



# Effect of helpers on reproductive output in a cooperatively breeding bird

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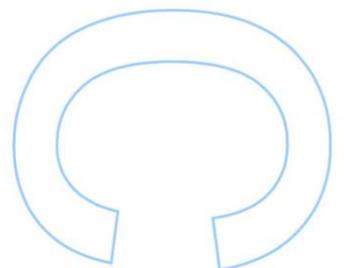
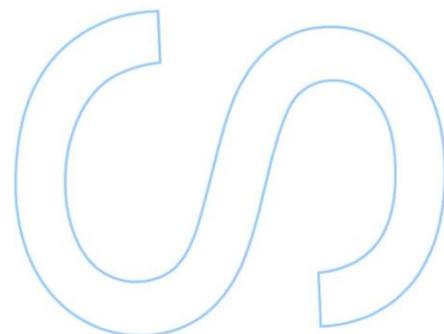
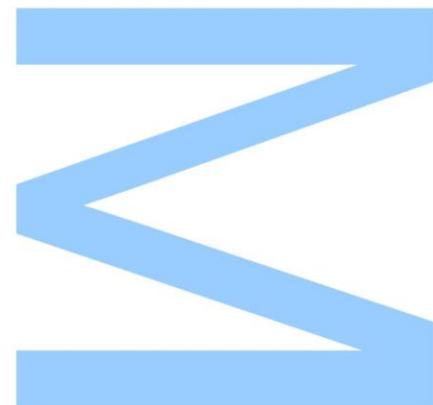
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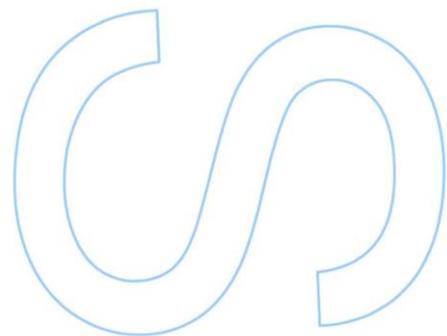
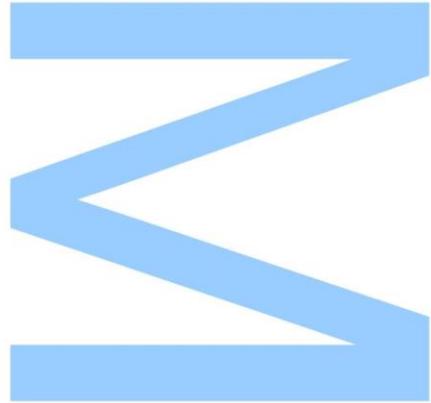




Todas as correções determinadas pelo júri, e só essas, foram efetuadas.

O Presidente do Júri,

Porto, \_\_\_\_/\_\_\_\_/\_\_\_\_



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## Abstract

In cooperation, individuals work together for some underlying benefit of the group. However, this poses a problem to evolution, as natural selection favors the selfish behavior of individuals. Nevertheless, cooperation has evolved and the hypotheses to explain it are broadly classified in two different ways: through direct fitness benefits when it benefits an individual's own reproduction and indirect fitness benefits through the gains from assisting their relatives. In birds, cooperation can be manifested in cooperative breeding, which can be defined as sexually mature individuals helping raising another individuals' offspring at the expense of forgoing their own reproduction. This is expected to improve the reproductive output and the survival of both breeders and chicks. However, studies on the effects of helpers in cooperatively breeding species show that a positive effect on the reproductive output is not always recorded, with works showing both no significant effects and negative effects. Understanding the mechanisms of helping behavior is therefore vital to understand the evolution of cooperative breeding. A possible explanation for this incongruity is that helpers may have a positive effect only when breeding conditions are adverse, and their effect might not be detectable under good conditions. Here, I used a well-studied population of a cooperatively breeding bird, the sociable weaver *Philetairus socius*, to explore the underlying mechanisms that might explain the potential benefits of helpers on the reproductive outcome. Specifically, I test if there is a positive effect associated with the presence of helpers through the analysis of breeding success by breeding attempt and breeding success by season. The results showed no significant effect of group size on the breeding success by breeding attempt which can be explained by breeders not maintaining the same effort regardless of helper number and rather compensate the work conducted by helpers by reducing their own effort. On the other hand, in the overall season reproductive success, the results suggest that it is advantageous for breeders to have helpers at the nest when the maximum temperature increases, as that is associated with increased production of the total number of fledglings. In short, this study illustrates that helping behavior might be flexible and the environmental context should be taken into account when assessing the effect of helpers.

Keywords: cooperative breeding, group size, kin-selection, *Philetairus socius*, reproductive success, sociable weaver.

## Resumo

Em cooperação, os indivíduos trabalham em conjunto para obter um benefício para o grupo. Contudo, isto representa um problema para a evolução porque a seleção natural favorece o comportamento egoísta dos indivíduos. No entanto, a cooperação evoluiu e é amplamente classificada de duas maneiras diferentes: por meio de benefícios directos quando beneficia a sua própria reprodução e por meio de benefícios indirectos através dos ganhos em assistir os seus parentes. Em aves, a cooperação pode-se manifestar em espécies que se reproduzem cooperativamente, isto é, espécies onde indivíduos sexualmente maduros não se reproduzem (“ajudantes”) para poder ajudar outros indivíduos a reproduzirem-se. É esperado que isto melhore o sucesso reprodutivo e a sobrevivência tanto dos pais como das crias. No entanto, estudos realizados nos efeitos dos “ajudantes” em espécies que se reproduzem cooperativamente, mostram que um efeito positivo no sucesso reprodutivo nem sempre é registado com trabalhos mostrando tanto a ausência de efeitos como efeitos negativos. Entender os mecanismos deste comportamento é portanto crucial para entender a evolução das espécies que se reproduzem cooperativamente. Uma possível explicação para esta incongruência é que os “ajudantes” podem ter um efeito positivo só quando as condições de reprodução são adversas e o seu efeito pode não ser detectável quando as condições são boas. Neste trabalho, eu usei uma população bem estudada duma espécie que se reproduz cooperativamente, o tecelão social *Philetairus socius*, de forma a explorar os mecanismos subjacentes que podem explicar os potenciais benefícios dos “ajudantes” no sucesso reprodutivo. Especificamente, eu testo se há um efeito positivo associado à presença de “ajudantes” através da análise do sucesso reprodutivo por tentativa de reprodução e o sucesso reprodutivo por época de reprodução. Os resultados obtidos mostraram que não há um efeito significativo do tamanho do grupo no sucesso reprodutivo por tentativa de reprodução, o que pode ser explicado pelo facto dos pais não manterem o mesmo esforço independentemente do número de “ajudantes” e preferem compensar o trabalho realizado pelos “ajudantes” através da redução do seu próprio esforço. Por outro lado, no sucesso reprodutivo por época, os resultados obtidos sugerem que é vantajoso para os pais terem “ajudantes” no ninho quando a temperatura máxima sobe, devido ao aumento na produção total de crias. Em suma, este estudo ilustra que o comportamento cooperativo pode ser flexível e o contexto social e ambiental deve ser levado em consideração quando se estuda o efeito dos “ajudantes”.

