The effect of helpers on the post-fledging period of a cooperatively breeding bird, the sociable weaver

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

O Presidente do Júri,

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Summary

To understand the evolution of cooperation it is crucial to determine the costs and benefits of this type of behavior. In cooperatively breeding species non-breeding individuals assist in raising offspring, and these 'helpers' are expected to increase reproductive output and/or breeders survival. While the effect of helpers on nestling conditions and breeders survival has been well studied, the effect of helpers on fledgings are rarely studied, mostly because of the difficulty in tracking mobile young. However, it has been suggested that besides improving juvenile future survival and dispersal probabilities, helper's presence might also have costs to the young. We monitored juvenile survival during the first three months of life in sociable weavers, *Philetairus socius*, raised in pairs alone versus pairs with helpers, and used capture-mark-recapture methods to control for individual detectability and estimate survival. Our results suggest a lower survival probability for juveniles with helpers from 17 to 30 days of age. Group size also seems to affect negatively survival. This is most likely true mortality, and not confounded by dispersal, since dispersers younger than 4 months are extremely rare. Colony size also seems to have a negative impact on juvenile survival, whilst rainfall has a positive effect. In order to understand this effect we investigated if juveniles with helpers fledged earlier using temperature inside the nest as a proxy for fledging date; however found no indication of significant differences. We also investigated if the breeders re-nesting interval after a successful brood could be shorter for parents with helpers, but also found no significant effect. Despite of this, our study gives new insights into the effects of helpers on the post-fledging period of cooperative breeders, demonstrating a cost that has now to be understood.

Keywords: *Philetairus socius*, sociable weaver, cooperative breeding, capture-mark-recapture, post-fledging survival, helpers.

Resumo

De maneira a entender de melhor forma a evolução da cooperação, é crucial determinar os custos e benefícios associados a este tipo de comportamento. Em espécies que se reproduzem cooperativamente, existem indivíduos não-reprodutores que assistem outros na criação dos juvenis. Estes são chamados de ‘ajudantes’ e espera-se que eles aumentem o sucesso reprodutor e/ou a sobrevivência dos casais que ajudam. Enquanto que os efeitos dos ajudantes nas condições físicas das crias no ninho, e na sobrevivência do casal, têm sido bem estudados, os efeitos dos ajudantes no período pós-ninho é raramente estudado, devido à dificuldade em detectar os juvenis em mobilidade. No entanto, tem sido sugerido que além de melhorar a sobrevivência futura dos juvenis e suas as probabilidades de dispersão, a presença dos ajudantes pode ter custos para as crias. Neste estudo, investigámos a sobrevivência juvenil durante os três primeiros meses de vida dos tecelões sociáveis, *Philetairus socius*, comparando crias criadas em pares com e sem ajudantes. Para isto, usámos métodos de captura-marcação-recaptura para poder ter em conta a detectabilidade individual e para estimar taxas de sobrevivência. Os nossos resultados sugerem que os juvenis criados com ajudantes têm menor probabilidade de sobrevivência dos 17 aos 30 dias de vida. O tamanho do grupo também parece afectar negativamente a sobrevivência. Esta estimativa não é confundida por dispersão, sendo considerada uma mortalidade verdadeira. Isto deve-se ao facto de nesta espécie ser raro haver dispersão antes dos 4 meses de vida. O tamanho da colónia também parece ter um impacto negativo na sobrevivência juvenil, ao contrário da chuva, que teve um efeito positivo. De maneira a tentar entender este efeito negativo tentámos perceber se os juvenis criados na presença de ajudantes saem do ninho mais cedo, usando para isto, como uma medida indirecta, a temperature dentro do ninho. No entanto, não encontrámos nenhuma diferença significativa. Além disso, investigámos também se após uma ninhada com sucesso os casais com ajudantes fazem outra tentativa de reprodução mais cedo, em comparação aos casais sem ajudantes. Também não encontrámos nenhuma variação significativa. No entanto, este estudo trás novas perspectivas sobre o efeito dos ajudantes do período pós-ninho em espécies que se reproduzem cooperativamente, e demonstra um custo que precisa de ser explicado.

Palavras-chave: *Philetairus socius*, tecelão sociável, reprodução cooperativa, captura-marcação-recaptura, sobrevivência pós-ninho, ajudantes.

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Introduction

Cooperative behaviour is commonly seen in the natural word, and it exists across all levels of biological organization. For example, bacteria cooperate when producing ‘public goods’ – products that are costly to the individual, but benefit the group; multicellular organisms can also be seen as a strong cooperation system between the eukaryotic cells that compose them (West et al. 2006; West, Griffin, and Gardner 2007). In higher orders of biological organization cooperation exists in various ways – some animals cooperate in the detection and/or defence against predators, or in foraging, while others cooperate to build societies – for example, ants (Alexander 1974). Others even breed cooperatively – species of insects, birds and mammals (Clutton-Brock 2002; Cornwallis, West, and Griffin 2009)

Cooperation is apparently costly to the actor (Hamilton 1964), but in order to evolve it should also provide a benefit to the receiver. This poses a problem to the evolutionary theory, in the sense that, this kind of behaviour can affect negatively the fitness of the individual that performs it. In order to better understand why cooperation is maintained throughout generations, it is important to understand its costs and benefits.

One of the first major breakthroughs to explain the evolution and maintenance of this type of behaviour happened in 1964, in a paper by W. D. Hamilton. He demonstrated that these cooperators may gain inclusive fitness through their positive impact on the reproduction of related individuals. By cooperating with close relatives, they are also indirectly spreading their own genes (indirect fitness benefits) (Hamilton 1964). To illustrate this theory, Hamilton devised a very simple rule which stated that cooperation occurs when $rb-c > 0$ (where r is the relatedness between the helper and the recipient, b is the fitness benefit to the recipient and c is the cost to the helper). Therefore, cooperation can evolve when the benefits to the recipient, and the genetic relatedness of the recipient to the actor, put together, outweigh the costs of performing that behaviour to the actor. Hamilton suggested that this could be achieved through kin recognition and actively choosing to cooperate with kin, or through limited dispersal, which creates genetically structured groups of related individuals (Axelrod and William D. 1981).

A specific case of cooperative behaviour is cooperative breeding. This happens in some species of vertebrates, mainly insects, birds and mammals (Clutton-Brock 2002; Cornwallis, West, and Griffin 2009). In these groups, sexually mature individuals called ‘helpers’ assist others with their breeding efforts, instead of engaging in reproduction themselves. This assistance consists mainly in bringing food to the developing young, and protecting the breeding site or territory against predators (Cockburn 1998).

Kin selection appears to be a major factor explaining the evolution of cooperative breeding (Cockburn 1998). However, kin selection may not be the only adaptive explanation for helping (Griffin and West 2002). Several studies have found that helping behaviour is not associated with relatedness (reviewed in Clutton-Brock 2002). For example, helpers can be unrelated to the young they’re feeding, or unrelated helpers might have the same investment in feeding than related helpers (Wright et al. 2009; Doutrelant, Dalecky, and Covas 2011). This suggests that these individuals might be getting another kind of benefit from helping. Some of these direct benefits can include payment of rent, i.e. work in exchange of other benefits of living on a territory or in a group; direct access to parentage; enhancement of the territory or group size in a way that improves later opportunities for direct reproduction, or improves survival; enhancement of social circumstances via formation of alliances that improve the prospect of reproduction; acquisition of skills or prolonged maturation that facilitates later reproduction (reviewed in Cockburn 1998, Clutton-Brock 2002).

To fully understand the evolution and maintenance of cooperative breeding, it is first necessary to understand the costs and benefits of the help provided. An important work has been performed on the effect of helping on reproduction (clutch size or litter size, juvenile condition, number of young produced and feeding rate). In general it has been found that helpers do increase the overall reproductive success of the individuals they helped (Hodge 2005; Woxvold and Magrath 2005; Doerr and Doerr 2007).

Helpers are also expected to affect offspring condition and survival after the nestling period. After they have fledged, juveniles are extremely vulnerable since they are still developing their foraging and predator avoidance skills. Helpers can make a difference, by continuing to give food and protection from predators (Langen 2000). For example, a study done on pied babblers showed that fledglings that received longer periods of care attained higher foraging efficiency and body mass than their counterparts at 6 months of age (Raihani and Ridley 2007). In cooperative meerkats, pups raised by helpers were more likely to breed at a younger age as subordinates and to compete successfully for alpha rank (Russell et al. 2007). And consequently, the extra food brought by the helpers can also have positive long-term effects on the body condition and survival of the juveniles. Nestling growth rates might increase due to the extra food, which means that chicks might be able to develop more quickly, and leave the nest earlier (Raihani and Ridley 2007). This will lead to a decrease in the predation rate which can be very important in many species given that predation can lead to the death of more than half of the nests in many species (Martin 1995; Cheng and Martin 2012). In agreement with this study, a recent comparative study showed that cooperative species tend to fledge their young earlier (Ridley and van den Heuvel 2012).

The benefices of helping might alternatively, or in addition, exist for the parents. Helpers are thought to increase the reproductive success of the parents, by alleviating parental work load, and thereby allowing them to have enough energy to relay more often or to survive better (Hatchwell 1999). In many species, it has indeed been found that parents work less in presence of helpers (Hatchwell 1999; Covas, Plessis, and Doutrelant 2008) or that mothers invest less in eggs (Russell et al,. 2007; Paquet, Covas, Chastel, Parenteau, & Doutrelant, 2013). A few studies have shown that the breeders' survival increased in presence of helpers (Kingma et al. 2010).

Furthermore, parents might decrease their re-nesting period in the presence of helpers. In pied babblers it has been shown that after fledging, parents start a new nest quicker in presence of helpers because helpers take on the task of feeding the juveniles (Raihani and Ridley 2008). A similar behaviour was observed for the cooperatively breeding apostlebirds (Woxvold and Magrath 2005). However, if helpers are less experienced (e.g. lower foraging or predator avoidance skills), or motivated carers this can have a negative impact on juvenile survival.

On the other hand, competition between juveniles and their former helpers may take place. For example, if staying in the natal colony and remaining in a family group is an important asset for survival and future access to mating, but there is an optimal group size, some individuals might be forced to disperse.

