# Maternal effects and life history trade-offs in a cooperative breeder, the sociable weaver (Philetairus socius)

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Par

Matthieu PAQUET

# Effet maternels et compromis évolutifs chez une espèce à reproduction coopérative, le Républicain social (*Philetairus socius*)

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## Maternal effects and life history trade-offs in a cooperative breeder, the sociable weaver (*Philetairus socius*)

Maximizing of the number copies of genes that are transmitted to the next generations involves a series of tradeoffs. In cooperatively breeding species some sexually mature individuals do not breed but instead help other individuals to raise their offspring. These helpers are particularly interesting in a life history context as they create a predictably favorable breeding environment and their presence can thus influence evolutionary trade-offs. A major evolutionary trade-off that is often neglected in studies on cooperative breeding is maternal allocation, notably through maternal effects that are epigenetic modifications of offspring phenotype. Here we investigate whether there are maternal effects induced by the presence of helpers and their possible consequences on females and their offspring in a colonial cooperative breeder of southern Africa, the sociable weaver *Philetairus socius*. Our results show that females lay smaller eggs in the presence of helpers and in addition these eggs have lower corticosterone and testosterone concentrations. Our results also show a higher survival probability of females breeding in groups, which may be partially due to their lower investment in eggs. In addition, a study of roosting chamber temperatures in relation to group size suggests further benefits for parents and helpers, particularly through lower costs of thermoregulation that could also allow energy savings for survival. To start understanding the consequences of helpers presence and differential maternal allocation for offspring we conducted a cross fostering experiment. Our results show that eggs produced by females breeding in larger groups produce chicks that beg at a lower rate, showing that maternal effects may influence chicks' behavior. Finally, we investigated post-fledging survival through capture-recapture analyses and, surprisingly, found that fledglings have a lower survival probability when raised with helpers. Taken together, these results demonstrate the importance of studying maternal effects on cooperative breeders and open several research prospects on family conflicts and life history trade-offs according to the presence of helpers.

***Keywords:*** *cooperative breeding, life history trade-offs, maternal effects, hormones, birds*

## Effets maternels et compromis évolutifs chez une espèce à reproduction coopérative, le Républicain social (*Philetairus socius*)

Maximiser le nombre de copies de gènes transmises aux générations suivantes implique une série de compromis. Chez les espèces à reproduction coopérative, des individus ne se reproduisent pas mais participent aux soins des jeunes d'autres individus reproducteurs. Ces assistants sont particulièrement intéressants dans le contexte des traits d'histoire de vie car ils forment un environnement prédictible favorable pour la reproduction, et leur présence peut aussi influencer les compromis évolutifs chez les reproducteurs. Un compromis évolutif majeur mais sous-étudié dans le cadre de la reproduction coopérative est l'allocation maternelle notamment via des effets maternels qui sont des modifications épigénétiques du phénotype de la descendance. Nous avons étudié l'existence d'effets maternels associés à la présence d'assistants et leurs possibles conséquences sur les femelles et leurs descendants chez un oiseau colonial et coopératif du sud de l'Afrique, le Républicain social *Philetairus socius*. Nos résultats montrent que les femelles pondent des œufs plus légers en présence d'assistants et que ces œufs sont moins concentrés en corticostérone et testostérone. Nos résultats montent aussi une plus grande probabilité de survie pour les femelles se reproduisant en groupe pouvant être en partie due à leur plus faible investissement dans les œufs. De plus, l'étude de la température dans les nids en fonction de la taille des groupes a permis de suggérer d'autres bénéfices pour les parents et assistants, en particulier via une réduction des coûts de thermorégulation qui pourrait aussi permettre de garder de l'énergie pour la survie. Pour comprendre les conséquences de la présence d'assistants et de l'allocation différentielle pour les poussins, une expérience d'adoption croisée a été réalisée. Elle a révélé que les œufs pondus par les femelles avec plus d'assistants produisent des poussins qui quémandent moins, montrant que des effets maternels pourraient influencer le comportement des poussins. Enfin nous avons étudié la survie des poussins après l'envol à l'aide d'analyses de captures recaptures et avons trouvé de manière surprenante que les poussins à l'envol ont une probabilité de survie plus faible lorsqu'ils sont élevés présence d'assistants. Ces résultats dans leur ensemble démontrent l'importance d'étudier les effets maternels chez les espèces coopératives et ouvrent de nombreuses perspectives de recherche sur les conflits familiaux et de compromis évolutifs associés à la présence d'assistants.

***Mots clés :*** *reproduction coopérative, compromis évolutifs, effets maternels, hormones, oiseaux*

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# RESUME ETENDU

Chez tous les êtres vivants, la maximisation du succès reproducteur des individus à l'échelle d'une vie implique une série de compromis évolutifs. Ces compromis sont fortement influencés par les conditions environnementales et leur variation. Par exemple en environnements fortement variables les espèces à stratégie itéropare, c'est-à-dire se reproduisant plusieurs fois au cours de leur vie, sont favorisées. Une stratégie de reproduction qui a depuis longtemps suscité un grand intérêt est la reproduction coopérative qui correspond au fait que certains individus retardent leur reproduction et aident à élever des jeunes qui ne sont pas les leurs. De façon intéressante, on observe particulièrement ce type de comportement coopératif chez des espèces longévives que l'on retrouve souvent dans des environnements imprédictibles telles que les savanes semi-arides où les précipitations varient considérablement d'une année à l'autre.

Chez certaines espèces la reproduction coopérative est la seule possibilité permettant de se reproduire avec succès mais chez d'autres ce comportement ne semble étonnamment pas augmenter le succès reproducteur des parents. Du fait leur stratégie longévive, on s'attend toutefois à ce que les espèces à reproduction coopérative favorisent l'investissement dans leur survie davantage que dans leur reproduction et en effet chez plusieurs espèces les parents présentent une probabilité de survie plus importante en présence d'assistants. Cependant chez les oiseaux une seule étude a utilisé des méthodes statistiques de capture recaptures permettant de discriminer la mort de la non détection des individus et cette étude n'a pas trouvé de relation entre la présence d'assistants et la survie des parents. Des mesures de survie par capture recapture sont donc indispensables pour déterminer les bénéfices de la reproduction coopérative.

Les assistants peuvent augmenter les chances de survie des parents de différentes manières. L'une d'elles, étonnamment négligée notamment chez les oiseaux, est une

augmentation de survie liée à une diminution des coûts de thermorégulation. En effet, les espèces coopératives dorment souvent en groupes et ceux-ci ne sont probablement pas indépendants des groupes reproducteurs.

Chez les oiseaux, le bénéfice des assistants le plus souvent avancé pour la survie des parents est une diminution du nourrissage des poussins mais pour les femelles d'autres possibilités existent et l'une d'elle serait de diminuer leur investissement dans les œufs, diminution pouvant également être compensée par la nourriture supplémentaire apportée par les assistants. L'existence d'effets maternels liés à la présence d'assistants n'a été que récemment proposée et encore peu examinée.

Ces modifications épigénétiques de l'allocation de la femelle dans les œufs sont particulièrement attendues pour varier en fonction de la qualité de l'environnement si celui-ci est prédictible. Dans ce contexte, la présence du nombre d'assistants qui crée un environnement prévisible représente un contexte idéal pour étudier l'allocation maternelle. Si une diminution du poids ou de la taille des œufs en présence d'assistants a bien été récemment observée chez quelques espèces, l'allocation hormonale dans les œufs n'a jamais été étudiée. Cette allocation hormonale est particulièrement intéressante à étudier car les hormones maternelles ont d'importantes conséquences sur le comportement des jeunes, telle que leur quémande et pourraient possiblement affecter aussi leur croissance et survie.

**Le but de cette thèse était dans un premier temps de déterminer si les effets maternels pourraient varier en fonction de la présence d'assistants. Il était ensuite de s'intéresser aux conséquences de la présence d'assistants pour la valeur sélective des parents et des jeunes et de déterminer dans quelle mesure ces conséquences pouvaient résulter d'effets maternels**.

Ces questions ont été étudiées chez le Républicain social *Philetairus socius,* un petit passereau colonial coopératif des savanes semi arides du sud de l'Afrique. Ces oiseaux sont particulièrement connus pour construire d'imposants nids communautaires, chacun composés de plusieurs chambres « individuelles » dans lesquelles ils se reproduisent mais aussi dorment tout au long de l'année. Ils sont relativement longévifs (le plus vieil oiseau capturé avait minimum 16 ans) ont une reproduction coopérative facultative, les parents pouvant nourrir seul ou avec 1 à 5 assistants. Les assistants sont majoritairement apparentés aux parents étant souvent des descendants des années précédentes. Enfin des études précédentes ont montré que les parents diminuaient leur taux de nourrissage en présence d'assistants et que la présence d'assistant augmentait peu le succès de reproduction (i.e. seulement quand les conditions de reproduction étaient mauvaises)

Pour déterminer si les stratégies d'investissement dans les œufs varier en fonction de la taille du groupe, nous avons tout d'abord pesé des pontes et récolté les premiers œufs pondus durant la saison 2010-2011 afin d'en analyser le contenu en terme de poids de jaune et de concentrations en caroténoïdes, androgènes et corticostérone. Le nombre d'assistants a été ensuite identifié pour un maximum de ces nichées. Nous avons trouvé que la masse des œufs était plus faible lorsque la taille du groupe reproducteur (parents et assistants) était plus grande. Nous n'avons pas trouvé de différence concernant les caroténoïdes mais les femelles aidées d'assistants ont pondu des œufs contenant moins de testostérone et de corticostérone. Ces résultats suggèrent que l'environnement que représente la présence d'assistants pourrait bien influencer l'allocation maternelle, notamment par une diminution de l'énergie allouée dans les œufs et un changement de leur contenu hormonal. Ainsi en présence d'assistants le phénotype des jeunes pourrait différer.

Pour déterminer si la taille des groupes pourrait apporter des bénéfices en termes de thermorégulation la température de chambres a été mesurée la nuit avant la période de reproduction de 2012-2013 et le nombre d'oiseaux dormant dans ces chambres a été identifié à l'aide de caméras au coucher. Parmi ces chambres certaines ont été le lieu de reproduction et le cas échéant la date de ponte, masse des œufs et taille des groupes ont été relevés. Les données récoltées ont montré que le nombre d'oiseaux dormant ensemble était fortement significativement corrélé à la température nocturne dans les chambres. Aussi il semble que les oiseaux dormant dans des groupes plus grands passent plus de temps au-dessus du seuil théorique de température au-dessous duquel des coûts de thermorégulation sont attendus. Les données récoltées ont aussi permis de déterminer que le nombre d'oiseaux dormant ensemble avant reproduction était corrélé avec la taille des groupes pendant reproduction indiquant un potentiel bénéfice additionnel des assistants pour la survie des parents. Enfin des données préliminaires suggèrent que le fait de dormir en groupe permet une date de ponte plus précoce. Le comportement de dormir en groupe et les bénéfices thermiques associés pourraient ainsi avoir des conséquences proximales et évolutives qui méritent d'être approfondies par d'autres études.

Nous avons par ailleurs cherché à savoir si la présence d'assistants était bien associée à une augmentation de la probabilité de survie pour les mâles et les femelles. Basées sur 14 années de captures recapture et 5 années de reproduction, des nous avons réalisé des analyses de Capture Marquage Recapture. Nous avons trouvé que les femelles ne bénéficiant pas de la présence d'assistants avaient une probabilité de survie plus faible que les autres individus reproducteurs l'hiver suivant la reproduction. Ce résultat indique clairement que des bénéfices propres à chaque sexe existent. Pour les femelles ce pourrait être des bénéfices telle que la diminution de l'investissement dans les œufs mais cela reste à démontrer par des études reliant la taille des œufs à la survie.

Concernant l'impact des assistants sur les jeunes en 2012-2013 nous nous sommes tout d'abord intéressés à leur effet sur le comportement de quémande des poussins. En effet ce comportement est un médiateur de conflits entre parents et jeunes qui est connu pour être affecté par les concentrations en testostérone et en corticostérone dans les œufs chez de nombreuses autres espèces. Nous avons donc réalisé une expérience d'adoptions croisées qui nous a permis de discriminer entre les effets pré et post natals associés au nombre d'assistants. Nous avons ensuite mesuré le taux de quémande des poussins à deux stade de croissance: quand le plus vieux poussin avait 4 jours (et donc très tôt après l'éclosion), et en milieu de croissance au jour 9. Nous avons trouvé que les poussins nourris par des groupes adoptifs de plus grandes tailles quémandaient à des taux plus faibles en accord avec le fait qu'ils reçoivent plus de nourriture et sont ainsi davantage rassasiés. En accord avec la prédiction que la taille du groupe prénatal influence aussi le comportement des poussins, il est apparu que les poussins originaires de groupes plus grands quémandaient aussi moins à 4 jours. Cette étude réalisée pour la première fois chez une espèce à reproduction coopérative montre que l'environnement prénatal comme post natal influencent le comportement de quémande des poussins. Une des choses changeant dans l'environnement prénatal étant les hormones déposées dans les œufs, les femelles pourraient contrôler le comportement de quémandage des poussins. Une telle hypothèse nécessite d'autres études pour être confirmée.

Enfin la survie des jeunes en fonction de la présence d'assistant a été analysée par des analyses de Capture Marquage Recapture. En 2012-2013, les jeunes ont été observés au coucher du soleil toutes les semaines ou deux semaines après leur envol et ce durant trois mois. Les résultats suggèrent étonnamment une plus faible survie des jeunes élevés en présence d'assistants entre 17 et 30 jours, c'est à dire tôt après l'envol puisque celui-ci a généralement lieux aux alentours du 25ième jour. Ce résultat ne semble pas être lié à une plus forte dispersion car un tel comportement est extrêmement rare dans les trois mois suivant l'envol. Il suggère ainsi un coût majeur dû à la présence d'assistants pour les poussins et l'étude approfondie des interactions parents-assistants-jeunes est nécessaire pour en comprendre la cause. Cela pourrait être dû à une compétition au sein des familles ou au fait qu'après l'envol les parents laissent relèguent le soin de leur jeunes aux assistants qui sont moins expérimentés qu’eux. Ce transfert aurait des coûts pour les poussins mais pourraient permettre aux parents de se remettre à se reproduire plus vite.

Dans le but de comprendre si la présence d’assistants restait néanmoins bénéfique pour les femelles malgré la plus faible survie de leurs jeunes, des simulations de modèles de dynamique de populations ont été réalisées. Basé sur les paramètres de survie et de reproduction estimés au cours de cette thèse ainsi que dans précédentes études, nous avons trouvé que la plus faible survie des jeunes était en effet largement surcompensée par la plus forte survie des femelles.

Dans leur ensemble, les résultats de cette thèse démontrent l’importance d’étudier les effets maternels chez les espèces coopératives et ouvrent de nombreuses perspectives de recherche sur les conflits familiaux et les compromis évolutifs associés à la présence d’assistants. Ces effets maternels peuvent permettre aux femelles d’investir moins dans leurs œufs et plus dans leur survie mais aussi de manipuler le comportement des poussins et donc possiblement leur propre comportement de nourrissage ou celui de leurs partenaires et assistants. Nos résultats montrent aussi l’importance de regarder l’effet des assistants à la lumière des stratégies d’histoire de vie puisque la plus faible survie des jeunes en présence d’assistants peut représenter un moindre coût pour les femelles et les assistants qui y sont apparentés comparé à l’augmentation considérable de la survie des femelles.

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# Maternal effects and life history trade-offs in a cooperative breeder, the sociable weaver (*Philetairus socius*)

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A color ringed sociable weaver bringing back food to its nest.

# INTRODUCTION

## *Life history traits and cooperative breeding*

All living organisms have evolved as the result of one common mechanism: maximizing the number of copies of their genes that are transmitted to the next generation (Dawkins 1976). It is thus extremely surprising and fascinating to see the incredible diversity of the evolutionary pathways taken by organisms, from morphology to behavior, for a same shared purpose.

One reason behind this diversity is that maximizing an individual's reproductive success at a lifespan scale can involve a variety of trade-offs between life history traits. For example, there is a major trade-off between allocating energy to current reproductive effort and survival, and can explain a wide range of reproductive strategies (Stearns 1992).