Palavras chave: reprodução cooperativa, tamanho do grupo, selecção de parentesco, *Philetairus socius*, sucesso reprodutivo, tecelão social.

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## List of Abbreviations

AIC – Akaike Information Criterion

Average Rain - Average Rainfall (mm)

EV – Environmental Variable

GLMM - Generalized Linear Mixed Model

Higher - Number of days above 33°C

LMM - Linear Mixed Model

Sum Rain - Sum of Rainfall (mm)

Sum Rain Season - Sum of Rainfall of a Season (mm)

TMax - Maximum Temperature (°C)

TMax Season - Average Maximum Temperature (°C) of a Season

TMin - Minimum Temperature (°C)

TMin Season - Average Minimum Temperature (°C) of a Season

# Introduction

When considering evolution by means of natural selection, competition and the survival of the fittest, are established mechanisms. In spite of strong competition, almost everywhere in nature, there are also examples of cooperation. Cooperation is a process where individuals of the same species (or different species) work together for a common or mutual benefit (Lindenfors 2017). This poses a problem to the evolutionary theory because in natural selection, genes that increase the ability of an organism surviving and reproducing are favored and in cooperation, if too costly, the genes and behavior from assisting individuals might not pass on to the next generations (Hamilton 1964). Moreover, cooperation could impair the probabilities of an individual surviving and reproducing because individuals have to dedicate their time and energy, and in some cases incur risks like predation. Nevertheless, cooperation is present throughout nature among both invertebrates and vertebrates.

The major breakthrough in the study of cooperation was the kin selection theory which proposed that the fitness of individuals can be impacted by their own reproductive success (direct fitness benefits), as well as by the reproduction of related individuals (indirect fitness benefits). Indirect fitness benefits may improve the reproductive outcome of their relatives through indirectly passing copies of their genes on to the next generation and it is expected that the degree of genetic relatedness of an individual may affect the level of cooperation towards kin. Both actors and recipients might benefit in cooperation systems through both direct and indirect fitness benefits, which means that cooperation in this case is mutually beneficial and not altruistic (West et al. 2007). Therefore, the evolution of cooperation systems (or any behavior) might have occurred due to the gain of genetic fitness and maintained by a combination of direct and indirect fitness benefits (Clutton-Brock 2002; Richardson et al. 2003).

One specific form of cooperation is cooperative breeding, in which sexually mature individuals (“helpers”) postpone their own reproduction and assist other breeding individuals in raising their offspring (Hatchwell 1999). Most cooperatively breeding species live in family groups and this has led to the suggestion that kin selection plays a powerful explanation in the evolution of cooperative breeding through an increase in fitness of both parents and young through for instance, an increase in reproductive output (Emlen 1991; Cockburn 1998; Griffin and West 2003). It is therefore essential to determine whether helpers do indeed contribute to increase reproductive output.

Helpers may improve reproductive output through the quality and or quantity of food brought to the nest, thereby increasing the offspring' food intake and potentially alleviating parental work load, which may lead to improved survival in parents (see Paquet et al. 2015). For instance, in superb fairy-wrens (*Malurus cyaneus* Ellis, 1782), breeding females with helpers lay smaller eggs that produce smaller chicks due to the fact that helpers will fully compensate the investment reduction, allowing the breeding females to have an increased fitness in the next breeding season (Russell et al. 2007). In the red-cockaded woodpecker (*Picooides borealis* Vieillot, 1809), when helpers are present, the risk of a breeder dying declined by 21-42% in males and 0-14% in females, most likely due to a significant reduction in the breeders' workload (Khan and Walters 2002). Another way in which helpers can contribute to increase the reproductive success is by protecting the nest against predators or intruders (Mumme 1992). In a cichlid fish like *Neolamprologus pulcher* Trewavas & Poll, 1952, the primary benefits of sociality are the enhanced safety from predation provided by a cooperative defense system (Groenewoud et al. 2016). However, in some cases no significant effect of helpers is detectable (Legge 2000; Eguchi et al. 2002) and even negative effects of helpers on breeders and their offspring have been reported (Covas et al. 2011). Such contradictory results demand more studies and explanations. Therefore, understanding to which extent helpers are or not important to increase the reproductive output of the parent is central to understand the evolution and maintenance of helping behavior in any given system.

Environmental factors influence and explain the social behavior of cooperative breeders and their reproductive strategies mostly through the role of habitat heterogeneity in influencing dispersal decisions (Rubenstein 2011). However, studies have shown that the complex social behavior of birds can be influenced by the unpredictable breeding conditions (erratic and variable climatic environments) in which they are living (MacColl and Hatchwell 2002; Rubenstein and Lovette 2007; Covas et al. 2008). Therefore, helpers that live in fluctuating environments may influence the reproductive success exclusively under adverse conditions or under both adverse and good conditions. All these strategies help shape the evolution of cooperative breeding. When the contribution of helpers is only significant under harsh conditions, it goes unnoticed under more favorable conditions (Cockburn 1998; Magrath 2001; Covas and Du Plessis 2005; Rubenstein and Lovette 2007). For example, it may happen when the breeding pair is inexperienced (Magrath 2001), when the brood reduction is common (Hatchwell 1999) or under poor or unpredictable breeding conditions (Koenig and Mumme 1987; Curry and Grant 1990; Canário et al. 2004). Given this, it is important that the analysis of helper effects investigate not only the overall reproductive success but also the effect of helpers under adverse

breeding conditions and for this, the analyses should aim at containing simultaneously environmental, individual and social factors of helper effects.

Here I used the sociable weaver (*Philetairus socius* Latham, 1790), to investigate this question and so to understand the causes of variation in breeding success and if there is a positive effect associated with the presence of helpers. A previous work on the sociable weaver attempted to study this effects and concluded that the effect of helpers on the reproductive output was detectable under adverse conditions such as, low rainfall and when breeding in large colonies (Covas et al. 2008). However, those results were based on only 2 breeding seasons and used only rainfall as measure of environmental variation (Covas et al. 2008). Here, I conduct a more conclusive analysis using 7 years of data and used an additional proxy such as maximum temperature. This will help to better assess the importance of environmental factors.