Hence, the effect of helpers on the post-fledging period can be beneficial, but may also be associated with trade-offs. In a study on Siberian jays, retained juveniles constrained settlement decisions of dispersers by aggressively chasing dispersers off their territory (Griesser et al. 2008). Thus, juveniles born into a group with helpers might actually face higher mortality or dispersal rates, as it was found for sociable weavers (Covas, Deville, Doutrelant, & Spottiswoode, 2011).

Studying the survival of the individuals after they have fledged is often a hard task. In most species of birds, individuals disperse when they become independent, hence the difficulty in detecting these individuals, and obtaining long term data on their survival. Specific statistical methods are used in this case, like capture-mark-recapture (CMR) analyses. These models estimate survival by taking into account the recapture probability. This is essential because an animal that has not been seen for a long time might not be actually dead. It might have not been observed due to chance or biological reasons (Gimenez et al. 2008).

The effect of helpers on post-fledging survival has been seldom studied and these studies revealed contradictory results (McGowan, Hatchwell, and Woodburn 2003; Sankamethawee, Gale, and Hardesty 2009; Covas et al. 2011). However, CMR analyses were only used in three studies and the results were drastically different. In a study done on the puff-throated bulbuls, no effect of helpers on the survival of the juveniles was found (Sankamethawee, Gale, and Hardesty 2009); in one study done on long tailed tits, there was a positive effect (McGowan, Hatchwell, and Woodburn 2003) and in one study on sociable weavers, there was a negative effect (Covas et al. 2011). This puzzling result obtained on sociable weavers could be due to either a higher mortality or to increased dispersal away from the study area (Covas et al. 2011). In the present study the goal was to better understand the potential negative influence of the presence of helpers on the post-fledging survival of sociable weavers, *Philetairus socius*.

Determining the mechanisms that trigger such negative effects and its consequence on adult behaviour is extremely important. If, for example, helpers have a negative effect on juvenile survival, but allow parents to reproduce more often, and thus fledge more young, this will allow us to estimate more precisely the cost and benefits of cooperation in this species and can explain its evolution.

Objectives

The main goal of this study was to determine whether lower juvenile survival in the presence of helpers is due to a higher mortality or to increased dispersal. To achieve this, we 1) used CMR methods to analyze juvenile survival during the first 3 months post-fledging, comparing nests with and without helpers. In this species, dispersal before the birds are 4 months old is extremely rare (it has only been observed once, over 6 years of observations in 15 colonies). Focusing on the first 3 months post-fledging thus allowed us to exclude dispersal as a major explanation for the disappearance of juveniles, and assess if juveniles with helpers suffer from true mortality after fledging. In addition, in order to gain a better understanding of the factors affecting juveniles in the first days post-fledging, we also 2) investigated whether the presence of helpers affected the duration of the nestling period, and 3) if parents that had helpers during the previous successful brood have a shorter relaying interval than parents that did not have help.

Methods

Study species

The sociable weaver, *Philetairus socius*, is a colonial cooperatively breeding passerine that inhabits the semi-arid savannahs of the southern Kalahari and in Southern Africa. They feed on a large variety of insects, but also on seeds and other plant products (Maclean 1973a). They build a very large communal nest (the colony), which is made of *Stipagrostis* grasses, and is built most commonly on *Acacia* trees (Mendelsohn and Anderson 1997). The colonies have several independent nest chambers where breeding and roosting take place, and vary in size from less than 10 to more than 200 individuals. Sociable weavers can breed in pairs or with one to five helpers (Covas et al. 2006; Covas, Plessis, and Doutrelant 2008). Both sexes can help, but helpers older than 1 year are normally all males (Doutrelant, Dalecky, and Covas 2011). The breeding group is usually stable during the breeding season, but group composition can change between years as older helpers leave, or young from the previous season become helpers. The regions that the weavers inhabit are characterized by an unpredictable rainfall both in timing and quantity, which affects food abundance, and which, in turn, affects breeding activity (Maclean 1973a; Covas, Plessis, and Doutrelant 2008). For this reason, this species does not restrict reproduction within a season, but seems to extend it as long as conditions are suitable (Maclean 1973b).

In this species the helpers have been shown to be most commonly offspring of the breeding pair (Covas et al. 2006). Nonetheless, unrelated individuals also help and may invest more in feeding the young than more closely related individuals (Doutrelant, Dalecky, and Covas 2011). These studies suggest that both direct and indirect (kin selected) fitness benefits are important to maintain the helping behaviour in this species.

The presence of helpers on sociable weavers was shown to have a positive effect on reproductive output, counteracting some of the negative effects of breeding under unfavourable conditions, such as large group size or low rainfall (Covas, Plessis, and Doutrelant 2008). In addition, a recent study found that females assisted by helpers produce smaller eggs, while fledging mass did not change, which suggests that helpers can compensate for the reduced investment in eggs (Paquet et al. 2013). Eggs from nests with helpers also had lower hormonal concentrations, specifically testosterone and corticosterone levels. Both these results suggest that the presence of helpers influences maternal investment in offspring.

Field Methods

This study was conducted at Benfontein Nature Reserve in the Northern Cape Province, South Africa. This project is part of a long-term study conducted on a population of the sociable weaver that aims to understand the evolution and maintenance of helping in this species. Since 1993, the resident birds at each colony are captured with mist nets every year, before the breeding season, to track juvenile dispersion and to mark immigrants. All the captured individuals are ringed with a uniquely numbered aluminium ring and a unique colour combination. All nest chambers in each colony are individually numbered with a plastic tag.

This study was conducted on 12 colonies. Six of these colonies were protected with cling film in order to keep away the snakes, since ca. 70% of the breeding attempts are normally depredated (Covas, Plessis, and Doutrelant 2008). Boomslangs *Dyspholidus typus* and Cape cobras *Naja nivea* are the main nest predators.

All nest chambers were inspected every 3-4 days during the breeding season to detect initiation of new clutches, and obtain information on hatching and nestling number and order. As soon as the first egg was found, the nests were inspected everyday to mark every new egg with a soft blunt pencil, in order to know the laying sequence. The sociable weavers lay 1 egg per day, with a total of 2-5 eggs per clutch (in most cases the clutch size is 3-4). The incubation period lasts 15 days, and after that the eggs hatch asynchronously at 1-day intervals. The nests were visited everyday to know the hatching order, and every chick was individually marked by removing specific down feathers from the neck and/or wings. It can happen that 2 chicks hatch in the same day. On day 9, we visit the nest and put a uniquely numbered metal ring on the chicks. At this time, the individual marks done after hatching were still visible. The nestling period lasts 21-24 days (Maclean 1973a) however 19 days old juveniles have been seen outside the nest (personal observation). This might be due to the fact that if disturbed after day 17 the nestlings can fledge prematurely (R. Covas, personal observation). Therefore, when the oldest nestling is 17 days old we put the colour rings in the chicks, weigh and measure them. A small temperature data logger (also called thermocron) was placed hidden inside the nests, underneath the chicks, to record the temperature every 5 minutes from day 19 to day 25. After this, recovering the temperature data logger would not disturb the juveniles, since they had already fledged.

To identify the individuals feeding at a given nest we conducted observations, during the nestling period, from a hide placed 2-5 m from the colony for 1-2h a day over 3-5 days. An individual is considered to be part of the breeding group after having been observed feeding the juveniles on 3 or more observations in different days. The day in which the first chick(s) of a clutch hatches is considered to be day 1 for the whole brood.

Observations associated to breeding monitoring also allow us to have information on re-nesting interval of the same parents.

Rainfall influences food availability, and the duration and success of the breeding season in sociable weavers. Therefore, we collected rainfall data in the study area using a rain gauge.

To determine the effect of the presence of helpers on juvenile survival in the first three months post-fledging, we started to conduct ‘visual recaptures’ after the chicks were 30 days of age, every 1 or 2 weeks for the following 3 months. These observations were done at the end of the day, when all the individuals come to the colonies to roost. Observations were conducted from under the same hide used to identify breeding groups. We began the observations at day 30 because prior to this age the fledglings spend most of the day in their chambers, making it hard to observe them. For each observation we would mark a 1 for seen, and a 0 for not seen. During the breeding season of 2012/2013 we conducted 10 ‘visual recaptures’ that were 1 or 2 weeks apart (the different time intervals between observations were later taken into account in the analysis). This implicated observing all colonies that had fledglings at each of the 10 different occasions. During the study new chicks would fledge and so in each ‘visual recapture’ we would observe new juveniles, and also record their presence. Day 17 was defined as the first occasion. Thus, in total we had information for 11 different occasions. For example, a capture-resighting history of a juvenile that fledged in the beginning of the breeding season could be 11111111111, if it was always seen during the 10 ‘visual recapture’ events, or 10000000000 if it was never seen after day 17. It would be 0000100000 for an individual that fledged in the middle of the breeding season and it was not seen afterwards.

In total, we had capture-resighting histories for 156 fledglings, 92 of these were raised by pairs without helpers, and 64 were raised by groups with helpers. All individuals we followed fledged between October 24th 2012 and January 31st 2013.

Statistical analyses

Capture-Mark-Recapture Analysis

Using the individual capture histories it is possible to estimate survival parameters via maximum likelihood methods (Lebreton, Jean-Dominique Burnham, Clobert, and Anderson 1992). In order to have a more correct inference of the survival rates, it is important to also calculate the probability of the animal being on the field site and being seen. Therefore, the probability of encountering a previously marked and released individual is a product of the survival probability and the re-sighting probability. Survival probability can be defined as the probability of surviving and returning to the sample area. Re-sighting probability can be defined as the probability of being encountered conditional on being alive and in the sample. Individuals that disperse are considered to have died, and so it is generally impossible to determine true survival probabilities. However, in the present study this problem was largely avoided since dispersal in sociable weavers before the birds are 4 months old is extremely rare (a single case was recorded in 6 years of monitoring). The statistical analyses were performed using program MARK (Cooch and White 1998).