Some species, so called semelparous, reproduce only once in their lifetime. They often exhibit a seasonal life cycle as it is the case for annual plant species or some moths for example, while other semelparous species can be long-lived. For instance in the Atlantic salmon (*Salmo salar*) the pre breeding period can last several years and in insects a sticking example is found in cicadas that feed underground for either 13 or 17 years precisely before emerging and breeding (Williams and Simon 1995). Finally, some species called iteroparous can breed several times during their lifetime, ranging from several times a year to once a year or even every second or more years (Bull and Shine 1979) and theoretical studies predict that iteroparity should be favored when environmental quality varies considerably (Orzack and Tuljapurkar 1989, Benton and Grant 1999, Ranta et al. 2002).

As iteroparous species can reproduce several times trade-offs can occur between their investment in the current or in future reproduction depending on age-specific mortalities and environmental variability (Stearns 1992, Charlesworth 1994). Comparative studies show that iteroparous species can even skip breeding opportunities when environmental conditions are too harsh, such as when breeding at high latitudes or low temperatures (Bull and Shine 1979) or when food is harder to find (Jouventin and Dobson 2002). For example the eastern tiger salamander (*Ambystoma tigrinum tigrinum*) was found to defer breeding in years when the risk of adult mortality is high (Church et al. 2007). In fact, during poor breeding conditions, maximum fitness can be achieved by saving energy by not breeding at all as supported by theoretical models (Erikstad et al. 1998).

During these non-breeding events individuals can increase their fitness by several ways. First of all they can accumulate reserves and invest in more in growth which is for example the case in Atlantic cods *Gadus morhua* (Jorgensen et al. 2006) or the meadow viper *Vipera ursinii ursinii* (Baron et al. 2013). Another possibility is to prospect and obtain social information about conspecific breeding success and breeding patch quality (Boulinier and Danchin 1997, Danchin et al. 1998) or future mates and dispersal opportunities (Young et al. 2005). Finally, a fascinating way of increasing their own fitness while not breeding is by helping other individuals to breed, typically by provisioning food to the brood which define cooperative breeding (Emlen 1991).

Helping behavior may seem particularly paradoxical as potentially costly and directed to other individuals (Hamilton 1964). However, potential benefits provided by helping behavior are various and commonly divided between direct and indirect benefits (Cockburn 1998, Clutton-Brock 2002). For example helpers may obtain direct benefits through group augmentation such as a reduction in predation probability (Kokko et al.

2001) or by signaling their parental care ability to potential future partners (Zahavi 1975, Lotem et al. 2003, Doutrelant and Covas 2007). Lastly helpers can also enhance their inclusive fitness by helping kin-related individuals and thus obtain indirect fitness benefits (Hamilton 1964) as helpers are often related to the breeders (Griffin and West 2003).

This type of cooperatively breeding behavior is typically found in long-lived species characterized by low annual mortality (Arnold and Owens 1998, Covas and Griesser 2007). Moreover these species often occur in variable, unpredictable environments, such as semiarid savanna habitats, which experience unpredictable rainfall. Indeed, the presence of helpers can be seen as an environmental improvement in breeding conditions that buffers other environmental variations (Duplessis et al. 1995, Arnold and Owens 1999, Rubenstein and Lovette 2007, Covas et al. 2008, Jetz and Rubenstein 2011).

In some species cooperative breeding is actually the obligate way to allow successful reproduction or survival of breeders. It is for example the case of white-winged choughs, *Corcorax melanorhamphos* (Heinsohn 1992) and banded mongooses, *Mungos mungo* (Cant 2000) where only groups of more than four and six individuals respectively provide a suitable environment to breed successfully. In several other species cooperative breeding is facultative but helping is still usually found to be beneficial as it increases offspring’s condition or number (see Cockburn 1998, Hatchwell 1999, Kingma et al. 2010 for reviews).

In this context it is *a priori* quite puzzling that some species exhibit only weak effects (Woxvold and Magrath 2005, Covas et al. 2008) or even no effects of helpers on reproductive success (as found in the rufous vanga Eguchi et al. 2002, and 12 other bird species reviewed in Kingma et al. 2010). However, since cooperative breeders are generally long-lived (Arnold and Owens 1998), it is expected that breeders might favor investment in own survival over reproduction. This may explain the weak effects of helpers if parents work less in presence of helpers to save energy for survival. Concurring with this prediction, a higher survival of parents in presence of helpers has been found in 10 out of 21 species (see Kingma et al. 2010 for a review). However, only one of those studies used a Capture-Mark-Recapture (CMR) method (McGowan et al. 2003) to account for the non-detection of individuals and its related bias (Gimenez et al. 2008) and didn't find any relation between breeders' survival and helpers' presence. Studies of survival based on CMR methods are thus essential to determine the effect of helpers on adult survival.

There are several ways through which helpers can allow breeders to increase their survival. However most of them have been overlooked. The presence of helpers can reduce predation rates though active mobbing behavior or a passive dilution effect of group size (Clutton-Brock et al. 1999). In addition helpers may reduce the costs of thermoregulation through communal huddling (Gilbert et al. 2010). For example, in Alpine marmots (*Marmota marmota*) both juvenile and adults' survival were found to increase with hibernating group size (Arnold 1990, Allaine et al. 2000). The most studied way by which parents can benefit from the presence of helpers in terms of survival is the reduction of their investment in current reproduction (Clutton-Brock 1988). Indeed it has been shown in several species that parents can reduce their feeding effort in presence of helpers, the so called 'load lightening' strategy, and that this increase can be compensated by the additional food provided by helpers (reviewed in Hatchwell 1999). By doing so, parents can save energy and thus have a better chance to survive and experience more future breeding opportunities. Load lightening effects of helpers are particularly predicted if the costs of egg production are high (Savage et al. 2013).

Females, in addition, may have another major mechanism for saving energy. They may allocate differential levels of energy to the formation of their young. Hence another potential, but largely unexplored way for females to save energy for survival in presence of helper is differential maternal allocation in egg production and thus maternal effects.

## *Maternal effects under a life history perspective*

Maternal effects are epigenetic mechanisms through which females can adjust the environment experienced by the developing offspring, thereby maximizing offspring and/or their own fitness (Mousseau and Fox 1998). In egg laying species, this variation in maternal allocation is allowed by a variety of egg components such as a nutrients (e.g. proteins, lipids, carotenoids), hormones (e.g. androgens, corticosterone, prolactine) or antibodies (Sheldon 2000, Badyaev 2008, Boulinier and Staszewski 2008). The adjustment by the mother of the offspring’s early environment is predicted to be influenced by the mother’s current and/or expected environment and several studies have shown maternal effect adjustments according to temperature, food availability or mate quality (Kaplan 1992, Sheldon 2000, Benton et al. 2005).

The best studied proxy of female investment in eggs is probably egg size (Bernardo 1996, Christians 2002). When investing in current reproduction, both semelparous and iteroparous females face a tradeoff between the number of propagules and the investment per offspring which varies depending on environmental conditions (Smith and Fretwell 1974, Parker and Begon 1986, Einum and Fleming 1999). Many experimental studies on insects, amphibians or fishes have found an increase in egg size under poor environmental conditions (Kaplan 1992, Fox et al. 1997, Taborsky 2006, Vijendravarma et al. 2010). A common explanation for such mechanism is a positive effect of propagule size on offspring survival under adverse conditions which does not occur (or only to a lesser extent) in better quality environments or conditions, where fecundity is favored rather than propagule size (Fox et al. 1997, Benton and Grant 1999).

A more specific way for females to modulate their investment in eggs is through allocation in yolk carotenoids. As they are exclusively obtained from food carotenoids are likely to vary with environmental quality such as food availability (Blount et al. 2000). These fat soluble pigments have antioxidant properties (von Schantz et al. 1999). As such, carotenoids are expected to play a central role during embryo development and at hatching (Biard et al. 2005), but are also important for the breeding female's own immunity.

Hormone deposition represents another major component affecting offspring and mother fitness. To date two sets of steroid hormones are recognized to be crucial for mother and offspring fitness: glucocorticosteroids such as corticosterone and androgens, particularly testosterone.

Egg deposition of both hormones has been shown to be affected by environmental variations (see Meylan et al. 2012 for a review). For example females experiencing an experimentally stressful pre-breeding environment were found to deposit more corticosterone (a glucocorticoid hormone) in their eggs in a wide range of species in tree-spined sticklebacks *Gasterosteus aculeatus* (Giesing et al. 2011), Japanese quails *Coturnix coturnix japonica* (Hayward et al. 2005) or barn swallows *Hirundo rustica* (Saino et al. 2005). Maternally derived yolk androgen steroids such as testosterone are also found to be differentially deposited in eggs depending on pre-breeding conditions such as diet quality or social environment in passerine birds (Mazuc et al. 2003, Gil et al. 2007, Sandell et al. 2007).

Both corticosterone and androgens are known to influence offspring early growth and behavior such as begging (see Smiseth et al. 2011 for a review). Moreover prenatal hormones can also have long lasting consequences on offspring life history traits (Groothuis et al. 2005, Meylan et al. 2012). Pre-natal corticosterone was found to affect dispersal behavior and survival in the common lizard, *Zootoca vivipara* (De Fraipont et al. 2000, Meylan and Clobert 2005). One study showed that androgens may also have an important effect on dispersal in great tits *Parus major* (Tschirren et al. 2007). Maternal effects driven by environmental variations can thus have strong impacts on life history traits even over many generations (Reznick and Yang 1993, Benton et al. 2005) and represent major elements to consider in evolutionary biology (Badyaev 2008).

## *Maternal effects, cooperative breeding and life history traits*

Maternal effects are especially expected to be favored when there is high environmental heterogeneity (Badyaev 2008). Cooperative breeding therefore provides an ideal system to study maternal effects as the varying number of helpers for different females and between different breeding attempts creates a considerable environmental variation of offspring rearing conditions (Russell and Lummaa 2009).

The number of helpers represents for females a predictable index of environmental quality and in long-lived species with high prospect of future reproduction we can expect females with helpers to invest less in offspring production (Russell and Lummaa 2009). Concurring with this hypothesis, to date a reduction in egg size in presence of helpers was found in one fish (Taborsky et al. 2007) and three bird species (Russell et al. 2007, Canestrari et al. 2011, Santos and Macedo 2011) and similarly, a reduction in gestational growth was found in meerkats (Sharp et al. 2013). However, no load lightening investment in eggs was found in the acorn woodpecker *Melanerpes formicivorus* (Koenig et al. 2009).

As maternally derived androgens and corticosterone are known to depend on environmental conditions (Meylan et al. 2012) are also expected to vary with the presence of helpers but to date no study has investigated this possibility.

The consequences of such maternal effects are of particular interest in cooperative species as they can influence offspring development but also the propensity for cooperative behavior (Komdeur 2006) as they may be involved in provisioning performances (Peters et al. 2002, Santema et al. 2013). Moreover, maternal effects of testosterone and corticosterone are known to play a role in parent-offspring conflicts (Smiseth et al. 2011) and such conflicts are especially expected in cooperative breeders (Russell and Lummaa 2009). For example, it can be of the mother’s interest to invest less per offspring (in eggs or in feeding behavior) as it can increase her survival probability and so her lifetime reproductive success, while it is of each offspring interest to receive as much investment as possible from their parents (Trivers 1974, Lessells and Parker 1999). Additionally maternal hormones can play a role in parent-parent conflicts as females may use them to manipulate their partners’ feeding behavior through offspring begging (Muller et al. 2007). Such family-conflicts are especially likely and interesting in cooperative breeders as fathers but also helpers can be manipulated by the mother.

## *Aims of the thesis*

In this thesis we investigate the consequences of the presence of helpers for parents and offspring fitness with a particular focus on the role of maternal effects as a mediator of helper effects in the sociable weaver (*Philetairus socius*), a colonial passerine endemic to the semi-arid savannahs of southern Africa (Maclean 1973, Mendelsohn and Anderson 1997).

First we looked for the potential influence of helpers on maternal effects and the associated fitness consequences for the breeders. Specifically, we investigated whether egg mass and contents (carotenoids, androgens and corticosterone deposition in eggs) in order to investigate a potential reduction of female investment in eggs and the possibility of maternally derived effect of helpers in offspring behavior and fitness (**Manuscript 1**). We also considered another potential benefit of the presence of helpers for parents' survival and reproductive investment through the thermoregulatory benefits of communal huddling (**Manuscript 2**). Then, by using CMR analyses, we investigated if the presence of helpers was associated with an increase in survival probability for males and females' breeders (**Manuscript 3**).

Simultaneously, we investigated the consequences of differential maternal allocation in egg hormones for offspring behavior and fitness. First, we examined whether the number of helpers was associated with a variation in chicks' begging behavior through a cross fostering experiment (**Manuscript 4**). In addition, together with MSc student Lara Broom, we studied the effect of the presence of helpers on offspring survival (through CMR methods) and the timing when such effect of helpers occurs during the first months of life (**Manuscript 5**)

We finally discuss these outcomes using the support of some additional results and their possible implications in terms of life history and population's dynamics.

## *Study species*

**Plate 1. Monday, August 02, 2010, 11:10:06 AM:** Rita Covas (in the background) amazed to find a sociable weaver caught 15 years ago as an adult (in the foreground). Photo by Claire Doutrelant.

The sociable weaver is a colonial passerine endemic to the semi-arid acacia savannahs of southern Africa (Maclean 1973, Mendelsohn and Anderson 1997). Sociable weavers build massive communal nests containing several independent nest chambers that are used for breeding and roosting. They are facultative cooperative breeders, breeding in pairs or with up to five helpers (the proportion of birds breeding in groups varies from ca. 30-80% between years Covas et al. 2006). Helpers are mainly offspring of one or both breeders (93%), although a small number of unrelated birds can also help (Covas et al. 2006) and direct benefits of helping may occur (Doutrelant and Covas 2007). Both sexes help, but in a previous study helpers older than one year were found to be only males (Doutrelant et al. 2004).

Sociable weavers provided an ideal species for these questions given the considerable background of knowledge available in terms of life history traits, cooperative breeding characteristics and maternal effects.

These facultative cooperative breeders are relatively long-lived (the oldest bird recorded was at least 16 years old; **Plate 1**) and the population average survival rate (including fledglings) is 66% (Covas et al. 2004a but see Manuscript 3 for breeders). As expected in long-lived species their population dynamic is very sensible to small change in survival (Altwegg et al. 2013). Their annual reproductive success is particularly unpredictable as it is strongly dependent on rainfall and as they suffer high rates of nest predation by snakes (ca. 70% of the clutches laid are taken by Boomslangs Dyspholidus typus and Cape cobras Naja nivea, see Plate 2; Covas et al. 2008). In very dry years, individuals may skip reproductive altogether or have extremely low reproductive output (e.g. there was a total of 11 fledglings produced in the second year of this PhD), while good breeding conditions may lead to massive reproductive output (195 in the first year of this PhD).

Concurring with the hypothesis that long-lived species living in unpredictable environment should maximize their survival, previous work as found evidence of ‘load-lightening’ in this population, as both parents were found to reduce their provisioning rates in presence of helpers (Covas et al. 2008). Moreover, despite an overall increase in total feeding rate per nest with the number of helpers, no average effect of helper presence on clutch size and fledgling mass was found (Covas et al. 2008). On the contrary a lower apparent survival was recently found for offspring raised in presence of helpers which may attest a cost of helpers in terms of offspring fitness suggesting that family conflict might occur in sociable weavers (Covas et al. 2011). This indicates the potential for a lower investment in eggs and chicks in presence of helpers. Sociable weaver females were previously found to modulate the amount of androgens and carotenoids deposited in eggs depending on colony size or laying order (van Dijk et al. 2012) indicating that external factors have the potential to lead to differential maternal allocation in this species.

**Plate 2.** Boomslang (on the left) and Cape cobra (on the right) both eating a 17 days old chick that should have been measured on this specific day.

# Summary of the main results obtained

(See manuscripts for more details)

# HELPERS AND PARENTS' FITNESS

## *Helpers' presence and maternal allocation in eggs* (Manuscript 1)

Here we aim to investigate the existence of maternal effects induced by the presence and number of helpers.

The first purpose of this study was to see if sociable weaver females may benefit from the presence of helpers by investing less in eggs. The benefits of a load lightening strategy in presence of helpers is particularly expected when nestling starvation is rare (Hatchwell 1999), future probability to breed is high (Russell and Lummaa 2009) and/or when costs of egg production are high (Savage et al. 2013). In sociable weavers, a load lightening strategy of the parents, through decreased feeding rate in the presence of helpers, was previously found at the nestling stage (Covas et al. 2008). This was compensated by the presence of helpers, as the total provisioning rate per nest actually increased with the number of helpers but fledgling mass surprisingly did not differ on average between nests with and without helpers (Covas et al. 2008). We then expected mothers to invest less in eggs with helpers and that the extra food provided by helpers compensate for this reduction.