In this semi-arid colonial cooperative breeding species, the breeding activity is closely linked to weather conditions through the duration and timing of the breeding season, the amount of breeding attempts and the survival of nestlings (Covas et al. 2008; Mares et al. 2017). Males are the philopatric helping sex and disperse less often than females (Doutrelant et al. 2004). The number of helpers may range from one to six (Covas et al. 2008) and these individuals are mostly offspring or first order relatives of one (50%) or both (43%) breeders or, more uncommonly, unrelated helpers (7%; (Covas et al. 2006). Adult helpers have a lower feeding rate and bring smaller prey when compared to yearlings (one year old helpers; Doutrelant et al. 2011). Helping tasks include providing additional food to the nestlings, building and maintaining the nest structure and protecting against predators. In this cooperative system, helpers may gain indirect fitness benefits through kin selection if their help results in increased reproductive output of their relatives. Within a reproductive season (may span from September to June in some years), the same female may have several breeding attempts and thus helpers may feed several broods.

The importance of individual, social and especially environmental variables on reproductive traits was studied, because it was of particular importance to check if there is an effect when the breeding conditions are poor or unpredictable. The effects of helper presence were analyzed in two different ways: analyzing the breeding success by breeding attempt and the breeding success by season.

# Methods

## Field Site and Study Species

The study took place at Benfontein Nature Reserve, near Kimberley, South Africa (28°530S, 24°890E; Figure 1). The landscape consists of open savannah typical of the southern Kalahari with a continuous herbaceous layer of *Stipagrostis* Nees grasses and a discontinuous arborescent layer of *Vachellia erioloba* (E.Mey.) P.J.H.Hurter (Mucina and Rutherford 2006). The study area covers approximately 15 km<sup>2</sup> and contains 30 sociable weaver colonies, many of which have been regularly captured and ringed since 1993 (Covas et al. 2002). Moreover, some colonies are regularly the subject of experiments through the provision of food and/or protection against snakes (plastic protections around the trunk of the tree where the colony is found). The climate is characterized by low annual rainfall, the majority of which falls between October and April, and by widely ranging temperatures of 20 – 35°C.

The sociable weaver is a colonial passerine endemic to the semi-arid acacia savannahs of southern Africa (Maclean 1973; Harrison and Cherry 1997; Figure 1). Sociable weavers build massive communal nests using sturdy *Stipagrostis* grasses with the largest structures containing up to 300 independent nest chambers that are used for both breeding and roosting. They are facultative cooperative breeders, breeding in pairs or with up to six helpers (Covas et al. 2006). Helpers are predominantly males (Doutrelant et al. 2004) and mainly offspring of one or both breeders (93%), although a small number of unrelated birds can also help (Covas et al. 2006). Breeding at the study site can start as early as August and extend to as late as June, but the majority of clutches are laid between September and March.

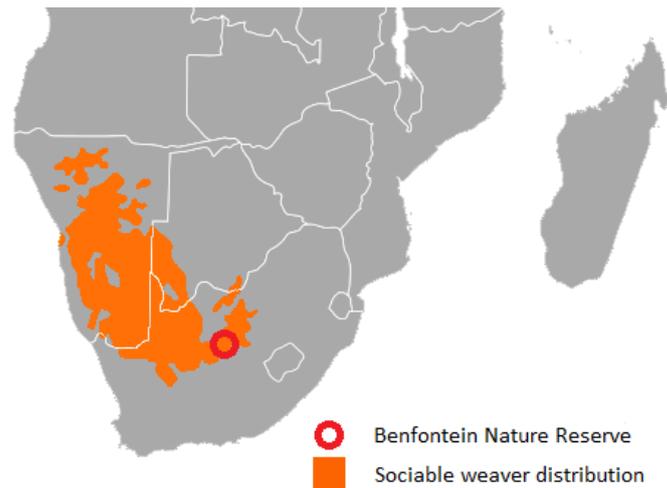


Fig. 2- Southern Africa map with sociable weaver distribution (orange) and Benfontein Nature Reserve location (red circle)

## Field Methods

Adults and juveniles were annually captured in 13 colonies at sunrise using mist-nets and each individual was marked with a metal ring and an unique color ring combination (which allows for visual identification) before the breeding season, including a specific color for each colony to help identify immigrants (see Covas et al. 2002 for more details on the captures). Blood samples were collected during this period for genetic sexing and determination of parentage and kin relationships among individuals. The number of individuals caught plus the ones that escaped in each colony are used as the measure of colony size.

Every year, breeding monitoring is conducted in detail in the captured colonies. This study is focused on seven breeding seasons (from 2011 to 2017). Colonies were visited every 1–3 days to check for new clutches and all nest chambers in each colony were individually identified with a numbered plastic tag. The nest mass was reached from the roof of a pick-up truck and a stepladder and the contents of each chamber were inspected using an extendable LED lighted mirror. The incubation period lasts 15 days and the nestling period lasts 21–24 days (Maclean 1973). In the nestling phase, the nests were visited 2 times: at day 9 to ring the chick with a unique numbered metal ring, collect a blood sample for sexing and genotyping analyses and weighing; and at day 17 (i.e. when chicks are 17 days old) to weigh, measure the wing and tarsus of the chicks and to ring them with a unique combination of plastic color rings. In order to avoid prompting premature fledging, nests were inspected for the last time 17 days after the first egg hatched and, therefore, it is referred to the survival of chicks up to this point as fledging (Covas et al. 2008).

Reproductive status (breeder versus helper) was determined by a combination of well-established genetic analyses (using 15 microsatellites markers; see Paquet, Doutrelant, et al. 2015 and Silva et al. 2018) and video analyses. For the video analyses, a camera (Sony Handycam HD) was placed during the early stages of incubation for 2 days and for ca. 2 hours in order to identify the breeders. Group identifications were also based on video camera recordings over the nestling period by dividing them in 2 different phases: phase 1 – from 8 to 12 days old, phase 2 – from 13 to 17 days old. Each stage was recorded for at least 2 hours a day during 2 days for each age block (4 days with 2 hours each). To avoid the hottest parts of the day (when birds are less active) and to standardize the data, all cameras were placed early in the morning (up to 2 hours after sunrise). This provided the identity of which birds were feeding nestlings at a given chamber and hence allowed to determine the breeding group size (Covas et al. 2006; Covas et al. 2008; Paquet et al. 2013). During video analyses, feeding visits and visits for other purposes (sanitation, building) were distinguished and only feeding visits were used to determine the breeding group size. Also, a criterion was used in which any given bird had to undertake at least 3 feeding visits to be considered as belonging to the breeding group due to the fact that some birds sporadically feed the juveniles but they are not actually part of the group. Only nests with chicks that reached day 17 were used in the analyses as group size is defined by the number of adults seen attending the chicks in the video recordings during the nestling period. Some adults might not be seen every day, therefore, if chicks die prematurely, there are less opportunity to record nestling feeding activity and to accurately estimate the group size (Preston et al. 2016).