Our final aim was to test the relative importance of helpers on juvenile survival. The effect of helpers was examined using two types of models: first, by treating helpers as a dichotomous factor (presence/absence), and second, as a linear variable – 'group size – ranging from 2 to 6 individuals. Other factors could affect the probabilities of survival, so we tested the following continuous covariates: weight at day 17, brood size, chick order, colony size, presence of snake protection (presence or absence) and rain (mm). We expected colony size to have a negative effect on survival probability, since it was previously found that larger colonies have lower fledging success (Covas, Plessis, and Doutrelant 2008). Rain was defined as the total amount of rain that occurred on the previous 30 days to day 17 (Dean and Milton 2001; Covas, Plessis, and Doutrelant 2008). We also tested the interactions between each covariate and the effect of helper presence/absence.

For the probability of resighting we tested the following variables: presence/absence of helpers and colony size. We expected colony size to have an effect on re-sighting probability, since the greater the colony, the harder could be for the observer to detect the presence of a juvenile.

To compare between different models we used the Akaike information criterion corrected for sample size (AICc). This method takes into account deviance and number of parameters. The model with the lowest AIC is the best model because it is most parsimonious given the data – i.e. it provides the best fit with fewest parameters. A difference of less than 2 in the AICc between this model and the others is not enough to support a significant difference between them. In these cases, to assess the significance of one or more factors on variation in a particular parameter of interest we used likelihood ratio tests (LRT) between nested models (Lebreton, Jean-Dominique Burnham, Clobert, and Anderson 1992).

In CMR analyses, several preliminary analyses have to be performed before testing the effect of the biological variables of interest (here, the effect of helper's presence) on survival. Here, we performed 3 steps of preliminary analyses

The first step of the analyses was to verify that the data set meets the Cormack-Jolly-Seber assumptions (no trap dependence and no transient effect). To do this we performed a Goodness-of-Fit test using the program RELEASE GOF. The general CJS model did not fit our data (Chi2 =97.016 P-level=0.00029754). Looking at the two tests separately (transient effect and trap dependence) showed that this was due to the presence of a transient effect, in this case, an age effect (P-level, two-sided test =0.00013056, P-level, one-sided test for transience =6.5282e-005). The test for trap dependence was not significant (P=0.86463). Hence, we assumed that our initial model was not a fully time-dependent model. In practice, this means that individuals of different age classes differ in the probability of surviving to the next age, i.e. as individuals get older they experience different mortality rates.

The second step was to test if both survival and recapture were time dependent or constant. With the knowledge that our final model would have to include age classes, due to the transient effect detected before, we constructed an age-dependent model for survival probability – Phi(age), which was a better fit than all the others, thus showing no time dependence. For the recapture probability, the best model proved to be time dependent – p(t). This model, Phi(age)p(t), gave us an estimate of the probability of survival for every interval between the 11 recapture occasions. The probability of survival for the interval between the 1st and 2nd occasions (immediately after the chicks fledge, i.e. between day 17 and 30) was of 0.777±0.037 (SE), while for the other intervals (after day 30) it was between 0.9 and 1. Therefore, we modelled the survival probability for 2 age classes. The first age class corresponded to the first interval, between 17 to 30 days of age, whilst the second age class included all the other intervals. The model Phi(2age)p(t) proved to be a better fit to the data than the previous one (Table 1).

Finally, the last step was to add the helper effect and colony size in the recapture probability, and chose the best model. By adding the group effect and covariate colony size to the model Phi(2age)p(t) we obtained the best model for the recapture probability - Phi(2age)p(t+c) (Table 2). Colony size had a positive effect on the probability of resighting of the fledglings.

Table 1: Modelling the survival probability (Phi) and recapture probability (p) in relation to time. The best model is in bold.

Model	AICc	Delta AICc	AICc Weights	Model Likelihood	Num. Par	Deviance
1.Phi(2age)p(t)	1048.011	0	0.00009	0.0007	12	1023.382
2.Phi(age)p(t)	1051.944	3.933	0.00001	0.0001	16	1018.839
3.Phi(t)p(t)	1057.502	9.4909	0	0	16	1024.397
4.Phi(age)p(age)	1059.607	11.596	0	0	16	1026.502
5.Phi(t)p(.)	1064.052	16.041	0	0	8	1047.764
6.Phi(.)p(t)	1068.835	20.824	0	0	11	1046.304
7.Phi(.)p(.)	1090.919	42.908	0	0	2	1086.896

Phi: survival probability, p: recapture probability, (t): time dependent, (.): constant, age: age-dependent, 2age: 2-age classes.

Table 2: Modelling the survival probability (Phi) and recapture probability (p) in relation to presence of helpers and colony size. The best model is in bold.

Model	AICc	Delta AICc	AICc Weights	Model Likelihood	Num. Par	Deviance
1.Phi(2age)p(t+c)	1040.722	0	0.00326	0.0263	13	1013.986
2.Phi(2age)p(t+h+c)	1042.722	2.0007	0.0012	0.0097	14	1013.872
3.Phi(2age)p(t+h)	1047.905	7.1831	0.00009	0.0007	13	1021.169
4.Phi(2age)p(t)	1048.011	7.2896	0.00009	0.0007	12	1023.382

Phi: survival probability, p: recapture probability, (t): time dependent, c: colony size, h: helper effect.

Phi(2age)p(t+c) constitutes our best model. However, because survival appears to be constant after 30 days, we investigate here the effect of helpers and other important variables on the survival probability specifically between 17 and 30 days. For this reason, hereinafter I will refer to the previous model as Phi(1age)p(t+c), in order to illustrate the fact that we tested the variables of interest only in the 1st interval, until 30 days of age. We did not test any of the variables mentioned in the period following 30 days.

Fledging period analysis

The aim of this analysis was to investigate if juveniles with helpers fledged earlier than juveniles without helpers. Fledging in this species usually occurs when the juveniles are 21-25 days old. This process does not appear to be synchronous for the different individuals of a same brood (personal observation), and, it is still unknown if hatching order has some influence in this. In most cases, after fledging, the juveniles move to another chamber that also belongs to that breeding group.

Determining the exact fledging date of 20 nests at different colonies only through observations is impossible for a single person, since it is unknown at what time of the day the juveniles leave the nest for the first time. Besides, after fledging, juveniles still tend to stay inside the nest for long periods of time, making it difficult to observe them outside. Thus, we decided to use the temperature inside the nest as an indirect measure of the exact day the juveniles leave the nest for the first time.

The temperature inside the nest was recorded from day 17 to day 25 for 20 broods (10 with helpers and 10 without helpers). In general, when the fledglings leave the nest, we can expect a decrease in the temperature inside the nest. We hypothesized that if juveniles with helpers fledged earlier, the occurrence of temperature drops would also happen earlier (when there are no birds on the nest), in comparison with nests without helpers.

To test this hypothesis, we analysed differences in average daily temperature from day 19 to 25 in nests with and without helpers (while controlling for outside temperature). Using the data collected by the temperature data loggers placed inside the nests, the average temperature for each nest each day from day 19 to day 25 was calculated between 6.30am and 5pm. Minimum and maximum outside temperature for the same days was collected from Kimberley Airport Station, 12 km from the centre of the study site. As temperature inside the nest is dependent on the temperature outside the nest, this needed to be taken into account in the analysis. For this reason, we calculated the average ambient temperature (by averaging the minimum and maximum outside temperature), and included it in all the models, never dropping it.

The effect of helpers was examined using two types of models - helpers as a dichotomous factor (presence/absence), and group size. The other variables tested were day (19-25), number of nestlings sleeping inside the nest (from 1 to 4) and laying date. We had repeated measures for the same nest over the days. This means that there was potential for non-independence of the data. For this reason, mixed models were used to analyse the data. These allow the incorporation of random effects. Nest identity was therefore included as a random term. This term was never dropped from the models even if it was non-significant to avoid pseudo-replication (Quinn and Keough 2002). For these analyses we conducted linear mixed models using the package nlme in R (Team and others 2005). The normality of the data was first verified. Models began with all the factors and interactions mentioned above, and the least significant terms (P>0.05) were sequentially dropped until obtaining a final model. The normality of the residuals was verified for this model. The following interactions were tested: helper absence/presence*day and group size*day. The significance for each term when it was dropped from the model is presented.

Inter-nesting interval

The aim of this analysis was to test if there was an effect of the presence of helpers on the inter-nesting interval. To achieve this, we calculated the number of days between the day on which a brood reached day 17, and the day on which the same parents laid the first egg of a new clutch. The analysis contained 30 pairs of individuals with inter-nesting intervals ranging from 8 to 64 days. Of these, 14 pairs had helpers (1 to 4) and 16 pairs had no helpers. The effect of helpers was examined in the same way as previously described. Other variables were taken into account: 1) the number of juveniles from the first brood that reached day 17; 2) the number of clutches laid by that pair since the beginning of the breeding season; 3) the total amount of rain in the month previous to the laying date, 4) colony size. The interactions between group type/number of helpers and all the variables were tested. There were no repeated pairs in the analysis; however, some parents came from the same colony. In order to control for colony identity we included the random term ‘colony’ in the analyses.

For these analyses we conducted linear mixed models using the package nlme in R (R Core Team 2013). Model selection was done in the same way as for the fledging period analysis.

Results

Capture-Mark-Recapture analysis: *Survival probability*

We were interested in understanding what was causing the lower survival probability immediately after the juveniles leave the nest. For this reason, we constructed models that enabled us to test the effect of the helper presence and other covariates on survival probability between 17 to 30 days – the 1st age class. We obtained 7 best models with a difference in AICc of less than 2, therefore we cannot distinguish between them. These were: Phi(1age+R+Co)p(t+c); Phi(1age+h+R)p(t+c); Phi(1age+h+R+Co)p(t+c); Phi(1age+h*Co)p(t+c); Phi(1age+R+Co+G)p(t+c); Phi(1age+R+G)p(t+c); Phi(1age+R)p(t+c) (where R: rain, h: helper presence, Co: colony size, G: group size) (Table 3).

Table 3: Modelling the survival probability (Phi) in relation to presence of helpers and other covariates. The seven best models are in bold (ΔAICc<2).