To study this hypothesis in 2010-2011 we weighted the eggs of clutches for which we subsequently identified the breeding group size. Additionally, we collected the first egg laid in each of these clutches and obtained yolk mass and carotenoids concentrations, as these pigments are costly to obtain and highly important for chicks' development (Blount 2004). We then determine the group size of the clutches that did not disappear before the fledgling period.

As predicted, we found that females laid lighter eggs as the number of helpers increased showing that mothers may have different reproductive strategies in presence /absence of helpers.

We did not find a reduction in yolk mass and carotenoids suggesting a reduction in albumen mass for the first laid eggs. This may represent a reduction in costs for females as albumen contains on average 71% of the eggs' proteins for altricial species (Carey et al. 1980) This pattern, however, is likely to differ for subsequently laid eggs as the energy peak demand for females during egg formation is expected to occur during albumen formation of the first egg (when the yolk is already produced) and yolk formation of the second and third eggs (Ruiz et al. 2000). More data will be needed to test this hypothesis.

In parallel the second aim of this study was to investigate if females' allocation of androgens (testosterone and androstenedione) and corticosterone in eggs differs when they are expected to be helped vs. when breeding in pairs. We expected females to deposit less androgens and corticosterone for several reasons (see **Manuscript 1**) including the following:

-As testosterone has positive effects on offspring growth in several species (Groothuis et al. 2005), females without helpers should deposit more testosterone in their eggs to compensate for the lack of help available as nestlings may compete more for food.

-Corticosterone is a stress induced hormone commonly assumed to be passively transferred in eggs (Gil 2008) and was shown to be positively linked with energy expenditure (Goymann and Wingfield 2004). As helpers may reduce females' stress and energy expenditure by sharing costly and/or stressing tasks we expected females to deposit less corticosterone in presence of helpers.

We analyzed testosterone, androstenedione (A4) and corticosterone in the collected eggs and found that females deposit less androgens and corticosterone in eggs when helped (The same trend was observed for A4 but only marginally significant after correcting for false recovery rates).

These differential hormone amounts in eggs are expected to have profound consequences on offspring behavior, growth and survival and thus provide a promising basis for the study of maternally induced effects of helpers on offspring behavior and fitness (**Manuscript 4 and 5**).

**Plate 3.** Colony 8 (on the top) and colony 31(down) seen from underneath revealing the individual chambers. Photos by Claire Doutrelant

## *Helpers' presence and thermoregulatory benefits* (Manuscript 2)

In this part we investigate huddling behavior as a potentially strong but frequently neglected benefit of breeding group size for parents' (and helpers) fitness in birds.

Huddling behavior has been associated with increased survival in several species and is particularly common in cooperative breeders (Gilbert et al. 2010). In addition, as huddling and feeding group size are likely to be correlated, such behavior may represent an additional benefit of cooperative breeding. Lastly temperature variation is known to affect reproductive output but surprisingly no studies have investigated consequences of huddling on reproduction.

Sociable weavers are particularly interesting candidates to study thermoregulatory benefits as they roost all year round in their massive communal nest structures (**Plate 3**) that were found to offer significant thermoregulatory benefits (see **ANNEX**).

We studied the relationship between roosting group size before breeding and 1) nighttime ambient chamber temperature 2) breeding group size 3) laying date and 4) egg mass.

For each focal chamber in the austral winter 2012 we placed one temperature logger inside on the top of the chamber and one outside at the entrance to control for the outside temperature. We then placed a video camera under the colonies that had temperature loggers in order to know the number of birds roosting in the same chambers.

Roosting group size was indeed strongly correlated with ambient chamber temperatures at night. After calculating a theoretical critical temperature of 23°c for sociable weavers (the temperature below which sociable weaver are theoretically predicted to spent energy in thermoregulation) we found that roosting group size significantly reduced the proportion of time spent below this lower critical temperature suggesting thermoregulatory benefits.

We found a correlation between roosting and breeding group sizes suggesting 1) the predictability of breeding group size which is a prerequisite for an effect of group size on egg mass and 2) an additional important thermoregulatory benefit provided by helpers. Crossing more roosting and breeding data is needed to study consequences of roosting temperatures on reproduction but the preliminary results obtained here indicate the possibility of such an effect.

## *Helpers' presence and parents' survival* **(Manuscript 3)**

Here we aim to examine the relationship between the presence of helpers and parents' survival with a particular focus on sex-specific effects.

Cooperatively breeding species are typically long-lived and hence are expected to favor investment in own survival rather than current reproduction. However the investigation of helper benefits for parental survival is surprisingly often neglected compared to reproductive success. Additionally, all studies that found a relationship between helpers' presence and "survival" actually did not use CMR methods and thus are in reality analyzing return rates and subject to misinterpretations.

By using sophisticated CMR analyses we investigated if the presence of helpers was associated with an increase in survival probability for male and female breeders. This study involved 14 years of capture history (from 1999 to September 2013) including five seasons of monitored breeding (with known breeding group composition, 1999-2000, 2000-2001, 2008-2009, 2010-2011, 2011-2012) that covers a large range of environmental conditions (namely rainfall taken into account in our analyses).

We expected the presence of helpers to be beneficial for both sexes notably because both parents were found to reduce their provisioning rates in presence of helpers (Covas et al. 2008) and because both should experience thermoregulatory benefits (**Manuscript 2**). Additionally the magnitude of the positive effect is expected to be greater for females as they were found to lay smaller eggs in presence of helpers (**Manuscript 1**).

Our best selected model indicated a considerably lower estimated survival probability for females without helpers (67%) than for other breeders (i.e. females with helpers and males; 85%).

This result clearly indicates female-specific benefits of the presence of helpers which can be due to more benefits and/or less costs associated with the presence of helpers for females. One specific benefit of helpers for females is the lower investment in eggs (**Manuscript 1**). A similar result was found on superb fairy-wrens (Russell et al. 2007), where females but not males have a higher return rate in presence of helpers (Cockburn et al. 2008). The absence of a positive association between survival and the presence of helpers for males may also indicate specific costs of helpers for males which might be related to dominance interactions, although more research is needed to understand the mechanisms underlying this result.

## HELPERS AND OFFSPRING'S FITNESS

### *Helpers' presence and offspring's begging behavior* (Manuscript 4)

Here we investigate whether maternal effects could influence offspring begging behavior.

Begging behavior is a typical manifestation of parent-offspring conflicts as it is commonly of the offspring's interest to receive more investment than it is optimal for parents to supply at each breeding attempt (Trivers 1974, Lessells and Parker 1999). Maternal hormones, especially corticosterone and testosterone, are usually found to be positively associated with begging behavior (Schwabl 1996, Saino et al. 2002, Smiseth et al. 2011). More specifically, by depositing different amounts of hormones into eggs females may modulate parent-offspring conflicts by acting on their young's begging behavior (Schwabl 1996) and then on their own and/or their partner's food provisioning (Muller et al. 2007, Tschirren and Richner 2008).

Cooperative breeders provide a promising system to study maternal control of begging behavior and family conflicts. In such systems the breeding groups involve parents and current offspring but also helpers that are often kin of one or both parents.

In order to test the possibility of maternal manipulation of offspring need, in 2012-2013 we used a cross fostering experiment and measured begging behavior at days 4 and 9.

As begging rate may vary with offspring need and satiation we expected chicks' begging rate to be lower when actually fed by more birds (foster group size). However, in addition, as eggs were found to contain less testosterone and corticosterone in presence of helpers (**Manuscript 1**), we expected nests with helpers to produce nestlings with lower begging rates than eggs laid in nests with helpers (original group size).

We found an effect of both foster and original group size. Chicks fed by more birds begged at a lower rate in accordance with the fact that they received more food (Covas et al. 2008). More interestingly, chicks originally from groups with helpers also begged less at day 4 (**Plate 4**).

The effect of original group size on offspring begging may be mediated by the differential levels of testosterone and corticosterone deposited in eggs depending on the presence of helpers. Experimental manipulation of egg hormones are however needed to test this hypothesis.

Female manipulation of carers provisioning can be particularly likely and advantageous in cooperative breeding species as not only one but several individuals can be manipulated. Hence, the joint study of maternal hormones, offspring begging and parents and helpers provisioning has the potential to be a fruitful field of research in cooperative breeders.

**Plate 4.** Begging chicks at day 4 during weight measurements. At this age we found that chicks begged less when expected to be fed by more birds. Photo by Lisa Malm.

## ***Helpers' presence and offspring's survival*** **(Manuscript 5)**

During her Master (University of Porto) Lara Broom studied the potential impact of helpers on the post fledgling period, especially fledgling survival.

While the effect of helpers on reproductive success has been well studied, the effect of helpers after fledgling is rarely studied, mostly because of the difficulty in tracking mobile young. However helper's presence might have costs to the young and apparent survival was found to be lower in sociable weaver yearlings raised with helpers than those raised by pairs alone (Covas et al. 2011). This result was suggested to arise from long-distance dispersal or a higher mortality. Here we attempted to distinguish between these two possibilities by studying post-fledging survival before dispersal took place.

Survival of 156 juveniles raised in pairs alone versus pairs with helpers was monitored during the first three months of life in 2012-2013, and CMR methods were used to control for individual detectability and estimate survival.

The results we obtained suggest a lower survival probability for juveniles with helpers from 17 to 30 days of age (i.e. around fledgling time) when fledgling survival rate was the lowest.

This is most likely due to true mortality and not long distance dispersal as dispersers younger than four months are extremely rare. One possibility is that fledglings come under the exclusive care of helpers that are less good carers than parents but allow parents to renest more quickly (Raihani and Ridley 2008). Here, we found no indication of a different timing of fledgling between broods with and without helpers. However this hypothesis needs further investigation as the method used as a proxy of fledgling date may not be accurate (see methods in **Manuscript 5**). Breeders re-nesting interval was also studied as it could have been shorter for parents with helpers, but on the relatively small sample size we have no effect was found. A deeper inspection of parents-helpers-fledgling interactions is thus needed to understand the mechanisms behind the lower early fledgling survival in presence of helpers. Nonetheless, these results add to the results of Covas et al. 2011, unambiguously suggesting that breeding with helpers also has costs.

# DISCUSSION

## *Summary*

We found that sociable weaver females with helpers laid lighter eggs and that maternal survival probability was higher for females with helpers. This is in agreement with life history theory suggesting that long-lived species should favor their survival over reproduction. Mechanistically we had results suggesting that females may anticipate the presence of helpers as the breeding group size was found to be correlated with pre-breeding roosting group size. Additionally the ambient temperature at night was found to be higher in chambers with more birds indicating a potential thermoregulatory benefit of helpers and that nest temperature may be a cue indicating good future breeding condition for females. In addition we found that eggs produced in presence of helpers have less corticosterone and testosterone, indicating that maternal effects are important in cooperative breeding species. Maternal effects are viewed as a way of manipulating offspring behavior and ultimately parental fitness. Concurring with this idea, our cross fostering experiment shows a lower begging rate early after hatching from chicks that should have been fed by more birds. Hence, we showed that mothers may manipulate the begging rate of their offspring. All these results added to previous ones obtained in this species (Covas et al. 2008) suggesting that the presence of helpers is beneficial for the parents. However by opposition we also obtained results showing a negative effect of helpers, as we found higher mortality rate after fledging for offspring raised with helpers.

## *Synthesis and prospects: from the limits of field studies to the opening of promising research perspectives*

Working on a natural population implies several limits and the two main ones that limit the power of the results presented here are small samples sizes and correlative results.

Small sample sizes were limited for three main factors. First, there is extreme variability in breeding conditions in the areas typically inhabited by this species (and at our study site) and this directly affects breeding success between years, as already mentioned. The second reason is nest predation by snakes, which take on average 70% of the broods (Covas et al. 2008). The last but not least interesting reason is infanticide that occurred particularly often when breeding conditions were bad. Interestingly, the 3 infanticides we were able to witness were performed by non-parent females, indicating a potential female competition for breeding (Nelson-Flower et al. 2013).

Another limitation of this study is that we did not manipulate the number of helpers pre-laying. Hence despite the fact that we included as many confounding factors as possible in our analyses we cannot be sure of any causal effect of the presence of helpers. However, if manipulating the number of helpers is essential to be sure of any causal effect of the presence of helpers, it would also mean the manipulation of many confounding factors we could not control for, as helper removal may profoundly disrupt group dynamics (Cockburn 1998). The effect of the number of helpers on egg size was experimentally tested only once in a cooperative fish (Taborsky et al. 2007) but was never tested on birds and in natural populations due to ethical and logistical limitations. Nevertheless, we were able to manipulate the number of helpers without affecting group composition through a cross fostering experiment. This allowed us to dissociate the maternal and rearing environments to test for the effect of the actual presence of helpers, although unfortunately not for the presence of helpers before laying, and hence quality remains a potential confounding factor. The most commonly cited confounding factor associated with helper presence is probably territory quality (Brown et al. 1982). The sociable weaver provides a particularly suitable system against this bias as they are not territorial and many breeders live in the same colony. In addition, we controlled for both random and size effects of the colonies. However, breeders' quality remains an issue (see **Manuscript 1**) as egg mass is usually very consistent within females but very variable between females (Christians 2002) an important step to avoid parental quality bias will be to study within-female variation in egg mass with the number of helpers between breeding seasons. This was initially planned to be part of the current thesis but the remarkably bad breeding season in 2011-2012 (13 fledglings from 12 broods) made a considerable gap in the data that prevented us to test longitudinal intra-female effects of helpers on egg mass.

Another possibility for the future is to identify and manipulate the proximal factors influenced by the presence of helpers that affect female allocation in eggs. Based on the results obtained in **Manuscript 2**, pre-laying roosting temperature is a possible candidate. Manipulating chamber temperature rather than the number of helpers before laying (within the natural range) is probably an easier and less disturbing experiment.

The effect of helpers on breeders' survival has never been experimentally tested and again confounding factors may occur, especially dispersal that is closely linked with cooperative behavior (Koenig et al. 1992). Even if very long range dispersion (i.e. outside of the 15 colonies we capture yearly) might occur, we partially took such bias into account by using CMR methods that correct for recapture probabilities. To our knowledge this is the first CMR analysis reporting a link between helper presence and survival. The lower survival of females without helpers may be the consequence of their higher investment in eggs. Maternal load lightening at the egg stage has been reported in four birds (including the present study) and 1 fish species (Russell et al. 2007, Taborsky et al. 2007, Canestrari et al. 2011, Santos and Macedo 2011), a lower survival of females without helpers was investigated and found in two of them (Cockburn et al. 2008 and the present study) but the direct relationship between egg investment and female survival remain to be investigated. Since 2010, egg mass is systematically measured in our studied population and CMR analyses should soon allow to test the hypothesis that higher survival of females in presence of helpers is mainly driven by their lower investment in eggs. A helper effect of females but not males' survival is likely to lead sexual conflicts linked to the presence of helpers. However helpers may be still beneficial for males by increasing their partner survival as sociable weaver pairs are relatively stable throughout life.