All colonies in which plastic protections experiments were conducted, were excluded from this study. Daily rainfall and temperature data were obtained from the Kimberley Airport weather station (28°48S, 24°45 E; 11km northwest of the study site).

## Statistical Methods and Explanatory Variables

The main goal of the study was to examine the effect of helpers' presence and their influence on breeding success, therefore, the variable breeding group size (number of birds feeding the chicks) was of particular importance.

To understand the underlying causes of variation in reproductive traits and reproductive outcome and whether there is an effect of the presence of helpers in this cooperatively breeding bird, the variation was analyzed in two different ways: the breeding success by breeding attempt (1) and the breeding success over the whole season (2). Moreover, the

analyses of breeding success by breeding attempt were estimated by two proxies: the number of chicks fledged at day 17 (1.1) and the survival of the chicks of each nest (1.2).

## 1. Breeding Success by Breeding Attempt

For this analysis, the aim was to see the effect of helpers at the breeding attempt level (i.e. when a female lays a new clutch in a nest). In the analysis of breeding success by breeding attempt, the breeding group size varied between two (breeding pair with no helpers) and eight individuals (the breeding pair plus six helpers).

### 1.1 Number of Chicks Fledged at Day 17

The aim was to test if having more helpers would result in more chicks by a potential combination of successfully hatching more chicks and increase their probability of reaching day 17 (number of chicks fledged varied between 1 to 4). Two analysis were conducted using a Linear Mixed Model (LMM). One including all breeding events (with or without helpers) in which it was tested if the number of chicks reaching day 17 was related with any of the following variables: Breeding Group Size (2 to 8 individuals), Colony Size (7-134 individuals), Breeding Female Age (258-4367 days), Sex Ratio of the Breeding Group (number of males divided by the total number of helpers), an Environmental Variable (hereafter EV; explained below); and the interactions: Breeding Group Size \* Colony Size, Breeding Group Size \* Breeding Female Age and Breeding Group Size \* EV (Analysis 1.1.1). Then in order to test other potential important variable, the Average Age of the Breeding Group (average age of all helpers in one group; 22-1386 days), nests without helpers were excluded and the following variables were used as independent variables: Breeding Group Size, Colony Size, Breeding Female Age, Average Age of the Breeding Group, Sex Ratio of the Breeding Group and an EV; and the interactions: Breeding Group Size \* Colony Size, Breeding Group Size \* Breeding Female Age and Breeding Group Size \* EV (Analysis 1.1.2). Breeding Pair Identity nested in Colony as well as Season were included in the analysis as a random effect to account for the non-dependency of data coming from the same colony or repeated breeding couples in different seasons.

## 1.2 Survival of All Chicks per Nest

Since helpers' effect might only be by maintaining chicks alive until day 17 (and have no effect on the number of chicks hatching), it was tested if group size would increase the probability of all chicks in the nest reaching day 17 i.e. surviving. A Generalized Linear Mixed Model (GLMM) was used for the survival of all chicks per nest and the dependent variable consisted on a binary variable in which 0 represented a nest that at least one chick died and 1 represented a nest in which all chicks survived. The independent variables used were: Breeding Group Size, Colony Size, Breeding Female Age, Sex Ratio of the Breeding Group, an EV and the Initial Number of Chicks in the Nest (number of eggs that hatched); and the interactions: Breeding Group Size \* Colony Size, Breeding Group Size \* Breeding Female Age, Breeding Group Size \* EV and Breeding Group Size \* Initial Number of Chicks (Analysis 1.2.1). Again, a sub-analysis was conducted following the same logic of the previous point where the Average Age of the Breeding Group was included. The variables used were: Breeding Group Size, Colony Size, Breeding Female Age, Average Age of the Breeding Group, Sex Ratio of the Breeding Group, an EV and the Initial Number of Chicks; and the interactions: Breeding Group Size \* Colony Size, Breeding Group Size \* Breeding Female Age, Breeding Group Size \* EV and Breeding Group Size \* Initial Number of Chicks (Analysis 1.2.2). Breeding Pair Identity nested in Colony as well as Season were used as random factors.

## 2. Seasonal Breeding Success

Since the effect of helpers might not be just at the breeding attempt level but also by allowing the breeding pair to reproduce more often (and additionally more successfully each time) I also tested the effect of helpers at the season level. I studied the number of chicks produced (i.e. chicks still alive in the nest at day 17) by a single couple during a season by testing the Average Group Size, Colony Size, Breeding Female Age (averaged over the breeding season) and an EV (explained below); and the interactions: Average Group Size \* Breeding Female Age, Average Group Size \* Colony Size and Average Group Size \* EV (Analysis 2.1). The number of chicks produced by one breeding pair varied between one to eight. Breeding Pair Identity nested in Colony as well as Season were used as random factors.

## Environmental Variables (EVs)

To test whether breeding conditions influence reproductive output and whether helpers may only have an effect when the breeding conditions are adverse, it was also included the effect of environmental variables. EVs are numerous (e.g. rainfall, maximum and minimum temperature) and a high number of variables can lead to over-parameterizing the models (Burnham and Anderson 2002). To avoid this, exploratory analyses were done to select which type of environmental variable available had a greater influence on my data set. LMMs were run to test the effect of five independent EVs on the number of chicks fledged at day 17: average minimum temperature (°C), average maximum temperature (°C), the number of days above 33 °C (see du Plessis et al. 2012; Cunningham, Kruger, et al. 2013; Cunningham, Martin, et al. 2013; Cunningham et al. 2015), the sum of rainfall (mm) and the average rainfall (mm). Additionally, to understand which time interval was more relevant for the data and hence the best to use in the final models, each of the mentioned EVs were computed for five different time intervals (15, 30, 45, 60, 75), before the fledging date. A similar analysis was conducted for the seasonal breeding success on the total number of fledglings per breeding pair per breeding season.

A correlation analysis was conducted to determine whether there was collinearity among all explanatory variables (Zuur et al. 2010). Pairwise correlations between potential predictors (fixed terms, detailed for each analysis below) were assessed using scatter plots and Spearman's correlation coefficients (Zuur et al. 2009), and terms with an absolute R greater than 0.35 were not included simultaneously in the models.

The final models were obtained by sequentially eliminating explanatory variables showing p values > 0.05 using a backwards stepwise approach. The random terms were never dropped from the models, even when they were non-significant, since this would inflate the degrees of freedom and hence would revert to pseudo-replication.