Model	**AICc**	**Delta AICc**	**AICc Weights**	**Model Likelihood**	**Num. Par**	**Deviance**
1.Phi(1age+R+Co)	1033.446	0	0.12384	1	15	1002.472
2.Phi(1age+h+R)	1034.347	0.9017	0.0789	0.6371	15	1003.374
3.Phi(1age+h+R+Co)	1034.663	1.2174	0.06738	0.5441	16	1001.557
4.Phi(1age+h*Co)	1035.087	1.6414	0.05451	0.4402	16	1001.981
5.Phi(1age+R+Co+G)	1035.158	1.7127	0.0526	0.4247	16	1002.053
6.Phi(1age+R+G)	1035.332	1.8858	0.04824	0.3895	15	1004.358
7.Phi(1age+R)	1035.402	1.9558	0.04658	0.3761	14	1006.551

Phi: survival probability, p: recapture probability, (t): time dependent, Co: colony size, h: helper effect, R: rainfall, G: group size.

Likelihood ratio tests (LRT) can be used to compare the fit of two models. One of the two models needs to be nested within the other; that is, one needs to be a more complex version of the other. Therefore, LRT tests were used to compare between the nested models that had a difference in AICc of less than 2. The difference between

Phi(1age+R) and Phi(1age+R+Co) was significant (Chi-sq=4,079 df=1 p=0,0434). This indicates that the model that includes rain and colony size as an effect is better than the model with only rain. The difference between model Phi(1age+R) and Phi(1age+h+R) was marginally significant (Chi-sq=3.177 df=1 p=0,0747). This indicates that the model with rain and helper effect seems to be slightly better than the model with only rain. All the other tests were not significant. Since it was impossible to choose a single best model, we decided to analyze and interpret all 7 best models mentioned above.

Helper presence had an effect in 3 models, either alone or in interaction with colony size. When helper effect was alone, survival was estimated to be lower immediately after fledging for individuals raised with helpers (0.732 ± 0.067 (SE)), being higher for individuals raised without helpers (0.867 ± 0.049 (SE)) (Fig. 1; estimates for Model 2 in Table 3). After 30 days of age survival probability for individuals raised with and without helpers was of 0.984 ± 0.012 (SE) (Fig.1, estimates for Model 2 in Table 3). Group size was present in 2 models, and had always a negative effect on survival (Fig. 2).

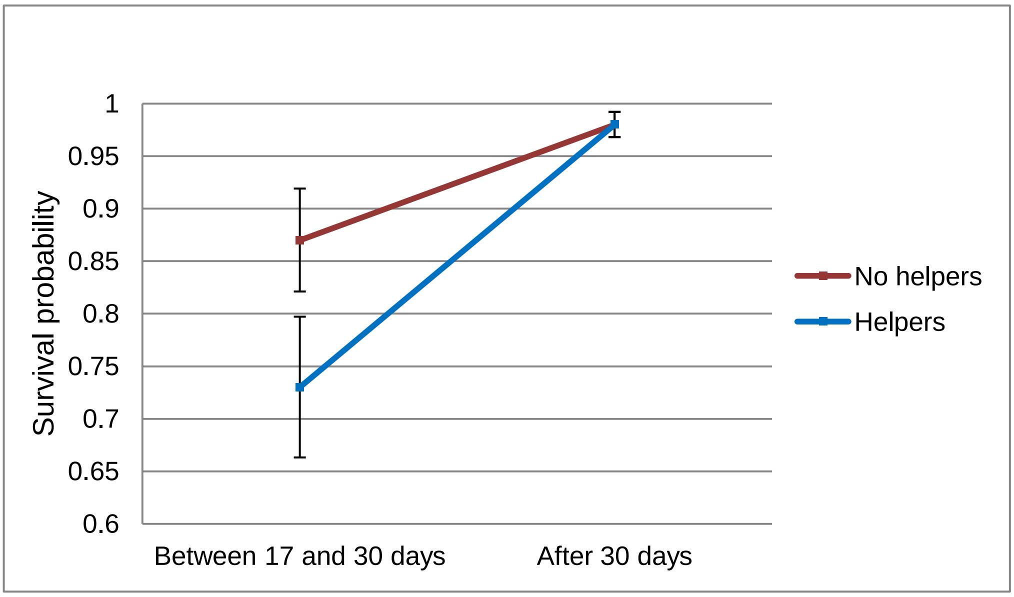

Figure 1: Survival probability between 17 and 30 days of age, and after 30 days of age, for juveniles raised in groups versus juveniles raised in pairs. Estimates taken from the model Phi(1age+h+R)p(t). Standard errors are given.

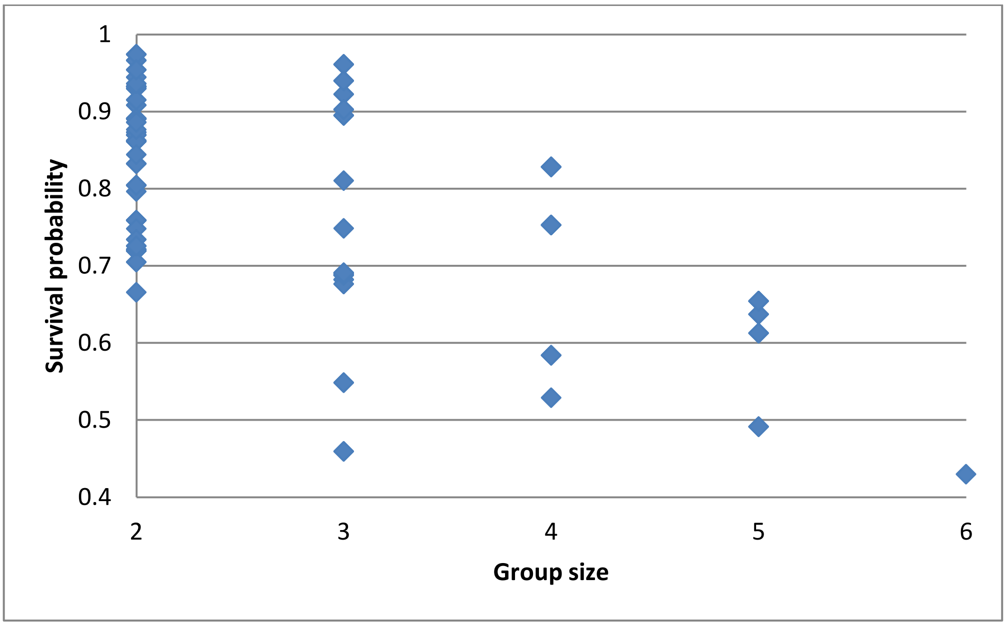

Figure 2: Survival probability (between 17 and 30 days of age) in relation to group size from the model Phi(1age+R+Co+G)p(t+c).

Rainfall was present in 6 models and had always a positive effect on survival probability (Fig. 3). Colony size was present in 4 models and had always a negative effect on survival (Fig. 4).

Finally, by looking at the estimates of survival for the model that includes the interaction of helper effect with colony size, it appears that the negative effect of colony size on survival is buffered by the presence of helpers (Fig. 5).

Survival was not affected by presence of snake protection, chick order, brood size, or weight at day 17 (for list of all the models see Annex 6).

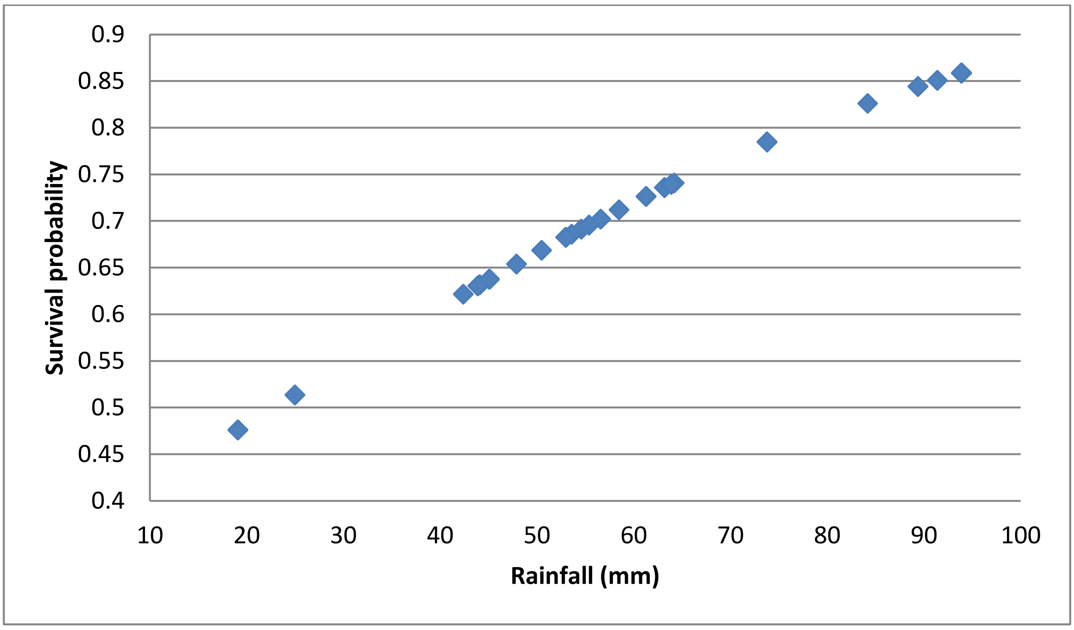

Figure 3: Survival probability (between 17 and 30 days of age) in relation to rainfall (mm) from the model Phi(1age+h+R)p(t+c).