The more classical explanation for an increase in parental survival when assisted by helpers is their lower food provisioning. However, by crossing information from Hatchwell (1999) and Kingma et al. (2010) the link between parental load lightening at the feeding stage and survival in birds seem inconsistent, especially for males (**Table 1**, Spearman rank correlation ; for males: $\rho = -0.054$, p-value = 0.847; for females: $\rho = 0.327$, p-value = 0.234). Indeed, several other benefits of helpers may occur in addition to load-lightening during the egg and chick stages and here we started investigating a poorly explored one: thermoregulation (**Manuscript 2**). Energetic benefits obtained through roosting allow important energy savings, particularly during cold nights (Gilbert et al. 2010)  and hence may represent important benefits not only for breeders but also for helpers. Communal roosting and associated thermoregulation benefits may ultimately play an important role in group cohesion in this and other cooperative breeders. It will be thus interesting to link the presence and the contribution of helpers during breeding to their presence with the parents for roosting in the following winter to investigate the existence of “pay-to-stay” mechanisms.

| Species | Male compensation | Male survival | Female compensation | Female survival | Egg mass/size reduction |
|---|---|---|---|---|---|
| Florida scrub-jay (*Aphelocoma coerulescens*) | + | + | + | + | |
| Sociable weaver (*Philetairus socius*) | + | 0 | + | + | + |
| Acorn woodpecker (*Melanerpes formicivorus*) | 0 | + | 0 | + | 0 |
| Bicolored wren (*Campylorhynchus griseus*) | 0 | + | + | + | |
| Dunnock (*Prunella modularis*) | 0 | 0 | 0 | 0 | |
| Red-cockaded woodpecker (*Picoides borealis*) | 0 | + | 0 | + | |
| White-fronted bee-eater (*Merops bullockoides*) | 0 | 0 | 0 | 0 | |
| Purple-crowned fairy-wren (*Malurus coronatus*) | + | + | + | + | |
| European bee-eater (*Merops apiaster*) | + | + | 0 | + | |
| Longtailed tit (*Aegithalos caudatus*) | + | +* | + | 0 | |
| White-browed scrubwren (*Sericornis frontalis*) | 0 | 0 | 0 | 0 | |
| Seychelles warbler (*Acrocephalus seychellensis*) | + | 0 | 0 | 0 | |
| Western bluebird (*Sialia Mexicana*) | + | 0 | + | 0 | |
| Superb fairy-wren (*Malurus cyaneus*) | + | 0 | + | + | + |
| Splendid fairy-wren (*Malurus splendens*) | + | 0 | + | + | |

**Table 1:** sex specific survival and compensation in relation with the presence of helpers pooled from Hatchwell (1999) and Kingma et al. (2010). For the 3 studies of egg mass/size reduction see Russell et al. 2007, Koenig et al. 2009 and the current study. *update from from Meade et al. 2010.

## *Maternal effects and family conflicts*

In addition to the reduced egg mass we found that females with helpers laid eggs with lower corticosterone and testosterone levels. This may be induced by environmental pre-breeding conditions (Meylan et al. 2012) such as social environment (Mazuc et al. 2003, Goymann and Wingfield 2004). For example corticosterone is a stress induced hormone (Saino et al. 2005, Giesing et al. 2011) which is assumed to be passively transferred to eggs (Groothuis et al. 2005) and has been found to be positively associated with energy expenditure (Goymann and Wingfield 2004). Considering the potential thermoregulatory benefits of roosting group size (**Manuscript 2**), one reason for the lower corticosterone level in eggs with helpers may be the lower energy expenditure of females roosting in large groups. For example on Greylag geese *Anser anser* excreted corticosterone metabolites were correlated negatively with the minimum ambient temperature of the night before (Frigerio et al. 2004). To investigate this possibility captured birds in the morning following the recording of the roosting group size at the evening and took blood samples within 3minutes in order to measure circulating corticosterone levels. We were only able to take samples for 9 roosting birds but the results we obtained clearly shows the opposite pattern as the corticosterone levels tend to increase with roosting group size (**Figure 1**). This may indicate a social stress related to roosting group size and for example in the previously mentioned Greylag geese, socially induced stress leads to corticosterone levels 10 times higher and baseline levels influence by ambient temperature (Frigerio et al. 2004). The influence of sociable weaver female pre-laying hormone levels on egg deposition still remains to be investigated.

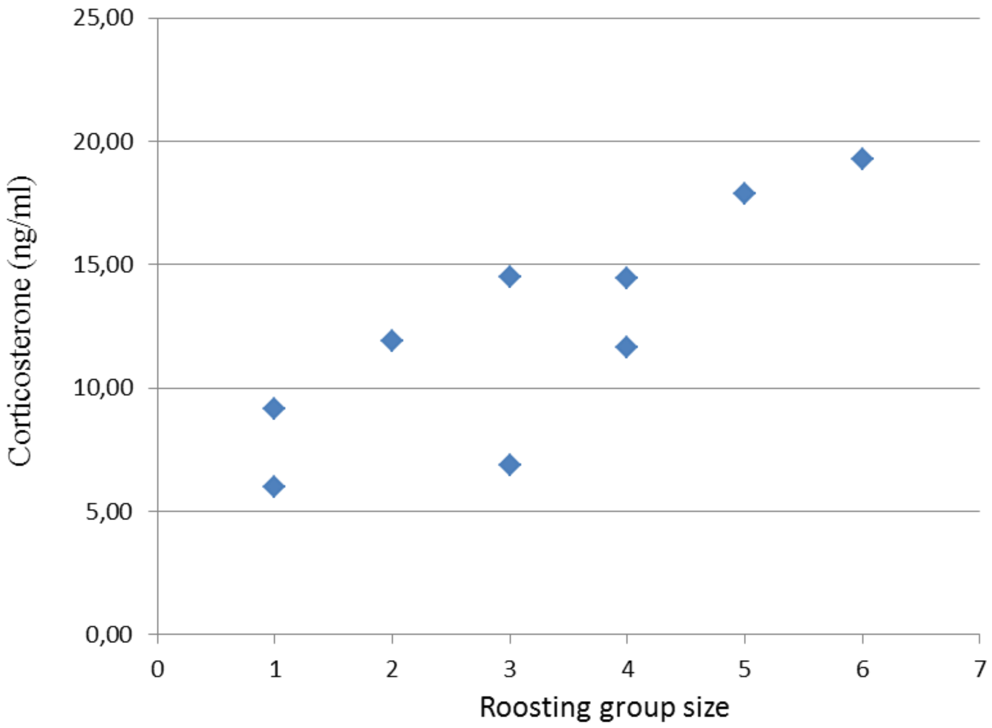

**Figure 1.** Circulating corticosterone levels of roosting birds in the morning in relation with the number of birds roosting in the chamber they were caught.

Both corticosterone and testosterone are known to affect offspring growth and behavior in several species (Groothuis et al. 2005) and a commonly reported effect of increased levels of these two hormones is the enhancement of begging behavior (Smiseth et al. 2011).

In agreement, through a cross-fostering experiment, we found that chicks originating from eggs produced by females breeding in larger groups begged at a lower rate early after hatching. Such result is also promising concerning the possibility of a hormonally derived maternal adjustment of carers feeding behavior (**Manuscript 4**).

Males and females' responses to begging signals have been shown to differ in several birds' species (Muller et al. 2007). In great tits, *Parus major*, for instance males adjust their food provisioning to visual begging displays, whereas females respond to visual and acoustic offspring signals (Kilner 2002a). Such differences in parents' provisioning rules may lead females to specifically manipulate her partner's provisioning behaviour, notably through differential yolk hormones' deposition (Muller et al. 2007) but evidence for this hypothesis is still missing (Kilner 2002b, Tschirren and Richner 2008, Muller et al. 2010). In cooperative breeders, females may in addition attempt to optimise their own, their partner's and helpers' behaviour. Hence, a next step would be to study breeding males, females and helpers responses to the variation of different begging signals and to yolk hormones levels. Indeed, nothing is known in cooperative breeding species about what type of stimuli (e.g. acoustic or visual) different types of providers respond to and whether there is any type of modulation from breeding females of their partners' and/or helpers' feeding effort. We predict this mechanism to be particularly likely and advantageous in such breeding system as not only one but several individuals' behaviour can be adjusted. Also a very interesting perspective would be to study how maternal effects vary with helpers' relatedness. Maternal manipulation of helpers' provisioning effort is expected to be more beneficial for females when helpers are unrelated to them and thus when they do not pay kin-related costs.

Individual responses to offspring begging were poorly studied on cooperatively breeding species but the results are in accordance with this hypothesis of manipulation. In Arabian babblers (*Turdoides squamiceps*), where there is high relatedness within breeding groups, parents and helpers showed the same provisioning rule in response to experimentally manipulated begging (Wright 1998). On the other hand, in superb fairy-wrens, *Malurus cyaneus*, where breeding males and helpers are most often unrelated to the brood, only these individuals, but not females, responded to increased begging (MacGregor and Cockburn 2002). Individual response to offspring begging has not yet been studied on the sociable weaver but individual provisioning behaviour of parents and helpers also reinforce the prediction of a higher manipulation of non kin feeders. Indeed, breeding males' feed at a higher rate than females and helpers (which were found to be first-order kin of the breeding female in 66% of the cases Covas et al. 2006, Doutrelant and Covas 2007). Additionally, adult helpers' feeding rates and prey sizes were negatively correlated with their relatedness to the breeding female (Doutrelant et al. 2011). Studying family conflicts on cooperative breeders depending on individual relatedness, the number of carers and maternal allocation in eggs hormones (that can be manipulated) is thus a promising research avenue.

## *Life histories strategies and population dynamics*

Maternal hormones may also have long lasting effects on offspring phenotype, affecting dispersal or survival (Groothuis et al. 2005, Meylan et al. 2012) and sociable weavers were found to have a lower survival probability at fledging when fed by parents and helpers than by parents only (**Manuscript 5**). However, when we analyzed the survival of the 57 cross-fostered fledglings, this lower survival does not seem to be the consequence of maternal effects. When we considered that the chicks survived at fledging when they were seen at least once during the three fist months after fledging and dead if not, we found that survival was negatively related to the foster group size (estimate = -1.89±0.59, df = 13, P = 0.007) but not by the group size of origin (estimate = 0.18±0.61, df = 12, P = 0.848, models glmm). This confirms that low survival is not due to a poorer quality of eggs produce in the presence of helpers or of a higher dispersal of nestling produced in nest with helpers, since dispersal in this species usually does not take place in the first four months of life

The effect of the actual presence of helpers on fledgling survival could be due to parental neglect if breeders transfer the care of the recently fledged brood to helpers, as observed in pied babblers (Raihani and Ridley 2008). Additionally, there might be competition between the recently fledged offspring and the helpers. For example in meerkats *Suricata suricatta* mortality of juveniles between emergence from the natal burrow and 6 months of age was lower in small groups than in large groups under low predation (Clutton-Brock et al. 1999). This was explained by a trade-off between the positive anti-predator effect of helpers for juveniles and their deleterious effect through competition.

To investigate the possibility of competition between offspring and helpers in sociable weavers, we analyzed the fledglings' plasma corticosterone levels in relation to the presence of helpers through a cross fostering experiment. We found indication of a positive effect of helpers presence on plasma corticosterone concentrations (Estimate = -3.401±1.69, df = 13, P = 0.0654, **Figure 2**) while the presence of helpers in the nest of origin has no effect (P = 0.92). While this result may be in accordance with a possible competition, corticosterone levels of the 89 samples fledglings in total were not related to survival (Glmm: Estimate = -0.0223±0.0616, df = 45, P = 0.7187; **Figure 3**).

Fledgling sociable weavers' plasma testosterone levels is remarkably low (< 0.2ng/ml) and were unfortunately not possible to measure (Charline Parenteau's analyses of our sociable weaver's plasma).

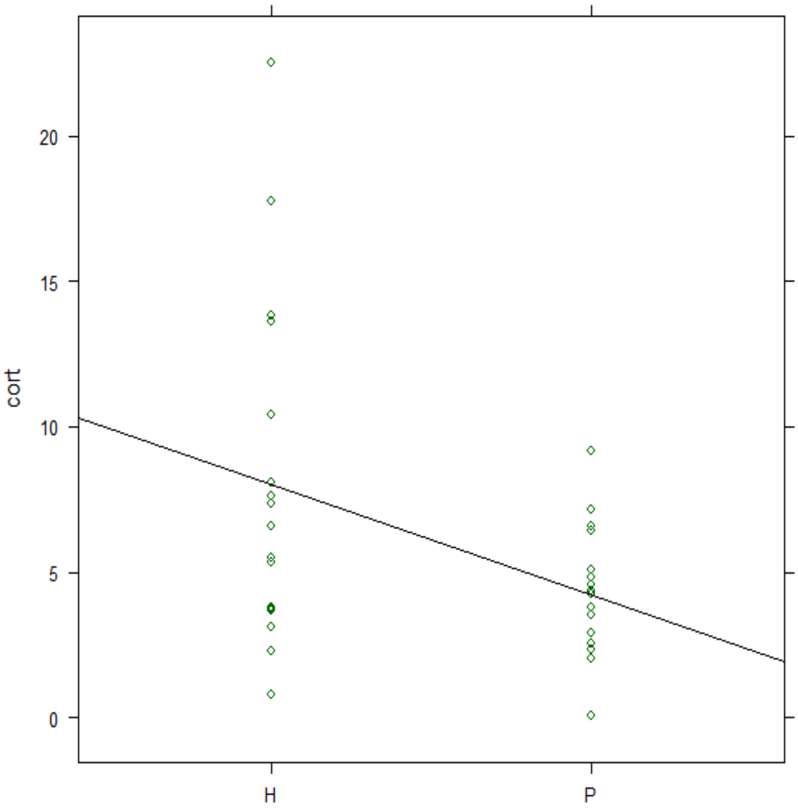

**Figure 2.** Relationship between plasma corticosterone levels (ng/ml) and foster helpers' presence**.**

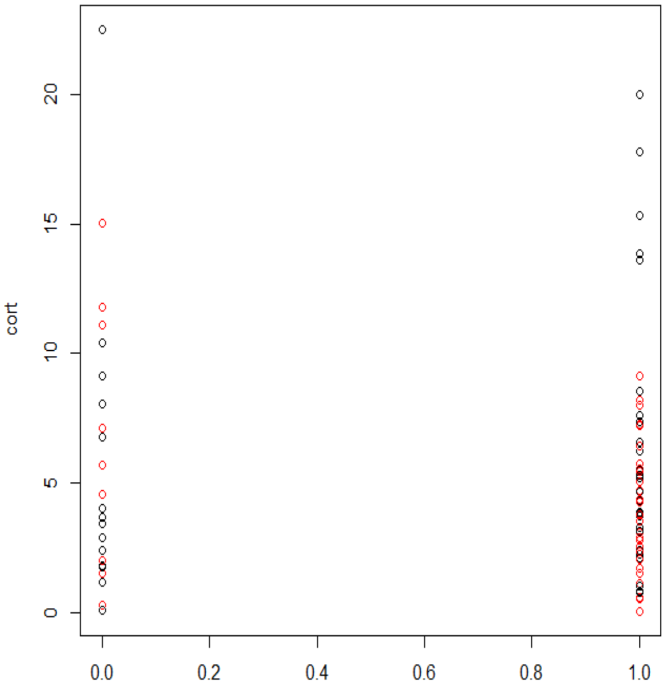

**Figure 3.** There was no relation between corticosterone levels and fledgling survival estimation (dots corresponding to fledglings raised by parents and helpers are in red).

A negative effect of helpers on offspring survival appears very surprising. Indeed why help (or accept help) if the offspring fed by helpers are less likely to survive? From the offspring point of view there is obviously a cost associated with the presence of helpers. However, we found that helpers may allow females to be considerably more likely to survive and thus a negative effect of helpers on offspring can be a low cost compared to the importance of the benefit for females.

We evaluate the pertinence of this hypothesis by using a simple population dynamic model (**Table 2**, **Figure 3**) with the ULM software (Legendre and Clobert 1995) and parameters estimations from the present and past studies (Covas et al. 2004a, Altwegg et al. 2013). This allows to compare the growth rate of a female population where all 3+ years old females are helped (Yearling survival s0 = 0.73, breeding females' survival s3= 0.85 from models in **Manuscript 3** and **Manuscript 5**) with a population without helpers (yearling survival s0 = 0.87, breeding females' survival s3 = 0.67 from models in **Manuscript 3** and **Manuscript 5**).

| **States** | **1** | **2** | **3** |
|---|---|---|---|
| **1** | 0 | 0 | f1*s0*σ |
| **2** | s1 | 0 | 0 |
| **3** | 0 | s2 | s3 |

**Table 2. Population matrix of the simple model (Figure 3).** For all modeled populations σ (sex ratio) = 0.5 (Doutrelant et al. 2004),survival from one year to two years (s1) and from two to three years (s2) = 0.66 (Covas et al. 2004a) and 3+ years females' fecundity (f1) = 0.7 (Altwegg et al. 2013).

