0.15
	video lentgh, neslting's age, rainfall, temperature, wind	509.95	1.71	0.14
Prey size	rainfall	342.18	0.00	0.37
	rainfall, time since sun rise	343.39	1.21	0.20
	nestling's age, rainfall	344.04	1.85	0.15
	rainfall, wind	344.09	1.91	0.14
	rainfall, temperature	344.12	1.94	0.14

Table S2. Relative importance of the weather variables.

Task	Predictors	Relative importance
Feeding	rainfall	0.65
	temperature	0.31
	wind speed	0.36
	time since sun rise	0.08
Brooding	temperature	1.00
	time since sun rise	1.00
Sanitation	temperature	0.19
Building	rainfall	0.60
	wind	1.00
	temperature	0.36
	time since sun rise	0.15
Prey size	rainfall	1.00
	wind	0.14
	temperature	0.14
	time since sun rise	0.20

Table S3. Results from the main model selection for the overall care analyses. All models and respective AICc weights within the ΔAICc=2 range are listed.

Task	Predictors	AICc	ΔAICc	AICc weights
Feeding	video length, nestling's age, brood size, colony size	1289.82	0.00	0.68
	video length, nestling's age, brood size, colony size, group size	1291.33	1.51	0.32
Brooding	video length, nestling's age, temperature, time since sun rise	507.19	0.00	0.62
	video length, nestling's age, colony size, temperature, time since sun rise	508.15	0.96	0.38
Sanitation	video length, nestling's age	395.32	0.00	0.33
	video length, nestling's age, brood size, colony size	395.76	0.44	0.26
	video length, nestling's age, colony size	396.09	0.78	0.22
	video length, nestling's age, brood size	396.47	1.15	0.18
Building	video length, nestling's age, wind	509.29	0.00	0.70
	video length, nestling's age, group size, wind	510.98	1.69	0.30

Table S4. Results from the main model selection for the transfer of care analyses. All models and respective AICc weights within the ΔAICc=2 range are listed.

Task	Predictors	AICc	ΔAICc	AICc weights
Feeding	video length, nestling's age, group size, status, nestling's age*group size, nestling's age*status	3743.25	0.00	0.43
	video length, nestling's age, col size, group size, status, nestling's age*group size, nestling's age*status	3743.64	0.39	0.35
	video length, nestling's age, brood size, colony size, group size, status, nestling's age*group size, nestling's age*status	3744.58	1.34	0.22
Brooding	video length, nestling's age, temperature, time since sun rise, status, nestling's age*status	1533.53	0.00	0.35
	video length, nestling's age, temperature, time since sun rise, group size, status, nestling's age*status	1533.62	0.09	0.33
	video length, nestling's age, brood size, temperature, time since sun rise, status, nestling's age*status	1535.01	1.47	0.17
	video length, nestling's age, brood size,group size, temperature, time since sun rise, status, nestling's age*status	1535.15	1.62	0.15
Sanitation	video length, nestling's age, brood size, group size, status	779.79	0	0.15
	video length, nestling's age, status	779.97	0.17	0.14
	video length, nestling's age, group size, status	780.09	0.3	0.13
	video length, nestling's age, brood size, group size, status, nestling's age*group size	780.09	0.3	0.13
	video length, nestling's age, group size, status, nestling's age*group size	780.25	0.46	0.12
	video length, nestling's age, brood size, group size, status, group size*status	780.36	0.57	0.12
	video length, nestling's age, brood size, status	780.49	0.7	0.11
	video length, nestling's age, group size, status, group size*status	780.78	0.99	0.09
Building	video length, nestling's age, wind, status, nestling's age*status	684.65	0.00	0.66
	video length, nestling's age, wind, status, nestling's age*group size, nestling's age*status	686.01	1.35	0.34