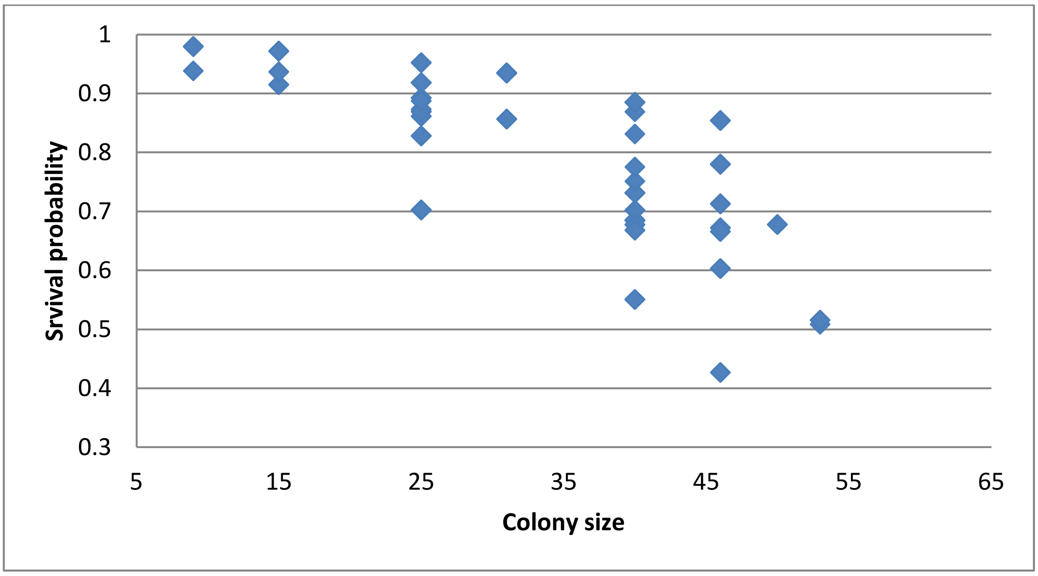

Figure 4: Survival probability (between 17 and 30 days of age) in relation to colony size from the model Phi(1age+R+Co)p(t+c).

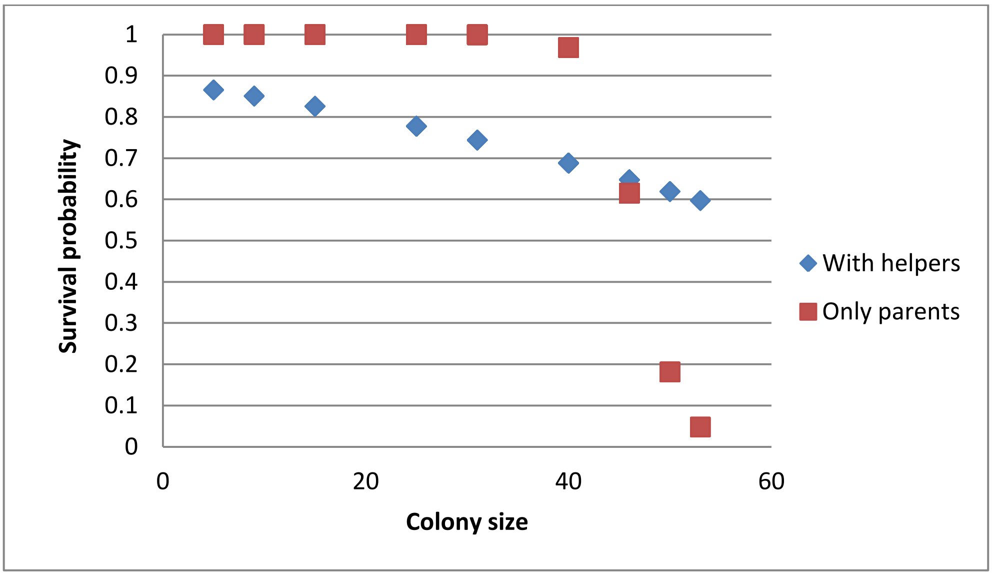

Figure 5: Survival probability (between 17 and 30 days of age) in relation to colony size for juveniles raised with and without helpers from the model Phi(1age+h*Co)p(t+c). For larger colonies (> 45 inds), 13 juveniles were raised without helpers, and 28 were raised with helpers.

Fledging period analysis

The temperature inside the nest during the day time was significantly affected by day (Table 4). Day had a negative effect, that is, temperature decreases from day 19 to day 25. This is in accordance with the fact that juveniles leave the nest during this time interval, which leads to a decrease in temperature inside the nest. The number of fledglings had a positive effect; that is, nests with more fledglings have higher temperatures. Laying date also had a positive effect, which makes sense, since as the season moves into the middle of summer, the temperatures inside and outside get warmer.

Finally, group type seems to slightly affect the temperature inside the nest. Nests with helpers are warmer than nests only with parents (Figure 6). However, group size had no significant effect, and neither did the interaction between helper presence (or number) and day (Table 4).

Table 4: Factors associated with the temperature inside the nest during the day.Estimates and standard error are given for significant explanatory terms included in the minimal model (in bold).The significance of each term when it was dropped from the model is presented. Model 1 and 2 included the same variables, and differed only by the presence of group type (Model 1) or group size (Model 2).

	numDF	denDF	F-value	p-value	Estimate	Std.Error
Intercept	1	104	1604.40	<.0001	-3632.16	1296.73
Model 1						
Day	1	104	33.95	<.0001	-0.39	0.0818
Average ambient temperature	1	104	57.27	<.0001	0.44	0.06
Number of fledgings	1	104	4.65	0.03	0.53	0.23
Laying date	1	18	7.96	0.01	0.09	0.03
Group type	1	17	3.40	0.08		
Parents					-0.60	0.50
Day x group type	1	103	0.58	0.45		
Model 2						
Group size	1	17	1.70	0.21		
Day x group size	1	103	0.86	0.36		

Day: from 19 to 25 days old; Number of fledglings: Number of nestlings sleeping inside the nest before fledgling.

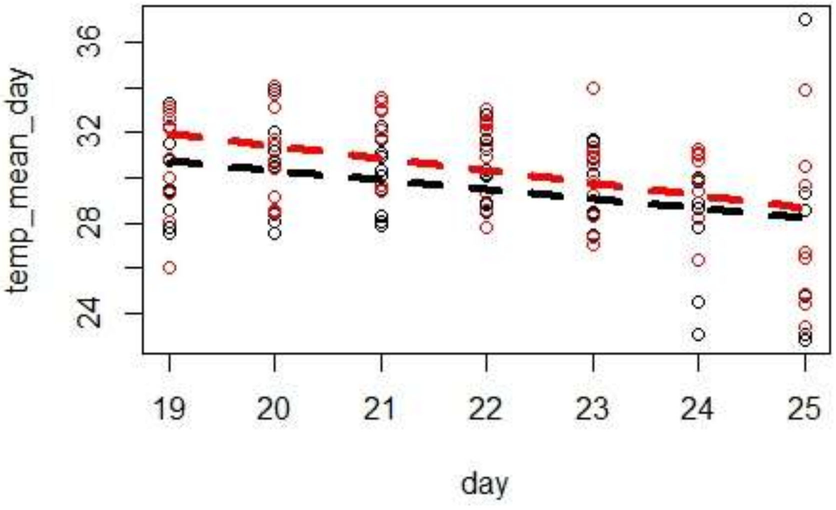

Figure 6: Daytime temperature for nests with only parents (black line) and with parents and helpers (red line), measured from day 19 to 25.

Inter-nesting interval

None of the variables tested had a significant effect on the inter-nesting interval. Despite the difference in the average number of days between nesting attempts for parents without (days=31) and with helpers (days=24.14) this factor was also not significant (see Table 5).

The result remains the same when the analysis is run without the breeders for whose fledglings were not re-sighted after 30 days of age. This rules out the hypothesis that the breeders started renesting earlier when their offspring was depredated.

Table 5: Factors tested for an effect on the inter-nesting interval. The significance of each term when it was dropped from the model is presented. Model 1 and 2 included the same variables, and differed only by the presence of group type (Model 1) or group size (Model 2).

	numDF	denDF	F-value	p-value
Model 1				
Group type	1	20	193.150	0.1799
Number of clutches before	1	19	0.19648	0.6626
Rainfall	1	18	0.02294	0.8813
Number of fledglings	1	13	0.00016	0.9902
Colony size	1	7	106.145	0.3372
Group type x Number of fledglings	1	13	0.05048	0.8257
Group type x Number of clutches before	2	15	0.34571	0.7132
Group type x Rainfall	2	17	0.72076	0.5007
Group type x Colony size	1	19	0.86869	0.363
Model 2				
Group size	1	20	139.913	0.2507
Group size x colony size	1	14	0.00008	0.9928
Group size x rainfall	1	15	0.0109	0.9182
Group size x Number of fledglings	1	16	0.01714	0.8975
Group size x Number of clutches before	1	17	0.02733	0.8706

Number of fledglings: number of juveniles that fledged before, Rainfall: rain on the previous 30 days to the laying date, Number of clutches before: Number of clutches laid by the parents throughout the breeding season.

Discussion

The aim of our study was first to investigate the effect of the presence of helpers on early juvenile survival. Capture-mark-recapture analyses showed that juvenile survival was lower between day 17 and day 30, and then more or less constant after that, indicating that the critical period is between day 17 and 30. In addition, our analyses showed that many factors are likely to affect the survival at this critical period, and helper's presence is probably one of them. Indeed, in addition to important factors known to affect juvenile survival such as rainfall and colony size (Altwegg et al. 2014, this study), 5 of the best 7 models show a negative effect of helper's presence on juvenile's survival probability. Colony size also had a negative effect on survival, whilst rainfall had a positive effect.

The negative effect of helpers on post-fledging survival is in accordance with a previous study that analysed annual survival on this species, and found that fledglings raised in groups had lower survival probability in their first year (Doutrelant, Dalecky, and Covas 2011). The present study shows that this mortality takes place in the first 10 days post-fledging. In addition, these results show that this is a true survival effect, and not confounded by dispersal, since dispersal does not take place in the first weeks post-fledging.

It was expected that juveniles would experience higher mortality immediately after leaving the nest, since this is an extremely critical period in their lives (Tarwater and Brawn 2010). Young are still developing their flying and foraging skills, and so they are more susceptible to depredation or loss of condition. The presence of helpers exacerbated this effect, which is an intriguing result. Helpers are expected to improve fledglings body condition through the additional food brought to the nest, and in sociable weavers helpers have a positive effect on body mass and fledging success under adverse breeding conditions, as under low rainfall or when breeding in larger colonies (Covas, Plessis, and Doutrelant 2008).