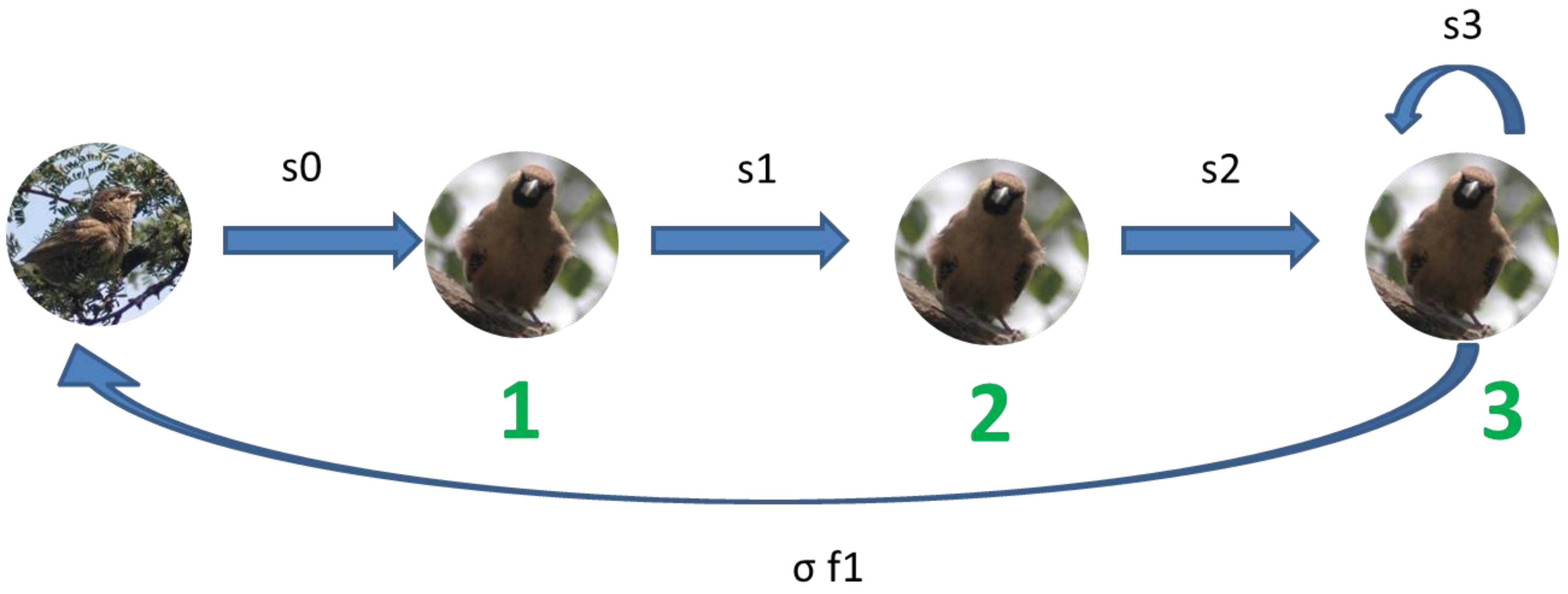

**Figure 4.** Simple females sociable weaver’s population model. For all modeled populations σ (sex ratio) = 0.5 (Doutrelant et al. 2004),survival from one year to two years (s1) and from two to three years (s2) = 0.66 (Covas et al. 2004a) and 3+ years females’ fecundity (f1) = 0.7 (Altwegg et al. 2013). Juvenile survival (s0) and 3+ years females survival (s3) depended on the presence/absence of helpers in a first time according to the models obtained in **Manuscript 3** and **Manuscript 5**. When compared to the model represented in **Figure 5** the variation due to the presence/absence of helpers was no more considered and s0 and s3 were obtained from the null models presented in **Manuscript 3** and **Manuscript 5**.

This returns a population growth rate (λ) of 0.969 in the population with helpers against 0.852 for a population without helpers. Despite the fact that both modeled populations are declining ($\lambda<1$) as recently reported for the studied population (Altwegg et al. 2013) the difference between the two λ is considerable. Indeed, starting with a population of 20 three years old females, a female population with helpers will be extinct ($n<1$) after 99 generations while a population without helpers will be extinct after 20 generations only. The presence of helpers is thus expected to be beneficial for females' fitness at a lifetime scale and is also expected to increase population growth.

As the facultative presence of helpers may profoundly impact population dynamics and life history traits, we formalized a second population model based on the previous model (where females were either always helped or never) that includes the possibility for females *to be helped or not* throughout years in the same population (**Table 3**, **Figure 5**). Sociable weavers can sometimes have helpers older than 2 years, but to simplify in this model, helpers are only one or two years old males, which are the offspring of the breeding female. Females can also first breed before 3 years old but again to simplify we let only them start when 3 years old as it is mostly the case. At this stage, they do not have helpers as they never bred before. When four years old, females can be helped (by one year old male helpers) if at least one of their male offspring of the previous year survived (state **4**). States **4**, **5** and **6** correspond to females with respectively only one year old, only two years old, and both one and two years old helpers. State **3** correspond to females without helpers. Again, survival estimators of 3+ years old females (with or without helpers s3h and s3p) and juveniles (with or without helpers s0h and s0p) were taken from the models in **Manuscript 3** and **Manuscript 5**. This model was run in ULM and the results were compared with a simpler model (as in **Figure 4**) that did not take into account the presence of helpers and used 3+ years old females and juveniles’ survival estimators from the null models without helper effect in **Manuscript 3** and **Manuscript 5** (**Table 4.a**).

| **States** | **1** | **2** | **3** | **4** | **5** | **6** |
|---|---|---|---|---|---|---|
| **1** | 0 | 0 | f1p*s0p*σ | f1h*s0h*σ | f1h*s0h*σ | f1h*s0h*σ |
| **2** | s1 | 0 | 0 | 0 | 0 | 0 |
| **3** | 0 | s2 | **s3p***(1-s0p)^((1-σ)*f1p) | **s3h***(1-s0h)^((1-σ)*f1h)*(1-s1)^(f1h*(1-σ)*s0h) | **s3h***(1-s0h)^((1-σ)*f1h) | **s3h***(1-s0h)^((1-σ)*f1h)*(1-s1)^(f1h(1-σ)s0h) |
| **4** | 0 | 0 | **s3p***(1-(1-s0p)^((1-σ)*f1p)) | **s3h***(1-(1-s0h)^((1-σ)*f1h))*(1-s1)^(f1h*(1-σ)*s0h) | **s3h***(1-(1-s0h)^((1-σ)*f1h)) | **s3h***(1-(1-s0h)^((1-σ)*f1h))*(1-s1)^(f1h*(1-σ)*s0h) |
| **5** | 0 | 0 | 0 | **s3h***(1-s0h)^((1-σ)*f1h)*(1-(1-s1)^(f1h(1-σ)s0h)) | 0 | **s3h***(1-s0h)^((1-σ)*f1h)*(1-(1-s1)^(f1h(1-σ)s0h)) |
| **6** | 0 | 0 | 0 | **s3h***(1-(1-s0h)^((1-σ)*f1h))*(1-(1-s1)^(f1h(1-σ)s0h)) | 0 | **s3h***(1-(1-s1)^(f1h(1-σ)s0h))*(1-(1-s0h)^((1-σ)*f1h)) |

**Table 3.** Population matrix of the model including the possibility for females to be helped (states 4, 5 and 6).
f1h=f1p=0.7 (Altwegg et al. 2013), s1 = s2 = 0.66 (Covas et al. 2004a), s3h: survival of females with helpers, s3p: survival of females without helpers, s0h: survival of fledglings with helpers, s0p: survival of fledgling without helpers.

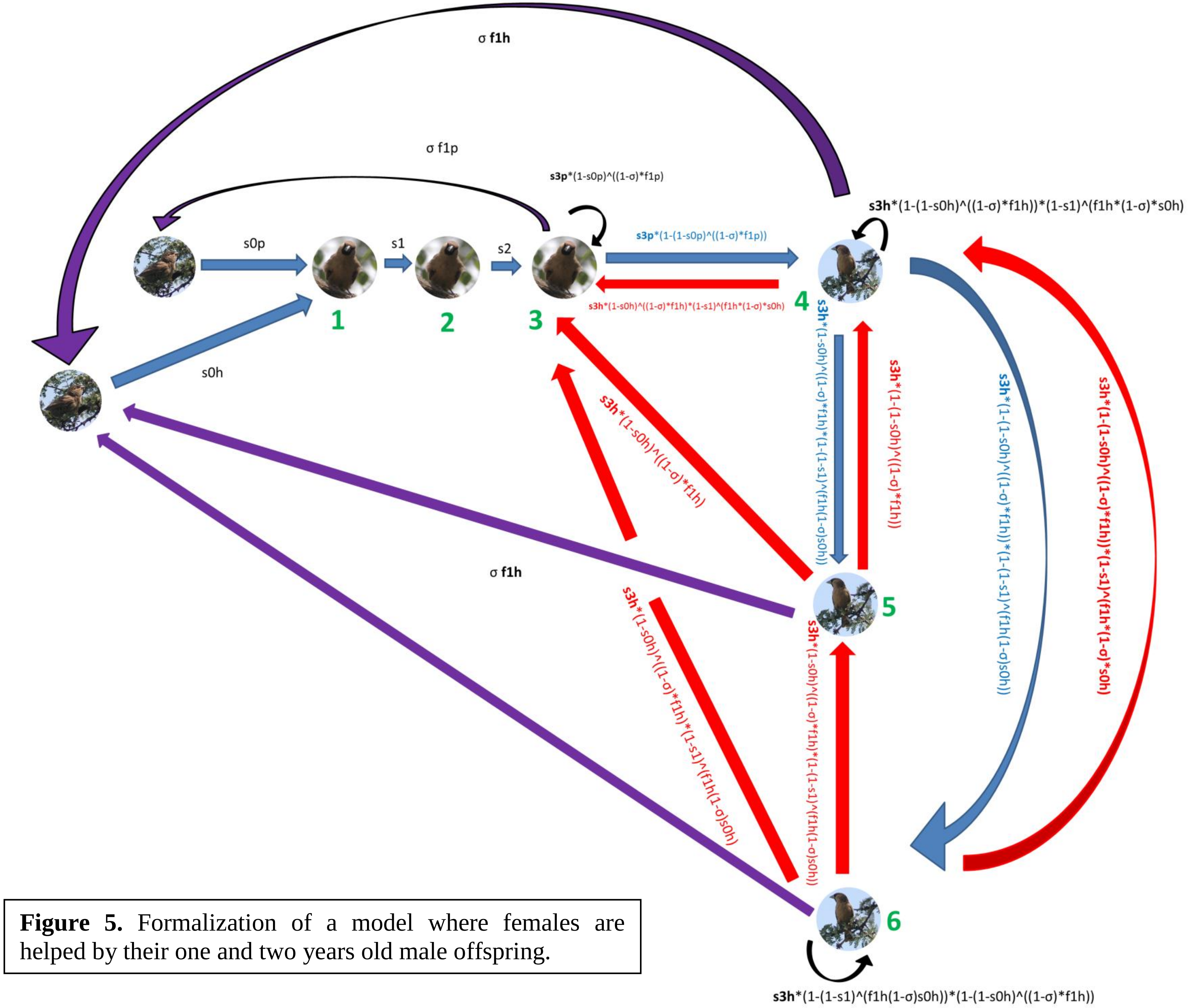

**Figure 5.** Formalization of a model where females are helped by their one and two years old male offspring.

| Parameter | Value | Elasticity |
|---|---|---|
| s0 | 0.777 | 0.108 |
| s1 | 0.66 | 0.108 |
| s2 | 0.66 | 0.108 |
| s3 | 0.82 | 0.676 |
| f1 | 0.7 | 0.108 |

**a**

| Parameter | Value | Elasticity |
|---|---|---|
| s0h | 0.73 | 0.07642 |
| s0p | 0.87 | 0.1407 |
| s1 | 0.66 | 0.1297 |
| s2 | 0.66 | 0.1201 |
| s3h | 0.85 | 0.3053 |
| s3p | 0.67 | 0.3344 |
| f1h | 0.7 | 0.06315 |
| f1p | 0.7 | 0.09487 |

**b**

**Table 4.** Estimators and elasticity of the parameters used in population models without differences associated with the presence of helpers (a, Figure 3) and with differences associated with the presence of helpers (b, Figure 4).

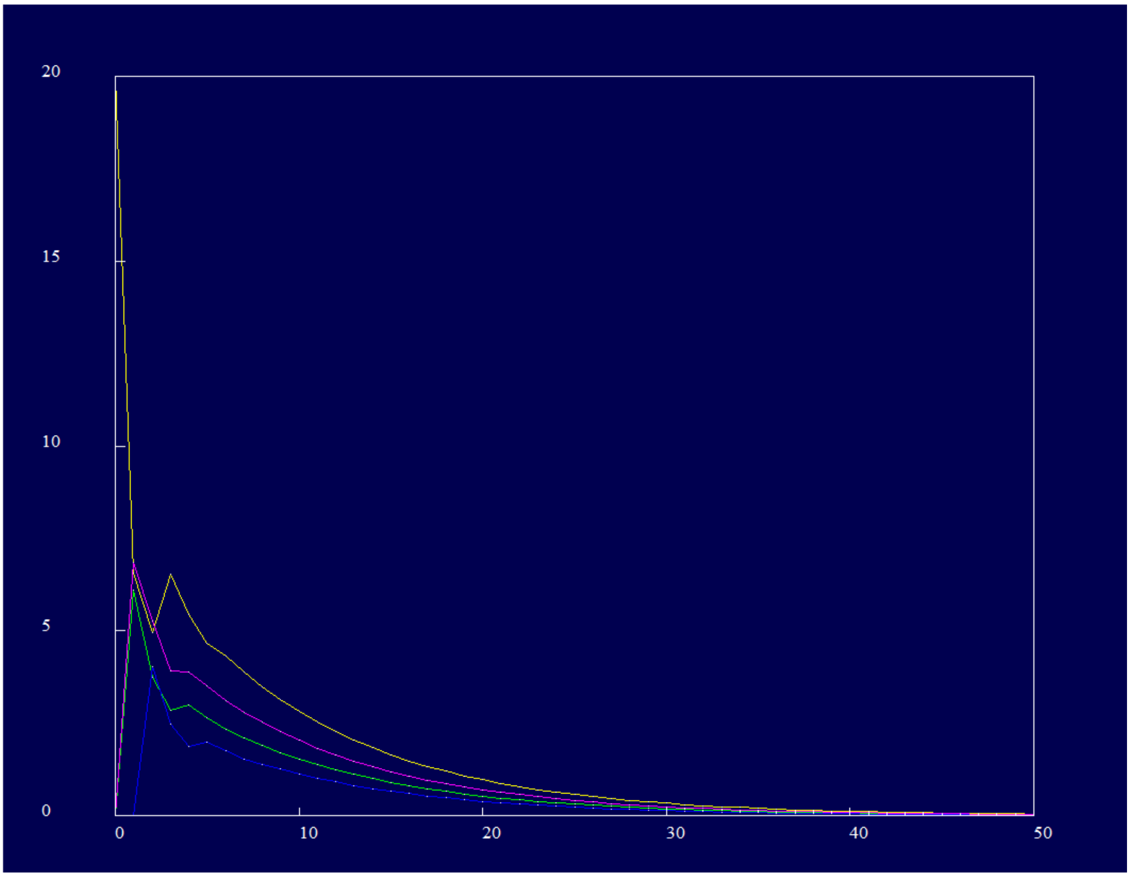

**Figure 6. Simulation of a population starting with 20 three years old females based on the model formalized in Figure 4.** One year old females in green, two years old females in blue, 3+ years old females without helpers in yellow and females with helpers in pink. Number of birds for each category is plotted against the number of generations.

The first main result is that the growth rate is 0.899 when taking into account the parameters' differences due to the presence of helpers compared to 0.951 for the simple model that do not consider any effect of helper. To illustrate this difference if we start with 20 three years old females we expect the population to be extinct after 28 generations (**Figure 6**) against 63 if we don't take into account the differences due to the presence of helpers. This clearly illustrates the need of taking into account the breeding system of a species when studying their population dynamics.

Another important result is the contribution of the reproductive parameters for the dynamic of the population (given by elasticity values of the fecundities and yearling survivals with and without helpers: f1h, f1p, s0h and s0p, **Table 4.b**). Indeed, juvenile survival contributes of 21.6% at the growth of the population (i.e. s0h+s0p elasticity values) against 10.8% for the simpler model without helper effect (**Table 4.a**). We can see that this difference is particularly due to the contribution of the reproductive parameters of the females without helpers.

According to our model, the only way for these females to have helpers and thus considerably increase their survival probability is by having at least one offspring that survive and thus to invest in reproduction. This is actually in accordance with the fact that when not helped, sociable weaver females invest more in offspring by increasing their investment in eggs (**Manuscript 1**) and feeding (Covas et al. 2008). Females that have one year old helpers (state **4** and **6** in **Figure 5**) should have less "pressure" to increase their reproductive investment as they have the guaranty to be helped the following year if their one year old helpers survived. Females with only two years old helpers may still use the presence of helpers to reduce their investment and then increase their survival but on the other hand they need to have offspring that survived to be helped the following year. It would be thus interesting to study females' differential investment in eggs and chicks in relation with the age of the helpers.