Continuous variables fitted as fixed terms were standardized by subtracting the mean and dividing by 2 s.d., to allow the direct comparison of their corresponding estimated effect sizes, and to facilitate the interpretation of the effects of variables involved in interactions (Gelman and Hill 2007).

Statistical analyses were conducted in the software R (v.3.2.1; R Development 2012; package lme4, Bates et al. 2014).

# Results

## 1. Breeding Success by Breeding Attempt

### Environmental Variables

Selection of the environmental variable - High temperatures had the strongest influence on reproductive success. The comparison of the EVs and their respective five intervals of days following the Akaike Information Criterion (AIC) is given in Table 1. Based on this, I decided to use in the final models the Average Maximum Temperature over the 15 days before the fledging date since it was the variable with the lowest AIC value (Table 1).

Table 1 - Results from the exploratory analyses including all the Environmental Variables with five different time intervals (15, 30, 45, 60, 75) before the fledging date. TMax - Maximum Temperature (°C). Higher - Number of days above 33°C. TMin - Minimum Temperature (°C). Sum Rain - Sum of Rainfall (mm). Average Rain - Average Rainfall (mm). Line in bold represents the variable that will be used in the following analyses.

	Df	AIC
<b>TMax 15</b>	<b>4</b>	<b>1139.8</b>
Higher 15	4	1140.6
TMin 75	4	1141.5
Higher 30	4	1142.5
TMax 30	4	1142.9
Higher 45	4	1143.1
Null Model	3	1143.3
TMin 60	4	1143.7
Sum Rain 75	4	1144.2
Average Rain 75	4	1144.2
TMin 15	4	1144.4
Higher 60	4	1144.5
TMax 45	4	1144.6
TMin 45	4	1144.7
TMax 75	4	1144.8
Higher 75	4	1145.0
Sum Rain 60	4	1145.1
Average Rain 60	4	1145.1
TMax 60	4	1145.2
Sum Rain 30	4	1145.2
Sum Rain 45	4	1145.2
Average Rain 30	4	1145.2

Average Rain 45	4	1145.2
TMin 30	4	1145.3
Sum Rain 15	4	1145.3
Average Rain 15	4	1145.3

## Correlations

The correlations among all the independent variables of interest are given in Table 2 and highlighted in bold are the significant values ( $P < 0.05$ ). Sex ratio was highly correlated with Group Age ( $R = 0.48$ ,  $P < 0.01$ ) and weakly correlated with Group Size ( $R = -0.16$ ,  $P = 0.04$ ) therefore, it was eliminated from the models. This correlation is expected because females usually disperse after one year, which leads to a male bias in the breeding group (Doutrelant et al. 2004). Since the remaining independent variables were not highly correlated (Spearman's rank correlations  $R < 0.35$ ), they were kept in the models.

Table 2 – Results from the correlation analysis between all the independent variables used in the Breeding Success by Breeding Attempt analysis. Values is bold highlight significant correlations ( $P < 0.05$ ).

	Breeding Female Age	Group Age	Colony Size	TMax 15	Group Size	Initial Chicks	Sex Ratio
Breeding Female Age	1.00	0.03	0.09	-0.01	0.06	-0.08	-0.08
Group Age	0.03	1.00	0.13	-0.08	-0.07	0.00	<b>0.48</b>
Colony Size	0.09	0.13	1.00	<b>0.26</b>	<b>0.32</b>	0.01	-0.02
TMax 15	-0.01	-0.08	<b>0.26</b>	1.00	<b>0.21</b>	<b>0.21</b>	-0.08
Group Size	0.06	-0.07	<b>0.32</b>	<b>0.21</b>	1.00	0.04	<b>-0.16</b>
Initial Chicks	-0.08	0.00	0.01	<b>0.21</b>	0.04	1.00	-0.11
Sex Ratio	-0.08	<b>0.48</b>	-0.02	-0.08	<b>-0.16</b>	-0.11	1.00

## 1.1 Number of Chicks Fledged at Day 17

1.1.1. A total of 188 breeding attempts were available. None of the explanatory variables used here were able to explain the variation in the number of chicks present in the nest at day 17. Group Size was not significant (estimate =  $0.0765 \pm 0.0629SE$ ,  $P = 0.22$ ; Table 3) providing no support for an effect of helpers. The remaining variables (Colony Size, Breeding female Age and Maximum Temperature) and the interactions were also non-significant ( $P > 0.05$ ; Table 3).

Table 3 – Results from the backwards stepwise approach of the Number of Chicks Fledged at Day 17. Analysis 1.1.1.

	Estimate	Std. Error	P
Breeding Female Age * Group Size	0.0169	0.0761	0.8200
Colony Size * Group Size	0.0495	0.0708	0.4764
TMax 15 * Group Size	0.0709	0.0687	0.2948
TMax 15	0.0035	0.0659	0.9577
Colony Size	0.0154	0.0653	0.8113
Breeding Female Age	-0.0493	0.0630	0.4306
Group Size	0.0765	0.0629	0.2223

1.1.2. The effect of Group Age was tested on a subset of the data ( $n = 141$ ), since it excluded all the breeding events by pairs alone. Breeding Female Age, Temperature and Group Age were not significant alone as well as in interactions with Group Size ( $P > 0.05$ ; Table 4). However, in this restricted subset of the data, the interaction Colony Size \* Group Size significantly influenced the number of chicks fledged at day 17 (estimate =  $0.0040 \pm 0.0017SE$ ,  $P = 0.02$ ; Table 4). The size of colonies was divided in 2 (through the median number of individuals in all colonies) for better plot visualization: Small Colonies (<60 individuals) and Large Colonies (>60 individuals). It appears that big colonies have bigger group sizes than small colonies, and produce more chicks than small colonies (Figure 1).

Table 4 – Results from the backwards stepwise approach of the Number of Chicks Fledged at Day 17, with Group Age. Line in bold represents the significant interaction. Analysis 1.1.2.