A possible explanation for the negative effect of helpers is that, after fledging, parents transfer their care to the helpers. For example, in pied babblers, the young are almost exclusively fed by helpers after leaving the nest while the parents move on to starting a new nest. A recent comparative analysis of reproductive performance in southern African birds with biparental and cooperative breeding strategies provided support for this hypothesis (Ridley and van den Heuvel 2012). They found that parents with helpers are able to raise more clutches per season, and suggested that this can be achieved if, after fledging, helpers are the ones taking care of the dependent fledglings. This allows breeders to re-nest while young are still dependent on adults for food. If the helpers are less efficient carers than the parents, i.e., if they bring less food, or do not efficiently protect the juveniles against predators or aggressive interactions from other individuals, then the fact that they are the only ones taking care of the fledglings can have a negative impact on juvenile survival (Raihani and Ridley 2008). In sociable weavers, parents are known to lower their feeding rates, during the nestling stages, when they have helpers (Covas, Plessis, and Doutrelant 2008).This might allow parents to invest more into reproduction. Lightening the parents work load can allow them to reduce the inter-nesting interval, and start preparing a new breeding attempt as soon as the juveniles fledge (Raihani and Ridley 2008). In sociable weavers, pairs with helpers also produce more fledglings at the end of the season, and a similar mechanism could take place (Covas, Plessis, and Doutrelant 2008). However, in our data set (30 nests) we did not find statistical differences in the re-nesting interval of parents with and without helpers. Nonetheless, parental neglect in the care of offspring might still exist in the presence of helpers, and this hypothesis, of whether in sociable weavers parents do effectively transfer the care of young to the helpers’ remains to be investigated with more data and behavioural observations.

In some cooperative species juveniles might fledge earlier when they are raised in a group with helpers (Ridley and van den Heuvel 2012). The extra food brought by the helpers might allow nestlings to grow faster, and leave the nest earlier, which can be an advantage in order to avoid depredation in the nest (Cheng and Martin 2012). In species with high nest predation, like the sociable weaver (where ca 70% of all clutches are lost to predation; (Covas, Plessis, and Doutrelant 2008)), this behaviour might have a great adaptive value. However, there can be costs associated with leaving the nest earlier, since juveniles have probably not developed completely their motor skills. This happens in pied babblers, where parents decrease their feeding rates in order to force juveniles to leave the nest earlier (Ridley and Raihani 2007). Here we did not find such a trend for parents with helpers to have shorter nestling periods. However, our analyses of the duration of the nestling period were based on the average temperature measured inside the nest using data logger (thermocrons). We acknowledge that this method might not be sensitive enough.

On the other hand, competition between juveniles and their former helpers may also take place. For example, if staying in the natal colony and remaining in a family group is an important asset for survival and future access to mating (Covas and Griesser

2007), but there is an optimal group size some individuals might be forced to disperse. In a study on Siberian jays, retained juveniles constrained settlement decisions of dispersers by aggressively chasing dispersers off their territory (Griesser et al. 2008). This is not the case in sociable weavers, since dispersal does not take place so early in life, however, we can not exclude that there might be still competition or some kind of aggressive interactions in the nests between juveniles and helpers.

Rainfall had a positive effect on the survival probability of the fledglings. Another study on sociable weavers found indications that rainfall was positively related to both survival and reproduction (Altwegg et al. 2014). This is in accordance with the fact that insect availability increases with rain, which is the main food source of sociable weavers (Maclean 1973a). Rainfall and not body mass at day 17 explained the variation in survival. This might be because rainfall captured more differences in condition than the body mass.

Colony size had a negative effect on survival probability. In a previous study it was found that larger colonies had lower fledging success, probably due to higher parasite loads (Spottiswoode 2007), and food depletion around the colonies (Covas, Plessis, and Doutrelant 2008). Another capture-mark-recapture study done on the cooperatively breeding Seychelles warbler found that survival decreased with increasing group size (Brouwer et al. 2006). Due to lack of predators in this species habitat, the authors attributed this effect to increasing competition for resources.

The presence on one of the models of an interaction between group type and colony size might be explained by the fact that there are more aggressive interactions towards juveniles in larger colonies (M. Rat, personal observation), but that the presence of helpers can buffer this effect. Parents alone might not be able to counter these aggressive interactions. On the other hand, if the decrease in survival in larger colonies is due to food depletion, the presence of helpers could counter it through the additional food brought. However, at this stage this suggestions remain speculative and behavioural observations are needed to test this hypothesis.

In some other studies, authors have not been able to find a positive effect of the presence of helpers on the reproductive success of cooperatively breeding species. Despite not being directly related to our results, they show how the presence of helpers might not be always beneficial to juveniles. For example, in laughing kookaburras it was found that group size does not have any effect on nest success (Legge 2000a). The authors suggest that this could be explained by the fact that in larger groups the parents reduce their own feeding effort, to compensate for the presence of helpers

(Sarah Legge, 2000). The same thing happens in other cooperatively breeding species: long-tailed tits (Meade et al. 2010), rufous vanga in Madagascar (Eguchi et al. 2002), and also in sociable weavers. In long-lived species, the benefits of reducing workload, and enjoying greater survivorship, might surpass the benefits of having more fledglings (Stearns 1992). For instance, in the presence of helpers, male long-tailed tits reduce their feeding rates more than females and this is reflected in increased survivorship for males (Meade et al. 2010).

We could not distinguish one best model from the other 7 best models presented, and none of the effects (rainfall, colony size or helper effect) was found in all models. This could due to a small sample size in comparison to other similar studies, for example, in McGowan et al. 2003 they analysed survival for 482 individuals. In addition, the different environmental and social factors affecting survival are likely to be complex and to interact among each other. Nonetheless, a negative helper effect was found in 5 out of 7 models and our results add to previous ones (Covas et al. 2011) that indicate a negative effect of helpers on nestlings’ survival.

This intriguing result leads to new questions: is it parental neglect that is driving this effect? Or is it conflict within the breeding group?

Whatever the mechanism, and despite of the negative effect of helper presence on post-fledging juvenile survival suggested here, it is still possible that in the sociable weaver helpers can have an overall positive effect on reproductive output. In the presence of helpers, parents are able to reduce their feeding effort (Covas, Plessis, and Doutrelant 2008), females have increased survival (R. Covas, A.-S. Deville, C. Doutrelant, C. Spottiswoode & A. Grégoire, unpublished data), lay smaller eggs (Paquet et al. 2013), and fledging condition is better under adverse conditions (Covas, Plessis, and Doutrelant 2008). Sociable weavers have a long lifespan (the oldest bird recorded was 16 years old) and suffer considerably high nest predation rates (ca. 70% of all clutched are lost to predation). Therefore, females might maximize their lifetime reproductive success by increasing the number of breeding attempts throughout their life, as opposed to putting all their effort in one brood (or a few broods). This suggests a trade-off between current and future reproductive efforts in the sociable weaver that remains to be tested and should be investigated by future work.

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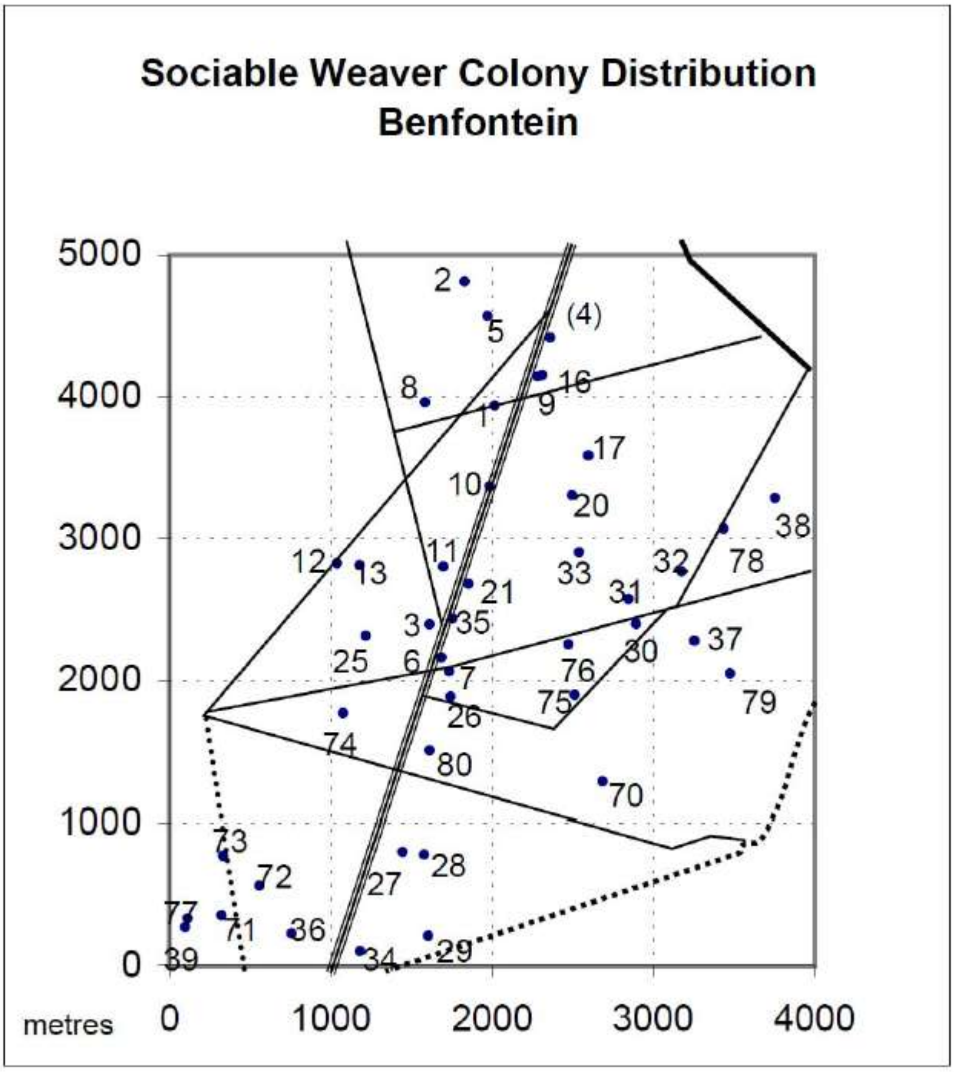
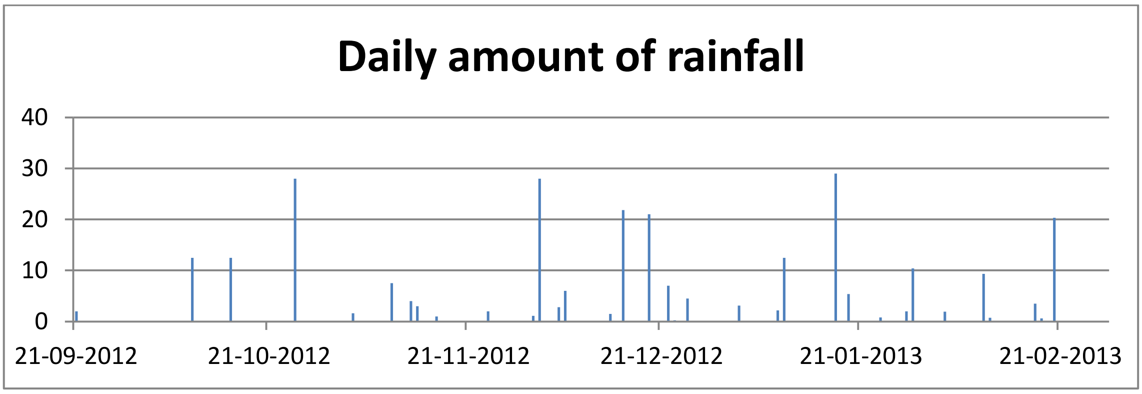
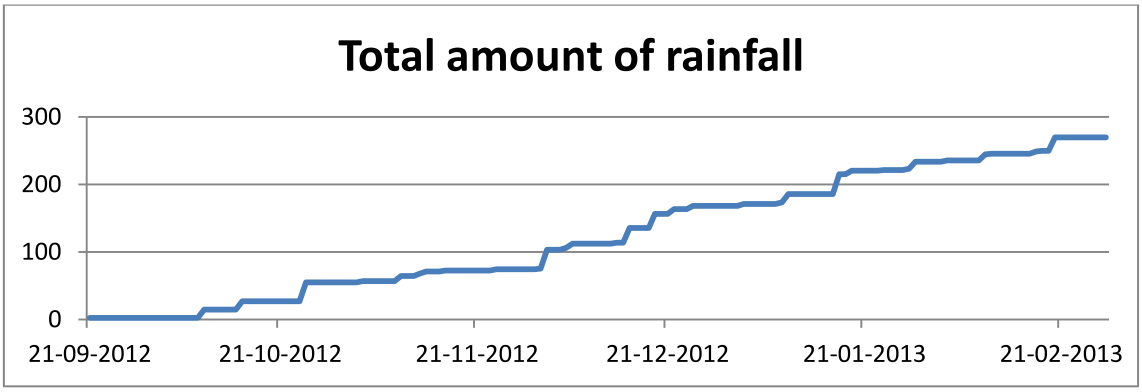
Annex 1: Sociable weaver colony distribution in Benfontein Nature Reserve (Kimberkey, Northern Cape, South Africa).