To conclude on this part and thus on the surprising results that fledglings from nests with helpers survive less, our results suggest different life history strategies depending on the presence of helpers and that the presence of helpers is globally very important despite this cost. Helpers presence is associated with reduce fledgling survival but this cost is overcompensated by the important increase of females' survival in presence of helpers. Since helpers in cooperatively breeding species are often closely related to the breeding female (typically offspring from previous breeding attempts Emlen 1995, Griffin and West 2003), for cooperative breeding species a non-negligible way for females to enhance their survival probability may be through increasing investment in reproduction and thus their chances of being helped for the successive breeding attempt. Cooperative breeders are typically described as relatively long-lived species that are expected to favor survival over reproduction (Arnold and Owens 1998) and this was our initial prediction. But our preliminary population based model shows that investment in reproduction may be more beneficial than commonly thought as this is the only way to get helpers and associated benefits. These may explain why these species are very sensible to reproductive conditions as shown in a previous experiment where improving reproductive condition brings one year old females to breed and helpers number to decrease (Covas et al. 2004b).

In conclusion, this thesis confirms the existence of maternal effects in relation to the presence of helpers and reveals some specific mechanisms through which maternal effects contribute to both females and offspring fitness in cooperatively breeding species. We also show the importance of considering the effects of helpers under a life history perspective to better understand the balance between costs and benefits of helpers. Finally, we showed that cooperative breeding may have consequences on life history traits and populations dynamics.

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# MANUSCRIPTS

# *Manuscript 1: Maternal effects in relation to helper presence in the cooperatively breeding sociable weaver*

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# Maternal effects in relation to helper presence in the cooperatively breeding Sociable Weaver

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## SUMMARY

In egg laying species, breeding females may adjust the allocation of nutrients or other substances into eggs in order to maximise offspring or maternal fitness. Cooperatively breeding species offer a particularly interesting context in which to study maternal allocation because helpers create predictably improved conditions during offspring development. Some recent studies on cooperative species showed that females assisted by helpers produced smaller eggs, as the additional food brought by the helpers appeared to compensate for this reduction in egg size. However, it remains unclear how common this effect might be. Also currently unknown is whether females change egg composition when assisted by helpers. This effect is predicted by current maternal allocation theory, but has not been previously investigated. We studied egg mass and contents in sociable weavers (*Philetairus socius*). We found that egg mass decreased with group size, while fledgling mass did not vary, suggesting that helpers may compensate for the reduced investment in eggs. We found no differences in eggs' carotenoid contents, but females assisted by helpers produced eggs with lower hormonal content, specifically testosterone, androstenedione (A4) and corticosterone levels. Taken together, these results suggest that the environment created by helpers can influence maternal allocation and potentially offspring phenotypes.

**Key-words:** cooperative breeding, maternal effects, egg mass, testosterone, androstenedione, corticosterone.

## INTRODUCTION

Maximising reproductive success over an individual's lifetime involves a series of trade-offs between current reproductive effort and survival between breeding events [1]. For females, an important way to adjust the costs of reproduction and influence offspring fitness is the possibility of varying maternal allocation during embryonic development in terms of nutrients, hormones or antibodies [2,3]. This differential allocation according to early, current or expected environment (e.g. temperature, food availability or mate quality) has been shown in several species [2,4,5,6].

In egg laying species, differential allocation in reproduction can occur first through the production of eggs of different sizes [7,8]. Many experiments have demonstrated that egg size is subjected to trade-offs and that these trade-offs change according to the species' life-history traits and breeding conditions experienced. Larger eggs are more costly to produce [9,10] but egg size correlates positively with early growth [8,11]. In particular, several experimental studies on insects, fishes and amphibians, have shown an increase in egg mass in poor environmental conditions, which can be explained by a greater positive effect of egg size on offspring survival under adverse conditions [4,12,13,14]. Similarly, different substances included in the contents of eggs may be submitted to trade-offs between allocation to offspring and mother self-maintenance [15]. For example, carotenoids are fat soluble pigments with antioxidant properties that protect against highly oxidative compounds produced during metabolic and immunological processes [16,17,18,19]. As such, carotenoids are expected to play a central role during embryo development and at hatching [20,21,22], but are also important for the breeding female's own immunity.

Another way through which egg-laying females can alter the environment experienced by their developing offspring is to alter the levels of maternally-derived yolk steroids, such as testosterone and androstenedione (A4), and glucocorticoids, such as corticosterone. In previous studies on birds, androgens (testosterone and A4) were associated with increased begging, growth and early offspring survival ([23] although potentially negative effects on offspring growth and survival have also been reported [24]). Conversely corticosterone is a stress mediated hormone which is assumed to be passively transferred to eggs [25,26,27,28] and overly high corticosterone levels seem mainly detrimental for offspring; reducing hatchling size and growth ([25,27,29,30,31] but see [32]). Prenatal hormones may also have long-lasting effects on offspring phenotype and fitness such as dispersal behaviour and survival [23,33,34,35]. Hormonal allocation into eggs is strongly influenced by female pre-breeding conditions. For example yolk testosterone deposition in eggs has been found to be influenced by diet quality [36], breeding density and social behavior [37] and females experimentally stressed before laying deposited more corticosterone in their eggs [26,27,31].

Maternal allocation in eggs is therefore an epigenetic mechanism influenced by the conditions experienced by the breeding females and by which females can adjust the environment experienced by the developing offspring in order to maximise either offspring or maternal fitness [38]. Previous studies show that the quality of the environment experienced by offspring and environmental predictability are key factors influencing the direction of maternal allocation [12,13,39,40].

Cooperatively breeding species offer a particularly interesting context in which to study maternal allocation and its effects (see also [41]). In these species, sexually mature individuals called 'helpers' forgo independent reproduction, but assist the breeders by providing care to their offspring through extra food brought to the nest [42,43]. Hence, the helpers create predictably improved conditions for offspring development, which is expected to affect female reproductive investment [41]. In addition, cooperative breeders are generally long-lived [44], and hence are expected to favour investment in survival over reproduction. One way in which breeding females may facilitate increased survival is by reducing investment in a current reproductive event when assisted by helpers [45]. For example, it has been shown that parents breeding in groups tend to compensate for the extra food brought by helpers by decreasing their feeding rate (see [46] for a review) which is expected particularly when the costs of egg production are high (Savage et al. in press). This 'load-lightening' effect of helpers can also occur through maternal effects.

The first study that investigated this hypothesis was conducted on a cooperatively breeding cichlid and showed that females reduced the size of their eggs according to the experimentally increased number of helpers [47]. In another study on superb fairy wrens *Malurus cyaneus* Russell and co-workers [48,49] showed that females used the extra food brought by helpers to decrease their own breeding investment. Specifically, these females laid smaller eggs, and experienced improved survival. Nonetheless, the extra food brought by the helpers compensated for the reduction in female investment and hence reproductive output did not differ between nests with and without helpers [48]. However, three additional studies that investigated this possibility obtained contrasting results. There was a similar reduction in egg size in the presence of helpers found in carrion crows *Corvus corone* [50] and southern lapwings *Vanellus chilensis* [51] but no clear support for this hypothesis in acorn woodpeckers *Melanerpes formicivorus* [52]. Hence, studying differential maternal allocation in the presence of helpers is particularly important in order to obtain an understanding of how fitness is maximised in different systems. Simultaneously, it could help explaining puzzling observations from previous studies that detected weak

[53,54] or absent [55,56] effects of helpers on reproduction. In these species breeding females might save energy in the presence of helpers by producing smaller eggs.

Investigations of egg contents in cooperative breeders are currently needed (see also [41]). Egg size is an important indicator of female energetic investment in reproduction, but more detailed studies of egg contents are required to understand the extent of this investment and the fitness consequences it may have for both mothers and offspring. Russell and collaborators [48] analysed the egg contents in lipids and proteins in superb fairy-wrens *Malurus cyaneus* and found lower levels of these nutrients in the presence of helpers. But to date no study has investigated whether mothers change the allocation of other important egg components such as carotenoids or hormones in relation to helper presence. Hormones, in particular, have a central role in mediating development, competition and sociality and therefore are of particular interest in studies of social and cooperative species [57].

Here, we investigate the effect of helper presence and breeding group size on egg mass and yolk components (carotenoids, testosterone, A4 and corticosterone) of first-laid eggs in a colonial cooperatively breeding bird, the Sociable Weaver, *Philetairus socius*. These weavers are relatively long-lived (the oldest bird recorded was 16 years old and the population average survival rate is 66% [58], although the figure appears to be above 80% for breeders Covas, Deville, Doutrelant and Gregoire unpublished data) and appear to favour investment in survival over reproduction [59]. In agreement with this, parents have been previously shown to reduce their nestling provisioning rates when assisted by helpers and a weak, albeit positive effect of helpers on fledgling mass was found mostly under adverse conditions (i.e. low rainfall or when breeding in large colonies) [54]. Finally, in this species, helpers do not have access to current reproduction and egg dumping has never been observed [60]. Hence, we predicted:

(i) a reduction in egg size and costly constituents such as carotenoids in presence of helpers;

(ii) an equivalent fledgling mass between nestlings raised with and without helpers, despite initial differences, if helpers compensate for the low maternal investment in eggs the overall feeding rate of a brood was previously found to increase with the number of helpers [54]);

(iii) a differential level of hormones in nests with and without helpers. Based on the positive effects of androgens on early offspring growth found in other studies [23], we expected that eggs laid by females without helpers should have higher levels of androgens to enhance the chicks' growth, thereby compensating for the lack of help available to raise the offspring (e.g., if nestlings compete more for food in nests without helpers than in nests with helpers and need to be fed more by parents to survive). Finally, corticosterone is thought to be directly related to female stress and likely to be passively transmitted to the eggs [25,26,27,28]. As corticosterone levels are linked with energy expenditure [61], we expected corticosterone levels in eggs to decrease with helper presence if the presence of helpers reduces energy expenditure and stress conditions experienced by females.

## METHODS

### *Ethics statements*

The work was conducted between September 2010 and February 2011 at Benfontein Nature Reserve in the Northern Cape province of South Africa (28°52' S, 24°50'E) with the permission of Northern Cape Nature Conservation. The Ethics Committee of the University of Cape Town specifically approved this study (permit number: 5869-2009). De Beers Consolidated Mines provided access to Benfontein Game Reserve.

### *Study species*

The sociable weaver is a colonial passerine endemic to the semi-arid acacia savannahs of southern Africa [62,63]. Sociable weavers build massive communal nests containing several independent nest chambers that are used for breeding and roosting. They are facultative cooperative breeders, breeding in pairs or with up to five helpers (mean group size 3.15 birds for this study, however the proportion of birds breeding in groups varies from ca. 30-80% between years [60]). Helpers are mainly offspring of one or both breeders (93%), although a small number of unrelated birds can also help [60]. Both sexes help, but in a previous study helpers older than one year were found to be only males [64]. [60].

### *Field methods*

Before the breeding season 503 individuals roosting in 14 colonies were captured and marked with a unique colour ring combination (see [65] for more details on the captures). Then to determine the onset of reproduction, all nest chambers in these study colonies (i.e. approximately 460) were inspected every 3 days. These chambers were marked with a numbered plastic tag

As soon as the first eggs were found, colonies were inspected every day in order to mark every new egg laid (with a soft blunt pencil) and thereby know the laying sequence (one egg is laid per day). Sociable weavers usually lay 3-4 eggs (average clutch size is 3.3 [54]). Two days after the first egg in a given nest was laid we weighed all eggs in that clutch to the nearest 0.001g with a digital Pesola balance (n=252 eggs from 84 clutches). On this occasion, we collected the first egg laid in that clutch, which was kept frozen until further analyses (n=84). Only the first egg was collected in order to allow the breeding activity to continue and hence to determine the breeding group size and identity of the individuals feeding at the nest from which we collected an egg. Nest chambers were checked the following day to weigh a possible fourth egg.

To associate every chick with its egg we individually marked 74 hatchlings of 38 clutches (from which we previously collected the first egg) by removing specific down feathers from the neck and/or wings. These marks were still visible 9 days after hatching when the chicks were ringed with a uniquely numbered metal ring. Due to high nest predation by snakes the number of clutches used in this study decreased from the initial 84 to 28 that actually fledged young. We weighed these chicks at 17 days old (46 chicks from 28 clutches).

To identify the individuals feeding at a given chamber and hence the breeding group size, we conducted 1 or 2 hours of daily observations for at least 3 consecutive days (min = 3, max = 10, average = 6.6 days). These observations started when the nestlings were around 6 days old since before the feeding activity is slower. Group size was established when no new birds were seen feeding after on average 5.5 consecutive sessions of observations. Observers were situated in a hide placed at 3-5m from the colony. We identified 34 breeding groups from chambers where we collected the first egg (18 groups with helpers and 16 without).

Rainfall closely influences food availability and the duration and success of the breeding season in sociable weavers [54,66,67]. We therefore monitored rainfall at the study site using a rain gauge.

### *Egg content assay*

Detailed methods of yolk content's analyses are available on supplementary electronic materials (protocol S1). Briefly, fresh yolk carotenoids concentrations were determined by colorimetry [68,69]. Yolk concentrations of testosterone, A4 and corticosterone were determined by radio-immunoassay [70]. Correlations between first egg mass and the different contents analysed are given in Table 1. As often found in the literature [71], testosterone and A4 concentrations were positively correlated. More surprisingly yolk mass and A4 were negatively correlated (Table 1).

### *Statistical analyses*

The aim of our analyses was to study the effect of breeding group size or type (with/without helpers) on egg mass, yolk carotenoids and hormonal contents. In addition, we analysed the effect of breeding group on fledging mass taking into account the egg mass. For all these analyses we conducted linear mixed models using the package nlme in R (R Development Core Team, 2011). The final models were obtained by sequentially eliminating explanatory variables with P values >0.1 using a backwards stepwise approach. The minimal model provided the P values of significant terms whereas P values for non-significant terms were obtained by reintroducing each non-significant variable into the minimal model [72].

For each of the following analyses we built two types of models. One using breeding group size as a dependant variable (studying linear and quadratic relationships) and one using breeding group type (i.e. with/without helpers) as the effect of helper presence may be significant but not additive (i.e. regardless of helpers' number). We present the results based on both group size and group type but as this represents multiple testing we adjusted the P values for false recovery rates [73]. Since, the relatively small sample sizes in this study do not provide strong statistical power, we also discuss the results when they were significant before false recovery rates corrections.

To study the effect of helpers on egg mass we fitted the random factor ´nest chamber´ in order to take into account the non-independence of eggs from a same clutch. The ´nest chamber´ factor was nested in a ´colony´ random factor as we had several nests from each colony. We fitted group size (from 2 to 6 individuals) or group type as a dependant variable and investigated both linear and quadratic relationships for group size. We also added the following co-variables that may affect egg mass in this species [74] and others [7,8]: laying order (1 to 4); clutch size (2-4); colony size (10-128 individuals); the number of previous breeding attempts in the season (22 eggs were collected during the first breeding attempt and 12 during the second) and rainfall over the 18 days before laying (13.9-94.5mm). The total rainfall over this period significantly correlated with the number of active clutches (i.e. clutches with eggs or chicks), the number of clutches laid per day and clutch size (Spearman rank correlations, respectively $\rho = 0.876$; $\rho = 0.409$; $\rho = 0.476$ all $P < 1.2\ 10^{-4}$)

For the analyses of yolk mass and contents (i.e. carotenoids and hormones) we included the same terms as above, except ´nest chamber´ and ´laying order´ (since we collected only the first egg of each clutch). In addition, we included ´egg mass of the first egg´ as a fixed term for the analyses of the yolk mass in order to know if the relative investment in yolk differed depending on the presence/number of helpers. As egg and yolk mass of the first eggs collected were not significantly correlated and as both are different indicators of female investment and offspring quality that may be influenced by the mother’s circulating hormones, even independently [75], we included both egg and yolk mass as fixed terms in the analyses of yolk contents. However, as the absolute allocation in yolk mass and contents may be more relevant for offspring fitness, we also present the results without taking into account egg and yolk mass when significant.

In order to investigate the effect of breeding group size and type on fledging mass we used ´nest chamber´ nested in ´colony´ as random factors and egg mass, the number of hatchlings, hatching order, colony size, the number of breeding attempts and the rain during the 18 days before laying as fixed factors.