	Estimate	Std. Error	P
TMax 15 * Group Size	0.0002	0.0769	0.9882
Breeding Female Age * Group Size	-0.0830	0.0816	0.2961
Breeding Female Age	0.0477	0.0731	0.5033
TMax 15	0.0644	0.0745	0.3780
Group Age	0.0784	0.0731	0.2757
<b>Colony Size * Group Size</b>	<b>0.0040</b>	<b>0.0017</b>	<b>0.0212</b>
Group Size	-0.1550	0.1379	
Colony Size	-0.0180	0.0075	

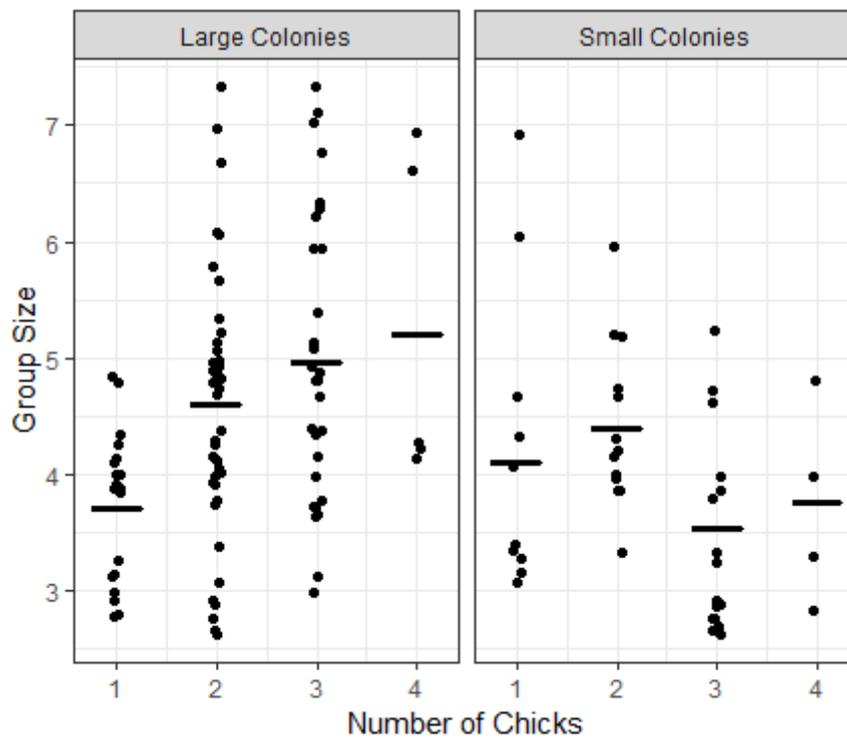


Fig. 2 - Effect of Group Size and Colony Size on the Number of Chicks Fledged at Day 17. Colony Size was divided in Large Colonies (>60 individuals) and Small Colonies (<60 individuals) for better visualization.

## 1.2 Survival of All Chicks per Nest

1.2.1. A total of 188 breeding attempts were available. Neither Group Size (estimate =  $0.1496 \pm 0.1575SE$ ,  $P = 0.34$ ; Table 5) nor the previously tested variables and their interactions significantly explained the variation in the chicks' survival per nest. However, the Initial Number of Chicks, a new variable introduced in this model, had a negatively influence (estimate =  $-0.5306 \pm 0.1600SE$ ,  $P < 0.001$ ; Table 5).

Table 5 - Results from the backwards stepwise approach of the Survival of All Chicks per Nest. Line in bold represents the significant variable.

	Estimate	Std. Error	P
Group Size * Breeding Female Age	-0.0211	0.1894	0.9114
TMax 15 * Group Size	0.0770	0.1823	0.6721
Group Size * Colony Size	0.2054	0.1762	0.2368
Initial Chicks * Group Size	0.3014	0.1899	0.1016
Breeding Female Age	0.0363	0.1540	0.8139
Colony Size	-0.0375	0.1636	0.8184
Group Size	0.1496	0.1575	0.3411
TMax 15	-0.1843	0.1547	0.2325
<b>Initial Chicks</b>	<b>-0.5306</b>	<b>0.1600</b>	<b>0.0006</b>

1.2.2. In the subset of data used for testing the effect of Helpers' Age ( $n = 141$ ), the Initial Number of Chicks was also negatively related to the Survival of All Chicks per Nest (estimate =  $-0.5406 \pm 0.1980SE$ ,  $P < 0.01$ ; Table 6). The interaction between Colony Size and Group Size was also significant (estimate =  $0.7751 \pm 0.2596SE$ ,  $P < 0.001$ ; Table 6), following the same pattern as the previous analysis when Group Age was added to the model. Again, the size of colonies was divided in 2, as mentioned previously, and it appears that Large Colonies have bigger group sizes and have more probability of having nests where at least one chick died (Figure 2).

Table 6 - Results from the backwards stepwise approach of the Survival of All Chicks per Nest, with Group Age. Lines in bold represent the significant variable and interaction.

	Estimate	Std. Error	P
Group Size * Breeding Female Age	-0.0820	0.2290	0.7200
TMax 15 * Group Size	-0.0901	0.2238	0.6872
Initial Chicks * Group Size	-0.4347	0.2404	0.0549
TMax 15	-0.1546	0.2004	0.4404
Breeding Female Age	0.1974	0.1920	0.3088
Group Age	0.3827	0.2065	0.0632
<b>Initial Chicks</b>	<b>-0.5406</b>	<b>0.1980</b>	<b>0.0047</b>
<b>Group Size * Colony Size</b>	<b>0.7751</b>	<b>0.2596</b>	<b>0.0004</b>
Group Size	0.3781	0.2096	
Colony Size	-0.2559	0.2225	

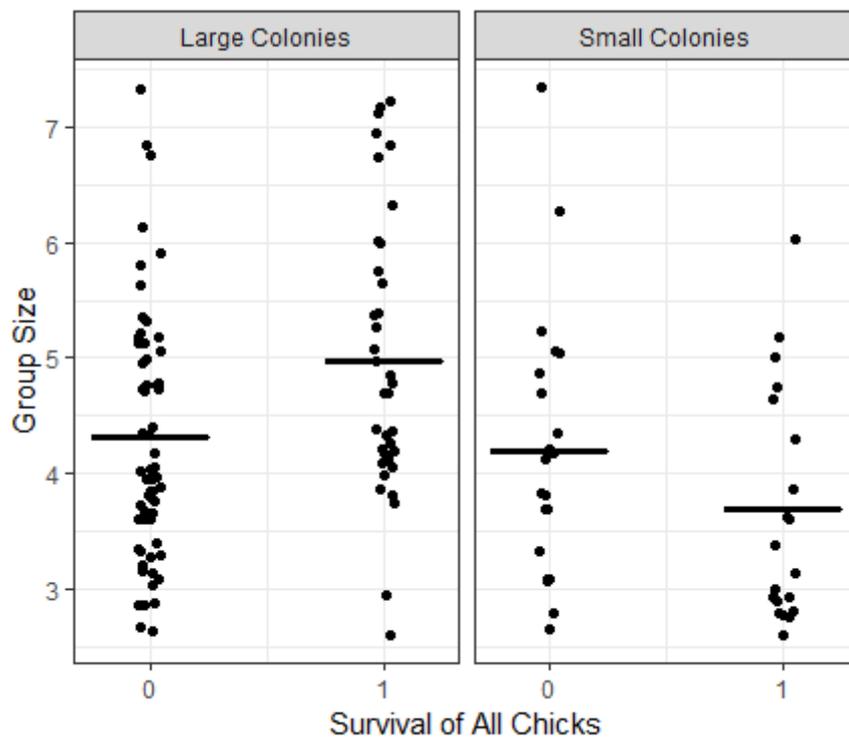


Fig. 3 - Effect of Group Size and Colony Size on the Survival of All Chicks per Nest. Colony Size was divided in Large Colonies (>60 individuals) and Small Colonies (<60 individuals) for better visualization.