Annex 2: Daily and total amount of rainfall (mm) for the breeding season of 2012/2013 (from 21-09-2012 until 28-02-2013).



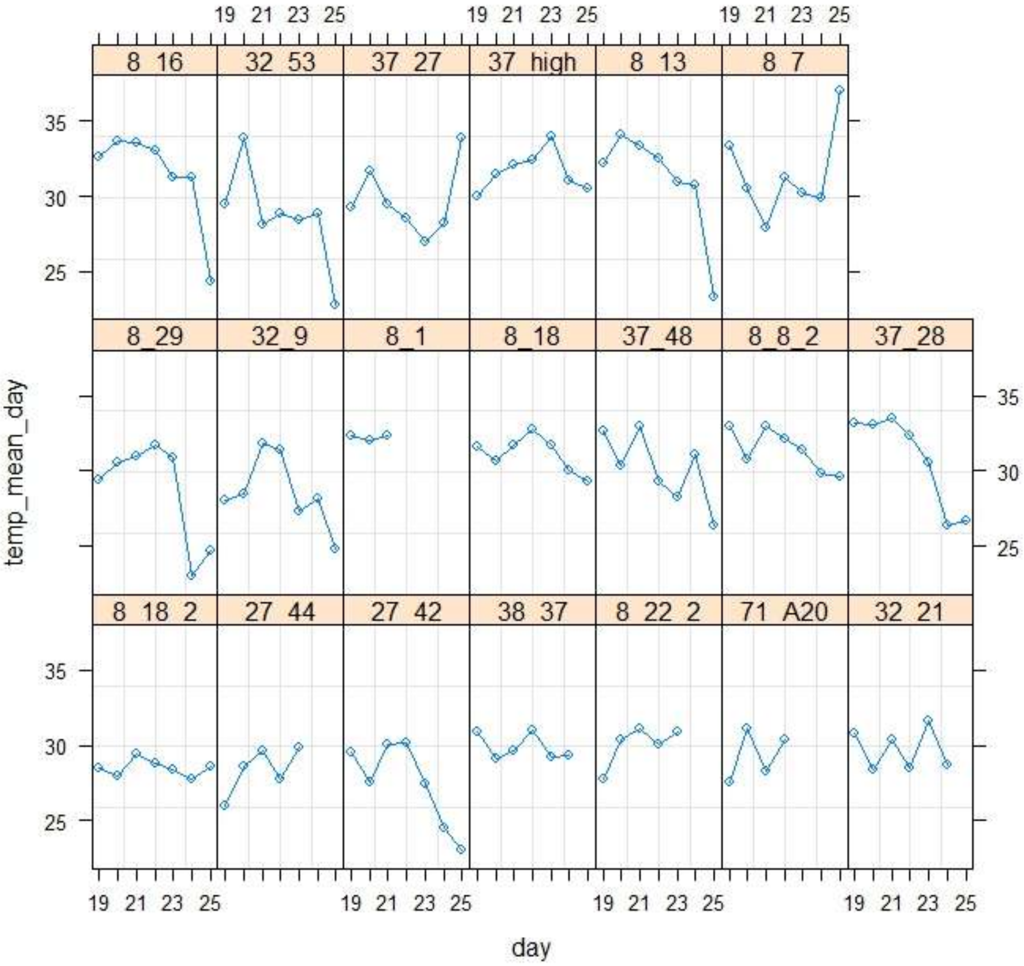


Annex 3: Number of individuals known to be present at the colonies analyzed. Colony sizes were deducted from the captures before the breeding season.

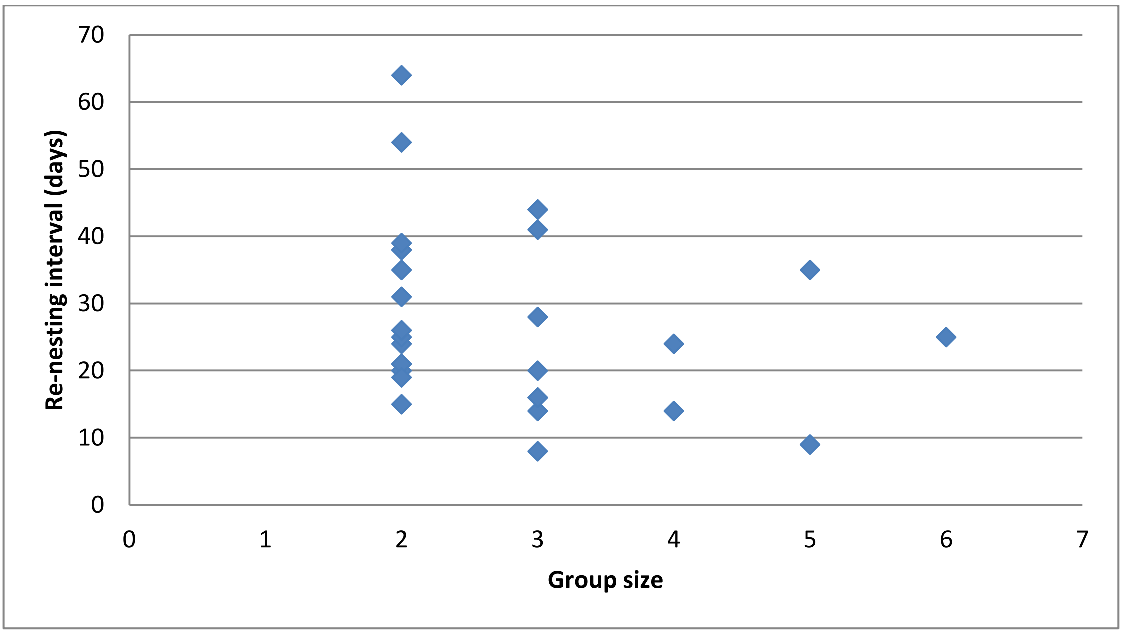
Colony ID	Colony size (Number of individuals)
2	15
6	5
8	40
11	31
20	25
27	15
31	50
32	25
37	46
38	53
39	9
71	9

Annex 4: Temperature for during the day (ºC) inside the nest from days 19 to 25 for 20 nests with and without helpers.

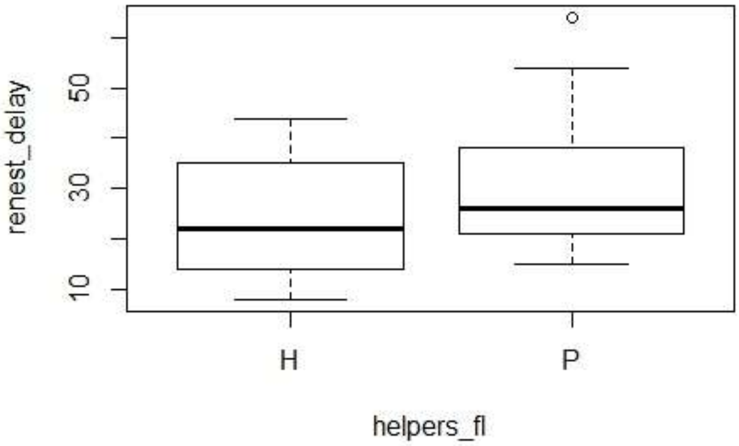
Legend: Identification of the colony _ Identification of the nest



Annex 5a: Re-nesting interval (in days) respective to the 30 breeding couples in groups with different sizes (2-7 individuals).