## RESULTS

### *Egg mass*

Egg mass varied between 1.932g and 3.050g and decreased significantly with the presence of helpers (group type: $F_{1,23} = 4.73$, $P = 0.040$, estimate = $-0.12 \pm 0.055$) and helper number (with a linear average decrease of 1.67% per additional helper; Table 2, Fig. 1). In addition, there was a laying order effect, second eggs being significantly heavier than first ones. There was no effect of clutch size, the number of clutches attempted before, colony size or rainfall (Table 2).

### *Yolk mass*

The yolk mass of the first egg, ranged between 0.541g and 0.798g. It varied in a negative quadratic way with the number of helpers, although this remained below significance (Table 3; Fig. 2; controlling for egg mass). The effect of the number of helpers was not significant without controlling for egg mass ($F_{1,22} = 1.84$, $P = 0.19$). Yolk mass was not affected by group type ($F_{1,22} = 0.84$, $P = 0.37$), clutch size, the number of clutches attempted before, colony size or rainfall, but increased with egg mass in a linear manner when taking into account the effect of the number of helpers ($F_{1,21} = 4.428$, $P = 0.048$, estimate = $0.138 \pm 0.066$) (Table 3).

### *Yolk carotenoids*

The concentration of carotenoids varied between $44.69\mu g.g^{-1}$ and $118.80\mu g.g^{-1}$. It was not affected by the number of helpers (linear term, $F_{1,22} = 0.081$ , $P = 0.78$; quadratic term, $F_{1,22} = 0.131$, $P = 0.72$), group type (with or without helpers; $F_{1,22} = 0.27\ 10^{-3}$, $P = 0.96$), or any other variable tested (i.e. egg mass, yolk mass, breeding attempts, colony size and rainfall, all $P > 0.27$). There was a tendency for carotenoids to decrease with clutch size, but this was only marginally significant ($F_{1,23}$ = 4.009, P = 0.057, estimate = -13.782 ± 6.883).

### *Yolk androgens*

Yolk testosterone concentration varied between 3.40pg.mg$^{-1}$and 7.37pg.mg$^{-1}$. It did not vary linearly with the number of helpers ($F_{1,22}$ = 2.03, P = 0.17) but was affected by breeding group type (Table 4 ) with a 13.58% reduction in testosterone for eggs laid by females in groups with helpers when compared to those in pairs (Fig. 3). Testosterone concentration tended to decrease with clutch size but this was below the significance threshold (Table 4). There were no effects of egg mass, yolk mass, the number of breeding attempts, colony size and rainfall (Table 4).

Yolk A4 concentration varied between 5.89pg.mg$^{-1}$and 13.32pg.mg$^{-1}$. There was a non-significant tendency for A4 to decrease with the number of helpers ($F_{1,22}$ = -1.79, P = 0.087, estimate = -0.38 ± 0.21) and to be lower for pairs with helpers than for pairs alone (with a 7.32% reduction in testosterone for eggs laid by females in groups with helpers when compared to those in pairs (table 5, Fig 4). Yolk A4 concentration also decreased with yolk mass (Table 5); A4 concentrations were higher for second clutches attempted than for the first ones (Table 5). No significant effects were found for the other variables tested (i.e. egg mass, clutch size, colony size and rainfall, all P = 0.38). Yolk A4 concentrations also tended to be lower for pairs with helpers than for pairs without controlling for yolk mass but this tendency was not significant ($F_{1,22}$ = 2.990, P = 0.098, estimate = -1.17 ± 0.68).

### *Yolk corticosterone*

Yolk corticosterone concentration varied between 7.31pg.mg$^{-1}$and 21.54pg.mg$^{-1}$. It did not vary with the number of helpers ($F_{1,22}$ = 2.64, P = 0.12) but tended to be lower for the first eggs of females with helpers than for females in pairs (Table 6) with an average reduction of 17.26% (Fig. 4). Corticosterone concentration also decreased with egg mass but no significant effects were found for yolk mass, clutch size, the number of breeding attempts, colony size and rainfall (Table 6). Yolk corticosterone concentration did not vary significantly between group type when egg mass was not in the statistical model ($F_{1,23} = 2.30$, $P = 0.14$).

### *Effects on fledging mass*

There was no effect of group type ($F_{1,18} = 0.11$, $P = 0.75$) or group size on fledging mass (Table 7), regardless of whether egg size was controlled for or not (see Figure S2 on supplementary electronic materials). The mass of 17 days old chicks decreased with clutch size and hatching order (Table 7). Fledglings were also heavier when coming from heavier eggs (Table 7; Fig 5). The fledging mass was not affected by colony size, the number of breeding attempts or rainfall (Table 7).

## DISCUSSION

Concurring with four previous studies on other cooperatively breeding species ([47,48,50,51] but see [52]), we found a decrease in sociable weaver egg mass as the breeding group size increased. In addition, we found a negative effect of helper presence on hormonal contents, with lower androgens and corticosterone concentrations in the presence of helpers. To our knowledge, this is the first study to indicate differential maternal allocation of egg hormones in relation to helpers' presence in an egg-laying species. Although this is a correlative study and experimentation is needed to fully test causality, these results suggest that the environment created by the presence of helpers can influence maternal allocation and offspring phenotypes.

### *Maternal investment in egg size and helper effects*

Maternal load lightening at the egg stage has been found in a broad range of species when a good offspring environment could be anticipated [12,13,39,40]. In cooperatively breeding species, when the breeding groups are already formed before egg laying or live birth, the additional care by the helpers represents a good environment for offspring and should allow females to invest less in their eggs or embryos. This is expected particularly in long-lived cooperatively breeding species where females are likely to keep their dominance status over several reproductive events [41]. In agreement with the previous studies on carrion crows *Corvus corone* [50] and superb fairy-wrens *Malurus cyaneus* [48], sociable weaver females were found to lay lighter eggs as the size of their breeding group increased. In this species egg mass decreased by, on average, 1.67% per additional helper. Egg production is known to be costly in birds ([76,77] see also [78,79]). Sociable weavers have protracted breeding seasons, which may last up to nine months under conditions of good rainfall, and have very high nest predation rates (ca. 70% on our study site). As a result, females usually lay several clutches a year (up to 9 clutches have been recorded in a single season; [54]). Under these circumstances, females assisted by helpers are likely to save a considerable amount of energy by producing lighter eggs. Interestingly, this reduction in female investment does not come with a cost for nestlings since we did not find any helper effect on fledging mass, despite a positive relationship between egg and fledging mass. As helpers provide additional food to the brood [54], this suggests that the helpers may compensate for the lower female investment in eggs. However, here we did not find any effect of helpers on fledgling mass even when correcting for egg mass. This might have been a consequence of removing one egg from the brood for analyses of egg contents, since by doing so we artificially reduced the cost of rearing offspring. In addition, the statistical power to detect this relationship might have been limited due to the reduced sample size at fledging, which was a result of nest predation. Additional work is currently underway to test whether the helpers have a compensatory effect on this species.

The energetic savings suggested here may allow females to survive better and therefore increase the number of potential future breeding attempts. Preliminary results suggest an increase in survival for sociable weaver females that have been helped to raise their offspring ([80]; Paquet, Grégoire, Deville, Doutrelant, Covas , in prep). This would indicate that the benefits of helping in sociable weavers may be greater than estimated by previous analyses on the effect of helpers on reproduction which showed that the effect of helpers is mostly positive under adverse conditions [54].

### ***Maternal investment in egg content***

Despite the negative effect of breeding group size on egg mass we did not find the same pattern for the first eggs' yolk mass. We only found a tendency for a negative quadratic effect of group size on relative yolk mass and did not found any effect of helpers on yolk mass when egg size is not taken into account. As eggs are only constituted by eggshell, yolk and albumen, this suggests that the reduction in egg mass according to group size is mostly due to a reduction in albumen mass. For altricial species, like sociable weavers, eggs are predominantly constituted by albumen [81] which contains on average 71% of the eggs' proteins [82]. Accordingly, in our study, yolk mass represented on average only 26% of the weight of an egg, the rest being albumen (and eggshell). An energetic model based on Audouin's Gull's *Ichthyaetus audouinii* three-egg clutches showed that, for egg formation, the energy-demand peak takes place during the formation of the first egg's albumen when yolk formation is already completed but females still have to complete forming the yolk of the two following eggs [83]. Therefore, the best way for females to save energy during egg formation is to reduce investment during this peak which can occur by reducing the amount of albumen for the first egg and yolk deposition for second and third eggs [83]. This model explains why first eggs' yolk mass is much less variable than yolk mass of second or third eggs which is also the case in sociable weavers [74]. Hence, while the reduction of first egg mass with group size seems to result in a reduction of the albumen mass, this may differ for the following eggs in the laying sequence.

This strategy of saving energy by reducing investment in albumen (or, to a lesser extent, eggshell) of the first egg might explain why we found no effect of group size on the amount of yolk carotenoids, which are costly nutrients. Moreover, the effect of helpers may be more complex than a simple expected reduction on carotenoid concentrations. We found that eggs were lighter as the breeding group size increased but on the other hand small eggs may experience a greater oxidative stress and then need more antioxidants like carotenoids to counter it [84]

### ***Hormones in presence/absence of helpers***

We found a clear indication of different levels of hormones in relation to helper presence. Females laid first eggs with lower yolk androgen concentrations (significantly lower testosterone and a tendency for lower A4, which was significant before correction for false recovery rates, for both relative and absolute quantities). Corticosterone concentrations are also lower (marginally significant after correction for false recovery rates), but only when we correct for egg mass. Corticosterone is a stress hormone that may be transferred passively [23] and has been found to correlate positively with energy expenditure associated with social status [61]. Hence, females experiencing more stressful or dangerous environments may deposit more corticosterone in eggs [26,31]. In the cooperatively breeding red-cockaded woodpecker breeding males, but not females, exhibit lower baseline corticosterone levels when assisted by two or more helpers [85]. This was suggested to arise from a reduced workload in the presence of helpers in males at a higher level than females [86]. In sociable weavers both parents reduce their feeding rate in the presence of helpers [54] and in addition helpers are involved in nest chamber defence, nest building and usually roost in the family chamber (Paquet, Covas, Doutrelant, per obs), which may have thermoregulatory benefits [87]. Hence, dominant females may be less stressed when breeding in groups with helpers, which in turn may result in lower circulating corticosterone levels and hence less corticosterone transferred into the eggs. This hypothesis, however, remains to be tested. The higher corticosterone levels transferred in eggs laid by females breeding in pairs may have detrimental consequences for offspring, as too high corticosterone levels were found to reduce nestling growth and begging ability ([25,27,30] but see [32]). However, as we did not find a significant lower corticosterone concentration without controlling for egg mass, chicks raised with and without helpers may not experience different circulating corticosterone levels.

The higher level of androgens in eggs produced by females breeding without helpers can be explained by at least three non-exclusive explanations. First, egg androgen levels may be influenced by female breeding condition and social environment. For example in house sparrows *Passer domesticus* the social environment experienced by the breeding female was affected by breeding density and female response to an intruder and this lead to increased yolk testosterone concentration [37]. In sociable weavers social interactions might also play a role if females in pairs are more often involved directly in aggressive interactions. Second, higher allocation of androgens and specifically, testosterone to eggs when breeding without helpers may be a female strategy to manipulate offspring metabolism and begging behaviour. Increasing testosterone levels in eggs has been shown to increase begging behavior and nestling growth [23,28,88]. Male sociable weavers bring more food to the nestlings than females [89], and thus, in the absence of helpers, this may contribute to enhance growth as chicks may beg more actively and have higher metabolic activity. In addition, higher testosterone levels may be important to produce more competitive nestlings, since they receive less food when raised by pairs alone [89], yet brood sizes are similar for pairs and groups. Conversely, in the presence of helpers, lower androgens levels should avoid the costs of rearing offspring that beg very actively and/or have enhanced metabolic activity, thus representing an additional way of saving energy [90]. As parents and helpers are likely to respond individually to the begging rate of the chicks [91], the lower testosterone levels in eggs with helpers may be responsible for the load lightening of the feeders. Finally, higher androgen levels could be a strategy to produce more competitive fledglings. For instance, higher concentrations of yolk A4 have been related to the production of more competitive phenotypes in communally breeding and colonial systems [71,92]. In the present study, A4 tended to be higher in nests without helpers, even if this was not significant. This could increase competitive ability of offspring, increasing their chances to stay in the natal colony and therefore act as helpers in subsequent years. In groups with helpers, competition for staying in the natal groups might be higher when the older, and presumably dominant, helpers are around [93,94]. Under these circumstances, lower yolk androgens could be beneficial by avoiding conflicts in the group. Further study is needed to test these different possibilities and to relate variation in hormone levels reported here to hormonal, behavioural and fitness variations in nestlings and fledglings.

Here for ethical and practical reasons (i.e. in order to determine group size and composition), we only collected the first egg laid. In order to know if the allocation patterns found here for the first eggs are representative of the female allocation for the whole clutch, a next step would be to collect complete clutches and investigate both yolk and albumen mass and contents in relation to the laying order and helper numbers. A previous study has found variation in yolk mass and carotenoids but not in yolk androgens contents in relation to laying order [95]. Sociable weaver nestlings hatch asynchronously and hence the first-hatched nestling has a higher chance of surviving, which could lead to a compensatory strategy by females. However, it is currently unknown whether this interacts with the presence of helpers. Moreover, the experimental manipulation of the number of helpers before laying remains the only way to fully test the causal effect of helpers on maternal allocation in eggs. As we did not manipulate the number of helpers before laying we cannot completely exclude the confounding factors that may explain the lower investment in eggs in presence of helpers found here. First, ´good quality´ females could produce more offspring that may become helpers in future broods. However, this confounding effect is unlikely to explain our results since, unlike what was found here, egg mass is expected to be positively correlated with female condition [8]. A second alternative explanation could be that females in groups experience more competition for resources in presence of helpers. This possibility is also unlikely as sociable weavers are non-territorial and the whole colony usually forages communally (authors personal observations; [66]). A competition effect is more likely to occur at the colony level but we controlled for colony identity as a random factor and also included the size of the colony as a covariate in our models and did not find any effects of these variables on egg mass.

In conclusion, our results suggest the existence of differential maternal investment in egg mass and show for the first time that hormonal contents of eggs vary in relation to helper presence in a cooperatively breeding species. These results have two important implications. First, they confirm that modulation of egg mass might be an additional mechanism to consider under the load lighting hypothesis [46] which suggests that helpers are beneficial because they allow parents to save energy for further reproductions. Second, given that the conditions experienced during the developmental stages may exert lifelong influences on adult phenotypes and health [96] the influence of helpers-at-the-nest in cooperative breeders is likely to go beyond the fledgling or independence stages and the effect commonly found on fledging condition or survival. This long-term influence has important implications for understanding the fitness gains of helping. However, the fields of maternal effects and cooperative breeding have so far remained largely apart, and these consequences have not been studied yet. The study of maternal allocation in cooperatively breeding species is therefore a promising research avenue that has the potential to help understanding the high inter- and intra-specific variability on the effects of helpers on key parameters such as reproductive output, survival, dispersal strategies and lifetime reproductive success in cooperative breeders.