## 2. Seasonal Breeding Success

### Environmental Variables

As above, a preliminary model selection was conducted to determine if all explanatory variables, including the null model, should be included in the final model. The environmental variables used here were the Average Minimum and Average Maximum Temperature (°C) over the whole season, and the Sum of Rainfall by season (mm). All the variables were compared following the Akaike Information Criterion and, again revealed a strong pattern that temperature explained better the variation in the data than rainfall did. The model with the lowest AIC was the Average Minimum Temperature (Table 7). However, this value differed from Average Maximum Temperature by < 2 and hence, for the sake of consistency, I decided to use Average Maximum Temperature in the seasonal reproductive success analysis (there are no qualitative changes if Average Minimum Temperature is used; Burnham and Anderson 1998; Burnham and Anderson 2002).

Table 7 - Results from the exploratory analyses including the Environmental Variables for the Seasonal Breeding Success. TMax Season - Average Maximum Temperature (°C) of a Season. TMin Season - Average Minimum Temperature (°C) of a Season. Sum Rain Season - Sum of Rainfall of a Season (mm). Line in bold represents the variable that will be used in the following analysis.

	Df	AIC
TMin Season	4	795.96
<b>TMax Season</b>	<b>4</b>	<b>797.30</b>
Sum Rain Season	4	801.47
Null Model	3	807.42

### Correlations

The independent variables used for studying the Seasonal Breeding Success were not highly correlated (Spearman's rank correlations  $R < 0.25$ ) and therefore, all were used to study the variation in the Number of Chicks Fledged per Breeding Pair per Season (Table 8).

Table 8 - Results from the correlation analysis between all the independent variables used in the Seasonal Breeding Success analysis. Values is bold highlight significant correlations ( $P < 0.05$ ).

	TMax Season	Average Breeding Female Age	Average Group Size	Colony Size
TMax Season	1.00	0.05	<b>0.18</b>	<b>0.24</b>
Average Breeding Female Age	0.05	1.00	0.01	0.07
Average Group Size	<b>0.18</b>	0.01	1.00	0.07
Colony Size	<b>0.24</b>	0.07	0.07	1.00

## 2.1 Number of Chicks Fledged per Breeding Pair per Season

A total of 144 data points were available. There was a significant interaction between Average Maximum Temperature and Average Group Size (estimate =  $0.1842 \pm 0.0785SE$ ,  $P = 0.02$ ; Table 9) revealing that the reproductive success increases more with group size under higher temperatures (Fig 3, Table 9). Colony Size, Breeding Female Age and their respective interactions with Average Group Size were not significant ( $P > 0.05$ ; Table 9), following the same pattern of the Breeding Success by Breeding Attempt analyses.

Table 9 – Results from the backwards stepwise approach of the Seasonal Breeding Success. Line in bold represents the significant interaction.

	Estimate	Std. Error	P
Average Group Size * Breeding Female Age	0.0126	0.0747	0.8594
Average Group Size * Colony Size	0.0024	0.0042	0.5545
Colony Size	0.0003	0.0041	0.9316
Breeding Female Age	-0.1043	0.0798	0.1888
<b>TMax Season * Average Group Size</b>	<b>0.1842</b>	<b>0.0785</b>	<b>0.0231</b>
TMax Season	0.3010	0.0789	
Average Group Size	0.0887	0.0803	

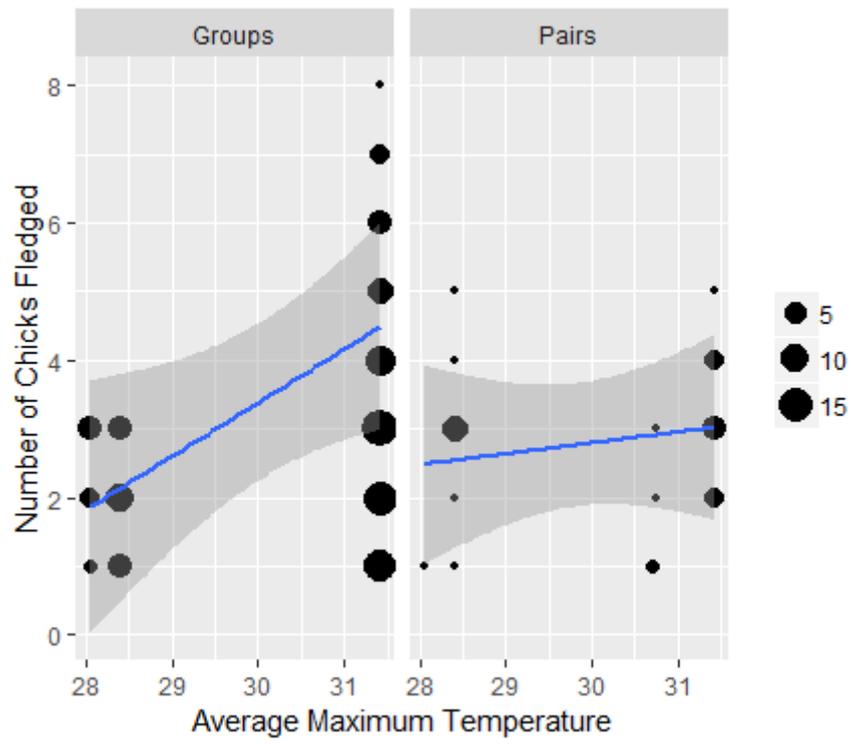


Fig. 4 – Effect of Number of Chicks Fledged per Breeding Pair per Season on the Average Maximum Temperature (°C) of a Season in Groups and in Pairs (blue lines). The grey area represents the Confidence Interval (95%).

## Discussion

The aim of this study was to understand the underlying causes of variation in the reproductive output in the sociable weaver in relation to the presence of helpers at the nest. The overall results obtained suggest that breeders benefit from having helpers when the temperatures are higher, but the effect of group size was only noticeable on the overall season reproductive success as this effect is not significant when running the analysis by breeding attempt.