Annex 5b: Average interval in days between one successful breeding event and another nesting attempt for parents with and without helpers.



Annex 6: List of all the models simulated on MARK.

Phi: survival probability, p: recapture probability, (t): time dependent, (.): constant, age: age-dependent, 1age: 1-age class, 2age: 2-age classes, Co: colony size, h: presence/absence of helpers, R: rainfall, G: group size, B: brood size, C: chick order; W: day 17 weight, S: presence/absence of snake protection.

Model	AICc	Delta AICc	AICc Weights	Model Likelihood	Num. Par	Deviance
{Phi(1age+R+Co+2age)p(t+co)}	1033.446	0	0.12384	1	15	1002.472
{Phi(1age+h+R+2age)p(t+co)}	1034.347	0.9017	0.0789	0.6371	15	1003.374
{Phi(1age+h+R+Co+2age)p(t+co)}	1034.663	1.2174	0.06738	0.5441	16	1001.557
{Phi(1age+h*Co+2age)p(t+co)}	1035.087	1.6414	0.05451	0.4402	16	1001.981
{Phi(1age+R+Co+G+2age)p(t+co)}	1035.158	1.7127	0.0526	0.4247	16	1002.053
{Phi(1age+R+G+2age)p(t+co)}	1035.332	1.8858	0.04824	0.3895	15	1004.358
{Phi(1age+Rain+2age)p(t+co)}	1035.402	1.9558	0.04658	0.3761	14	1006.551
{Phi(1age+R+Co+B+2age)p(t+co)}	1035.567	2.1215	0.04287	0.3462	16	1002.462
{Phi(1age+h*R+2age)p(t+co)}	1036.461	3.0156	0.02742	0.2214	16	1003.356
{Phi(1age+h+B+R+2age)p(t+co)}	1036.479	3.0337	0.02717	0.2194	16	1003.374
{Phi(1age+h+Co+2age)p(t+co)}	1036.664	3.2178	0.02478	0.2001	15	1005.69
{Phi(1age+Co+2age)p(t+co)}	1036.782	3.3361	0.02336	0.1886	14	1007.932
{Phi(1age+h+R+Co+B+2age)p(t+co)}	1036.791	3.3452	0.02325	0.1877	17	1001.545
{Phi(2age+h+R+h*R)+p(t+co)}	1036.933	3.4873	0.02166	0.1749	16	1003.827
{Phi(1age+h+2age)p(t+co)}	1037.216	3.7699	0.0188	0.1518	14	1008.365
{Phi(1age+R+G+B+2age)p(t+co)}	1037.452	4.0062	0.01671	0.1349	16	1004.346
{Phi(2age+c)p(t+co)}	1037.465	4.0197	0.0166	0.134	14	1008.615
{Phi(1age+G+Co+2age)p(t+co)}	1037.5	4.054	0.01631	0.1317	15	1006.526

{Phi(1age+R+B+2age)p(t+co)}	1037.509	4.0636	0.01624	0.1311	15	1006.536
{Phi(2age*h)p(t+co)}	1038.094	4.6486	0.01212	0.0979	15	1007.121
{Phi(1age+G+2age)p(t+co)}	1038.149	4.7035	0.01179	0.0952	14	1009.299
{Phi(2age+h+c)p(t+co)}	1038.253	4.8068	0.0112	0.0904	15	1007.279
{Phi(2age+G)p(t+co)}	1038.456	5.0099	0.01012	0.0817	14	1009.605
{Phi(1age+h*B+2age)p(t+co)}	1038.552	5.1062	0.00964	0.0778	16	1005.446
{Phi(1age+h+Co+B+2age)p(t+co)}	1038.657	5.2112	0.00915	0.0739	16	1005.551
{Phi(1age+h+Co+Gd+2age)p(t+co)}	1038.792	5.3459	0.00855	0.069	16	1005.686
{Phi(1age+Co+B+2age)p(t+co)}	1038.812	5.3658	0.00847	0.0684	15	1007.838
{Phi(1age+h*C+2age)p(t+co)}	1038.996	5.5507	0.00772	0.0623	16	1005.891
{Phi(1age+h*R+h*B+2age)p(t+co)}	1039.108	5.6625	0.0073	0.0589	18	1001.712
{Phi(1age+h+W+2age)p(t+co)}	1039.163	5.717	0.0071	0.0573	15	1008.189
{Phi(1age+h+C+2age)p(t+co)}	1039.21	5.7645	0.00694	0.056	15	1008.237
{Phi(2age+h)p(t+co)}	1039.274	5.8279	0.00672	0.0543	14	1010.423
{Phi(1age+h+S+2age)p(t+co)}	1039.282	5.8367	0.00669	0.054	15	1008.309
{Phi(1age+h+B+2age)p(t+co)}	1039.336	5.8902	0.00651	0.0526	15	1008.362
{Phi(2age+c)p(t+h+co)}	1039.536	6.0906	0.00589	0.0476	15	1008.563
{Phi(2age+h+c)p(t+h+co)}	1040.02	6.5744	0.00463	0.0374	16	1006.914
{Phi(1age+W+G+2age)p(t+co)}	1040.18	6.7344	0.00427	0.0345	15	1009.207
{Phi(2age+h*co)p(t+co)}	1040.187	6.7415	0.00426	0.0344	16	1007.082
{Phi(1age+C+G+2age)p(t+co)}	1040.225	6.7795	0.00418	0.0338	15	1009.252
{Phi(1age+B+G+2age)p(t+co)}	1040.237	6.7909	0.00415	0.0335	15	1009.263
{Phi(1age+S+G+2age)p(t+co)}	1040.265	6.819	0.00409	0.033	15	1009.291
{Phi(2age+h)p(t+h+co)}	1040.48	7.0345	0.00368	0.0297	15	1009.507
{Phi(2age)p(t+co)}	1040.722	7.276	0.00326	0.0263	13	1013.986
{Phi(1age+h*S+2age)p(t+co)}	1041.056	7.6104	0.00276	0.0223	16	1007.95
{Phi(1age+h*W+2age)p(t+co)}	1041.224	7.7782	0.00253	0.0204	16	1008.118
{Phi(1age+h+B+W+2age)p(t+co)}	1041.265	7.8194	0.00248	0.02	16	1008.159

{Phi(1age+h+C+B+2age)p(t+co)}	1041.302	7.8567	0.00244	0.0197	16	1008.197
{Phi(2age+h+S)p(t+co)}	1041.378	7.9323	0.00235	0.019	15	1010.404
{Phi(1age+h*B+h*C+2age)p(t+co)}	1041.471	8.0256	0.00224	0.0181	18	1004.075
{Phi(1age+C+h+2age)p(t+co)}	1042.428	8.9822	0.00139	0.0112	14	1013.578
{Phi(2age)p(t+h+co)}	1042.722	9.2767	0.0012	0.0097	14	1013.872
{Phi(1age+S+2age)p(t+co)}	1042.83	9.3847	0.00114	0.0092	14	1013.98
{Phi(1age+B+2age)p(t+co)}	1042.833	9.3873	0.00113	0.0091	14	1013.983
{Phi(1age+rain+2age)+p(t)}	1043.302	9.8559	0.0009	0.0073	13	1016.566
{Phi(2age+h+W+h*W)+p(t+co)}	1043.461	10.0152	0.00083	0.0067	16	1010.355
{Phi(t+co)p(1age+h+r+2age)}	1044.367	10.9216	0.00053	0.0043	13	1017.632
{Phi(1age+rain+2age+h+R+h*R)+p(t)}	1045.383	11.9372	0.00032	0.0026	15	1014.409
{Phi(2age+h)p(t+h)}	1045.397	11.9512	0.00031	0.0025	14	1016.547
{Phi(2age+h+R+h*R)+p(t)}	1046.046	12.6002	0.00023	0.0019	15	1015.072
{Phi(2age+h+c)p(t+h)}	1047.52	14.0742	0.00011	0.0009	15	1016.546
{Phi(2age+h)p(t)}	1047.805	14.3589	0.00009	0.0007	13	1021.069
{Phi(2age)p(t+h)}	1047.905	14.4591	0.00009	0.0007	13	1021.169
{Phi(2age)p(t)}	1048.011	14.5656	0.00009	0.0007	12	1023.382
{Phi(2age+co)p(t+h)}	1049.499	16.0537	0.00004	0.0003	14	1020.649
{Phi(2age+co)p(t)}	1049.877	16.4309	0.00003	0.0002	13	1023.141
{Phi(2age+h+co)p(t)}	1049.919	16.4734	0.00003	0.0002	14	1021.069
{Phi(2age+h+W+h*W)+p(t)}	1051.926	18.4798	0.00001	0.0001	15	1020.952
{Phi(age)p(t)}	1051.944	18.4986	0.00001	0.0001	16	1018.839
{Phi(1age+R+Co+2age)p(2age+co)}	1052.335	18.8895	0.00001	0.0001	8	1036.047
{Phi(1age+2age)p(1age+R+h+co)}	1055.754	22.3083	0	0	7	1041.53
{Phi(t)p(t)}	1057.502	24.0565	0	0	16	1024.397
{Phi(age)p(age)}	1059.607	26.1616	0	0	16	1026.502
{Phi(t)p(.)}	1064.052	30.6066	0	0	8	1047.764
{Phi(h*t)p(.)}	1067.985	34.5397	0	0	13	1041.25

{Phi(.)p(t)}	1068.835	35.3896	0	0	11	1046.304
{Phi(h)p(t)}	1070.843	37.3969	0	0	12	1046.214
{Phi(age)p(.)}	1072.468	39.022	0	0	7	1058.244
{Phi(h*t)p(t)}	1072.564	39.1178	0	0	26	1017.651
{Phi(t)p(h*t)}	1073.877	40.4312	0	0	27	1016.733
{Phi(h*t)p(h*t)}	1077.86	44.4143	0	0	32	1009.423
{Phi(.)p(h*t)}	1081.468	48.0219	0	0	21	1037.57
{Phi(.)p(.)}	1090.919	57.4736	0	0	2	1086.896
{Phi(1age+h+B+2age)p(t+co)}	1260.967	227.5216	0	0	15	1229.994