The results showed no significant effect of group size on the breeding success by breeding attempt analyses (number of chicks fledged at day 17, survival of all chicks per nest) with a larger dataset ( $n = 188$ ). The variable group age was relevant for the analyses because the experience of older helpers might be relevant for offspring care and therefore, have a positive or negative effect on the reproductive outcome of a breeding pair. On the restricted dataset ( $n = 141$ ), when group age was studied, an interaction between colony size and group size showed a positive effect on both the number of chicks fledged at day 17 and the survival of all chicks per nest. This might have happened because of the breeding pairs breeding alone being eliminated from the analysis, which resulted in a smaller and with less information sample size than the previous analysis. Despite this result being significant, there is no credible biological explanation for this outcome. Nonetheless, these results suggest that breeders do not maintain the same effort regardless of helper number i.e. helpers do not have an additive effect, but rather compensate the work done by helpers through decreasing their own effort in terms of parental care (Brown and Brown 1981).

Experience might not be that relevant for this species because age of breeding female showed no significant effect on both the survival of all chicks per nest and the number of fledglings at day 17. This indicates that younger females might provide the same parental care of an older female and that experience might not be important for nestling survival.

The initial number of chicks in the nest had a negative effect on the survival of all chicks per nest. This suggests that parents might have limited resources to raise their offspring and are not always able to adjust the number of eggs laid to the environmental conditions.

Colony size showed no significant effect in both analyses, which suggests that there is no difference for a parent on breeding in big or small colonies. This contrasts with a previous study on the sociable weaver that found a negative effect on hatching and fledging success in larger colonies, which was suggested to arise from food depletion, higher parasite loads at larger colonies and longer foraging trips (Covas et al. 2008). This can lead to a deficient incubation and therefore, an increase on hatching failure (Covas et al. 2008). However, in

the present study, there was a bias in the dataset, with more data coming from larger colonies, and this could explain the discrepancy between the two studies.

For the analyses run for each breeding attempt, the environmental variable maximum temperature in the 15 days preceding the fledging date was the one explaining better the variation in the number of chicks fledged at day 17, according to the exploratory analyses. In these analyses, temperature showed no significant effect on both the number of chicks fledged at day 17 and the survival of all chicks per nest. Temperature is an important variable in this study because sociable weavers live in arid and hot environments and high temperatures have been shown to influence foraging effort and reproductive success in these environments (du Plessis et al. 2012; Cunningham, Martin, et al. 2013; Cunningham, Kruger, et al. 2013; Cunningham et al. 2015). For instance, in Common Fiscals (*Lanius collaris* Linnaeus, 1766) and in Southern Pied Babblers (*Turdoides bicolor* Jardine, 1831), high temperatures significantly reduced body mass and foraging efficiency (du Plessis et al. 2012; Cunningham, Martin, et al. 2013).

As for the analyses of overall seasonal reproductive success, the results are different. Group size seems to have a positive effect on the total number of fledglings produced by breeding pair by season when the average temperatures are higher. As the temperature increases, the total number of fledglings being produced by breeders with helpers is bigger than the total number produced by parents breeding alone. This result is particularly interesting because it suggests a specific positive effect of helpers where needed. In this respect, in the sociable weaver system, a bird that inhabits fluctuating environments, helpers do indeed help raise more offspring under adverse conditions i.e. under high temperatures. It is also consistent with the results of a previous work where the brood size was manipulated and helpers had a positive effect on decreasing nest mortality and increasing the number of chicks fledged (Covas and Du Plessis 2005). Similar results were found in a cooperatively breeding mammal, the meerkat *Suricata suricatta* Schreber, 1776, which inhabits the same highly variable semi-arid Kalahari territories, in which environmental and social factors influence the reproductive success (Russell et al. 2002). High temperatures are probably a constraint when they look for food to bring to the chicks and helpers provide the necessary help to produce more chicks (du Plessis et al. 2012; Cunningham, Martin, et al. 2013). Another explanation might be the fact that breeding pairs with helpers could manage better to sustain their effort throughout the season when they have helpers, whereas parents without helpers fail when the conditions become very extreme (high temperatures). Previous works on the sociable weaver already showed that the presence of helpers allows females to save energy (Paquet et al. 2013; Paquet, Covas,

et al. 2015) and hence, females with helpers may be able to lay additional clutches per season.

Colony size and age of the breeding female showed no significant effects on overall breeding success, which is congruent with the results from the previous analyses at breeding attempt level, suggesting that female experience and the total number of birds in a colony do not influence the reproductive success.

However, my analyses only included the broods that survived to day 17, and hence it does not take into account the possibility that helpers might be effective at decreasing the effects of other adverse factors such as predation or infanticide. For example, in the pied babbler, *Turdoides bicolor*, predation is higher in smaller groups (Ridley and Raihani 2008). In the sociable weaver, snakes take approximately 70% of the broods laid, but it is unclear whether the presence of helpers can be effective against these predators (Covas et al. 2008). Moreover, in this species, infanticide occurs more frequently under adverse conditions (dry and hot) and the presence of helpers might reduce this event, which can contribute to increase the reproductive success (unpublished data). Therefore, a positive effect on the seasonal reproductive success is more meaningful than an effect per breeding attempt since it takes into account better the parental effort, predation and the reduction in infanticide.

It is expected that in cooperative breeders, the additional food brought to the nest by helpers may increase the reproductive output, however, some studies have failed to find this effect. This might happen because the contribution of helpers to offspring care can be used to reduce their own breeding effort or because the effect of helpers might only be significant under adverse conditions and go unnoticed under more favorable conditions (Cockburn 1998; Magrath 2001; Covas and Du Plessis 2005; Rubenstein and Lovette 2007). Previous work conducted on the sociable weaver provided support for both hypotheses. In the sociable weaver, the effect of helpers on the reproductive output was detectable under harsh conditions such as low rainfall and when breeding in large colonies (Covas et al. 2008). However, those results were based on only 2 breeding seasons (Covas et al. 2008). Here, with a more robust analysis, I showed that helpers do indeed have a positive effect and it is only noticeable under high temperatures. Moreover, similar results were found in a previous work where the brood size was manipulated showing a positive effect of helpers specifically in situations of greater demand (Covas and Du Plessis 2005). Therefore, all these studies indicate that helper effects' in the sociable weaver, contribute to buffer the effects of extreme and unpredictable conditions, while going unnoticed under good conditions.

To conclude, understanding the evolution and maintenance of cooperation and more specifically, the mechanisms underlying helpers' investment decisions and their effect on the reproductive success in the sociable weaver has revealed difficult with results providing support for both additive and compensatory behavior. Furthermore, this study suggests that there might be a flexibility of behaviors coming from both helpers and breeders in terms of parental care. Besides, both social and environmental context should be taken into account when assessing the effect of helpers due to the fact that the interaction between them are likely to exert a strong selection pressure in cooperative breeders.

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