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## TABLES

**Table 1.** Pearson correlations and associated p-values between egg mass and components of the first laid eggs.

| | yolk mass | carotenoids | Corticosterone | testosterone | androstenedione |
|---|---|---|---|---|---|
| egg mass | 0.27 (p=0.13) | 0.02 (p=0.91) | -0.21 (p=0.23) | 0.15 (p=0.38) | 0.01 (p=0.93) |
| yolk mass | | -0.24 (p=0.16) | -0.05 p=0.78) | -0.11 (p=0.56) | **-0.62 (p=1 $10^{-4}$)** |
| carotenoids | | | 0.11 (p=0.55) | 0.15 (p=0.15) | 0.18 (p=0.32) |
| corticosterone | | | | *0.33 (p=0.054)* | 0.13 (p=0.45) |
| testosterone | | | | | **0.46 (p=0.006)** |

**Table 2.** Factors affecting egg mass. Estimates and SE are given for significant explanatory terms included in the minimal model (bold characters). 'Group size' referred to the number of individuals that were feeding a given clutch.

| **Explanatory terms** | **F** | **d.f.** | **P** | **Estimate** | **SE** |
|---|---|---|---|---|---|
| **Intercept** | | | | **2.666** | **0.082** |
| **Group size** | **4.82** | **1,23** | **0.04** | **-0.048** | **0.022** |
| **Laying order** | **4,073** | **3,64** | **0.0104** | | |
| **2** | | | | **0.083** | **0.024** |
| **3** | | | | **0.036** | **0.025** |
| **4** | | | | **-0.005** | **0.058** |
| Group size$^2$ | 0.87 | 1.22 | 0.36 | | |
| Colony size | 2.51 | 1,8 | 0.15 | | |
| Clutch size | 0.36 | 1,22 | 0.55 | | |
| Breeding attempts | 0.22 | 1,22 | 0.64 | | |
| Rainfall | 0.15 | 1,22 | 0.70 | | |

**Table 3.** Factors affecting yolk mass. Estimates and SE are given for significant (bold characters) and nearly significant (italic characters) explanatory terms included in the minimal model. 'Group size' referred to the number of individuals that were feeding a given clutch.

| **Explanatory terms** | **F** | **d.f.** | **P** | **Estimate** | **SE** |
|---|---|---|---|---|---|
| Intercept | | | | 0.133 | 0.207 |
| ***Group size$^2$*** | ***4.095*** | ***1,21*** | ***0.0559*** | ***-0.014*** | ***0.007*** |
| ***Group size*** | ***3.938*** | ***1,21*** | ***0.0604*** | ***0.103*** | ***0.052*** |
| **Egg mass** | **4.428** | **1,21** | **0.0476** | **0.138** | **0.066** |
| Clutch size | 0.002 | 1,20 | 0.96 | | |
| Clutches attempted before | 0.524 | 1,20 | 0.48 | | |
| Colony size | 0.151 | 1,8 | 0.71 | | |
| Rainfall | 0.587 | 1,20 | 0.45 | | |

**Table 4.** Factors affecting yolk testosterone concentrations. Estimates and SE are given for significant (bold characters) and nearly significant (italic characters) explanatory terms included in the minimal model. 'Group type' referred to the presence (H)/absence of helpers feeding a given clutch.

| **Explanatory terms** | **F** | **d.f.** | **P** | **Estimate** | **SE** |
|---|---|---|---|---|---|
| **Intercept** | | | | **6,426** | **0,958** |
| **Group type (H)** | **6,396** | **22** | **0,0382** | **-0,71** | **0,281** |
| ***Clutch size*** | ***3,337*** | ***22*** | ***0,0813*** | ***-0,562*** | ***0,308*** |
| Egg mass | 0,189 | 21 | 0,67 | | |
| Yolk mass | 0,491 | 21 | 0,49 | | |
| Clutches attempted before | 0,187 | 21 | 0,67 | | |
| Colony size | 0,874 | 8 | 0,38 | | |
| Rainfall | 0,316 | 21 | 0,58 | | |

**Table 5.** Factors affecting yolk androstenedione concentrations. Estimates and SE are given for significant (bold characters) and nearly significant (italic characters) explanatory terms included in the minimal model.

| **Explanatory terms** | **F** | **d.f.** | **P** | **Estimate** | **SE** |
|---|---|---|---|---|---|
| **Intercept** | | | | 22,21 | 2,691 |
| ***Group type (H)*** | ***4,985*** | ***21*** | ***0,0732*** | ***-1,17*** | ***0,524*** |
| **Clutches attempted before** | **5,520** | **21** | **0,0287** | **1,285** | **0,547** |
| **Yolk mass** | **21,519** | **21** | **0,0001** | **-18,983** | **4,092** |
| Egg mass | 1,082 | 20 | 0,31 | | |
| Clutch size | 1,075 | 20 | 0,31 | | |
| Colony size | 0,007 | 8 | 0,94 | | |
| Rainfall | 0,604 | 20 | 0,45 | | |

**Table 6.** Factors affecting yolk corticosterone concentrations. Estimates and SE are given for significant (bold characters) and nearly significant (italic characters) explanatory terms included in the minimal model.

| **Explanatory terms** | **F** | **d.f.** | **P** | **Estimate** | **SE** |
|---|---|---|---|---|---|
| **Intercept** | | | **0,0019** | **37,461** | **10,656** |
| ***Group type (H)*** | ***5,621*** | ***22*** | ***0,0538*** | ***-3,330*** | ***1,405*** |
| **Egg mass** | **4,749** | **22** | **0,0403** | **-8,987** | **4,124** |
| Yolk mass | 0,067 | 21 | 0,80 | | |
| Clutches attempted before | 0,055 | 21 | 0,82 | | |
| Clutch size | 1,056 | 21 | 0,32 | | |
| Colony size | 1,178 | 8 | 0,31 | | |
| Rainfall | 0,018 | 21 | 0,90 | | |

**Table 7.** Factors affecting fledgling mass. Estimates and SE are given for significant explanatory terms included in the minimal model (bold characters). 'Group size' referred to the number of individuals that were feeding a given clutch.

| **Explanatory terms** | **F** | **d.f.** | **P** | **Estimate** | **SE** |
|---|---|---|---|---|---|
| **Intercept** | | | | **21,673** | **4,690** |
| **Egg mass** | **12,515** | **16** | **0,0027** | **5,659** | **1,600** |
| **Hatchling size** | **13,241** | **19** | **0,0017** | **-2,868** | **0,788** |
| **Hatchling order** | **10,678** | **16** | **0,0048** | **-1,500** | **0,459** |
| Group size | 0,283 | 18 | 0,60 | | |
| Group size2 | 0,298 | 18 | 0,59 | | |
| Clutches attempted before | 0,009 | 18 | 0,93 | | |
| Colony size | 0,087 | 6 | 0,78 | | |
| Rainfall | 0,066 | 18 | 0,80 | | |

## FIGURES

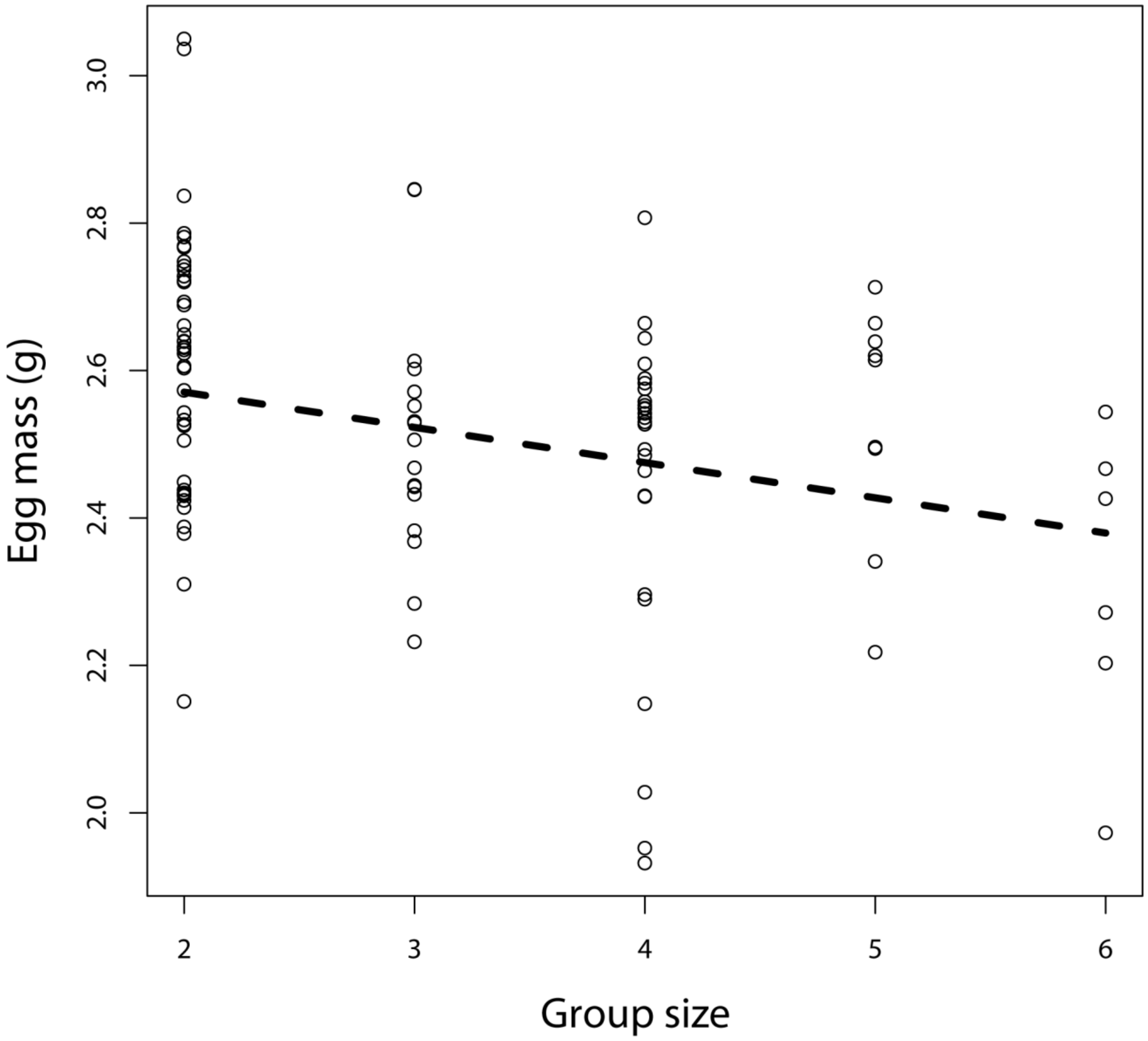

**Figure 1.** Egg mass decreased in relation to breeding group size. The line indicates the predicted values.

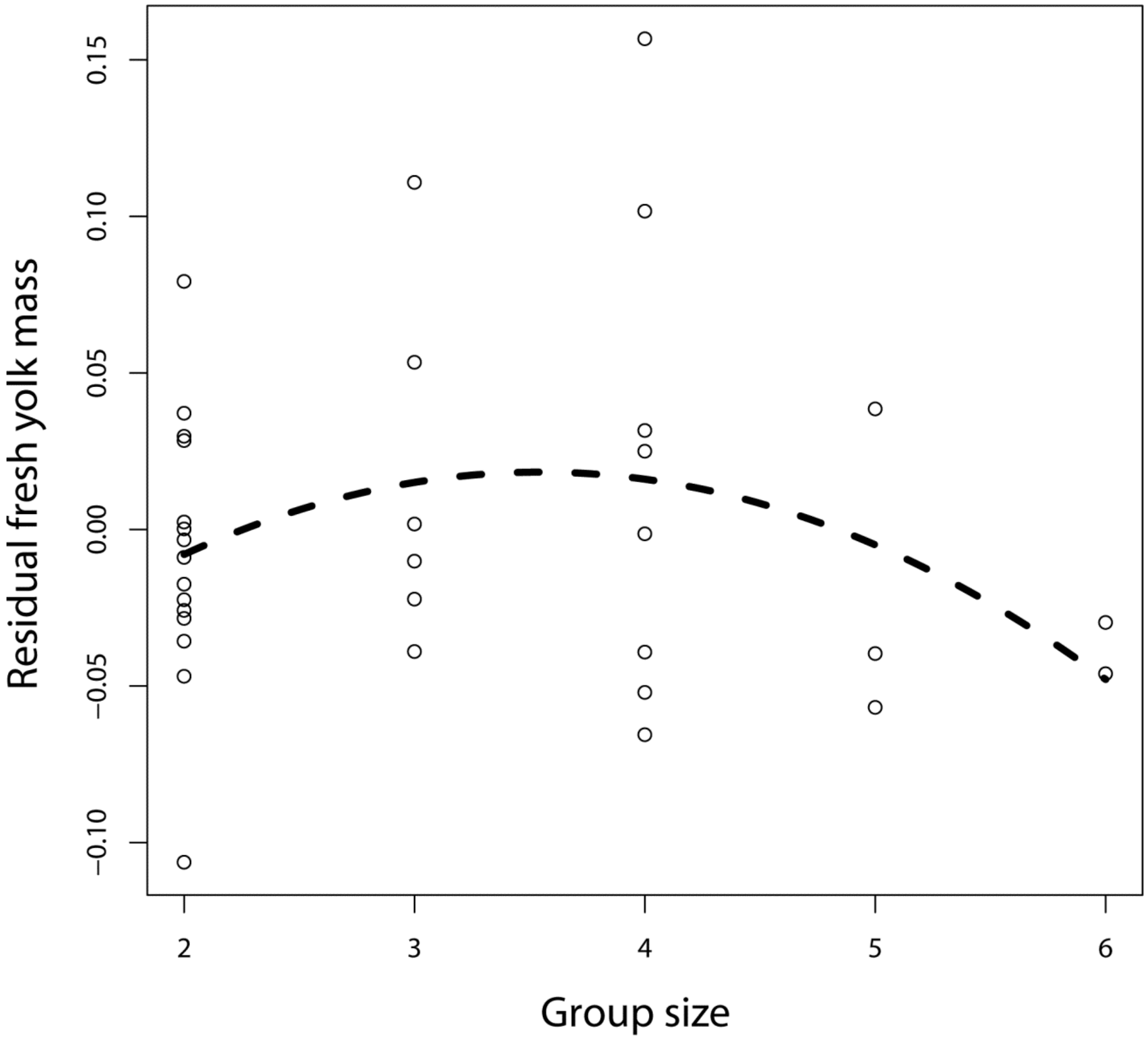

**Figure 2.** Relationship between fresh yolk mass of first laid eggs (corrected for egg mass) and breeding group size. Dashed line indicates predicted values from the linear mixed-effects model.

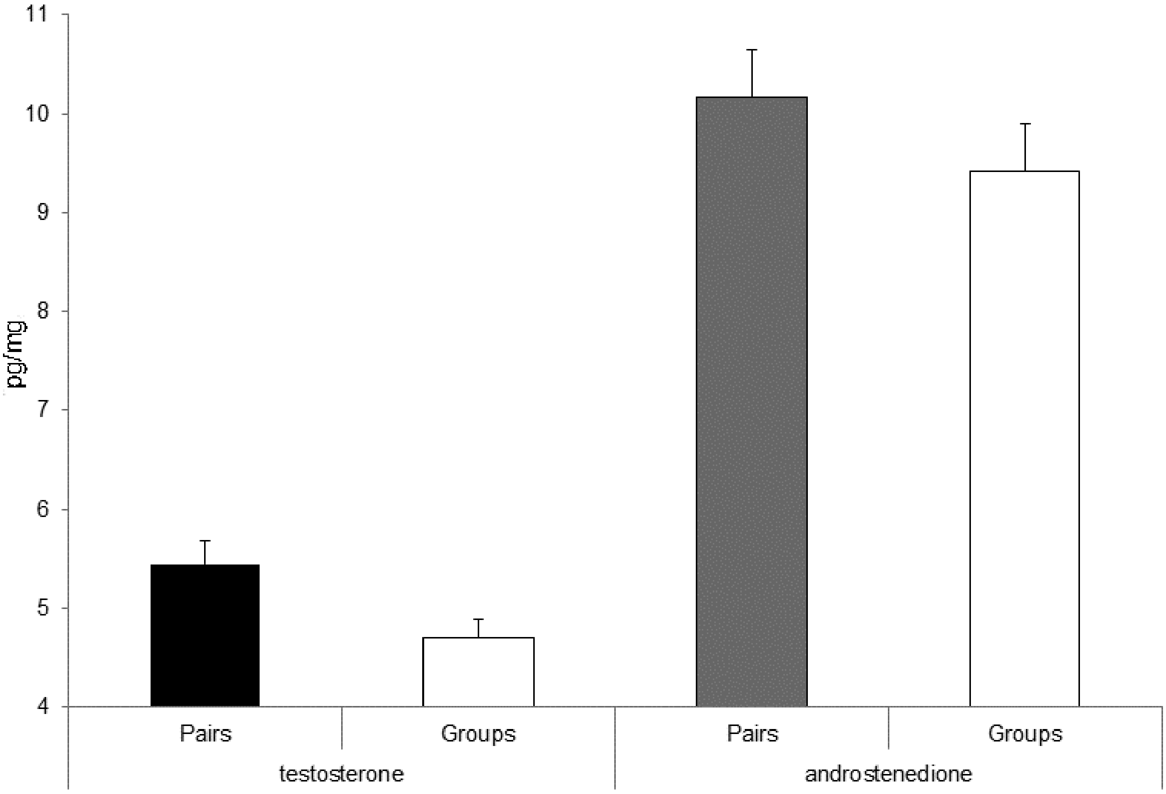

**Figure 3.** First eggs yolk androgen levels were lower for clutches raised with helpers than for clutches raised in pairs (means and SE are shown). This was significant for testosterone but only marginally for androstenedione (A4).

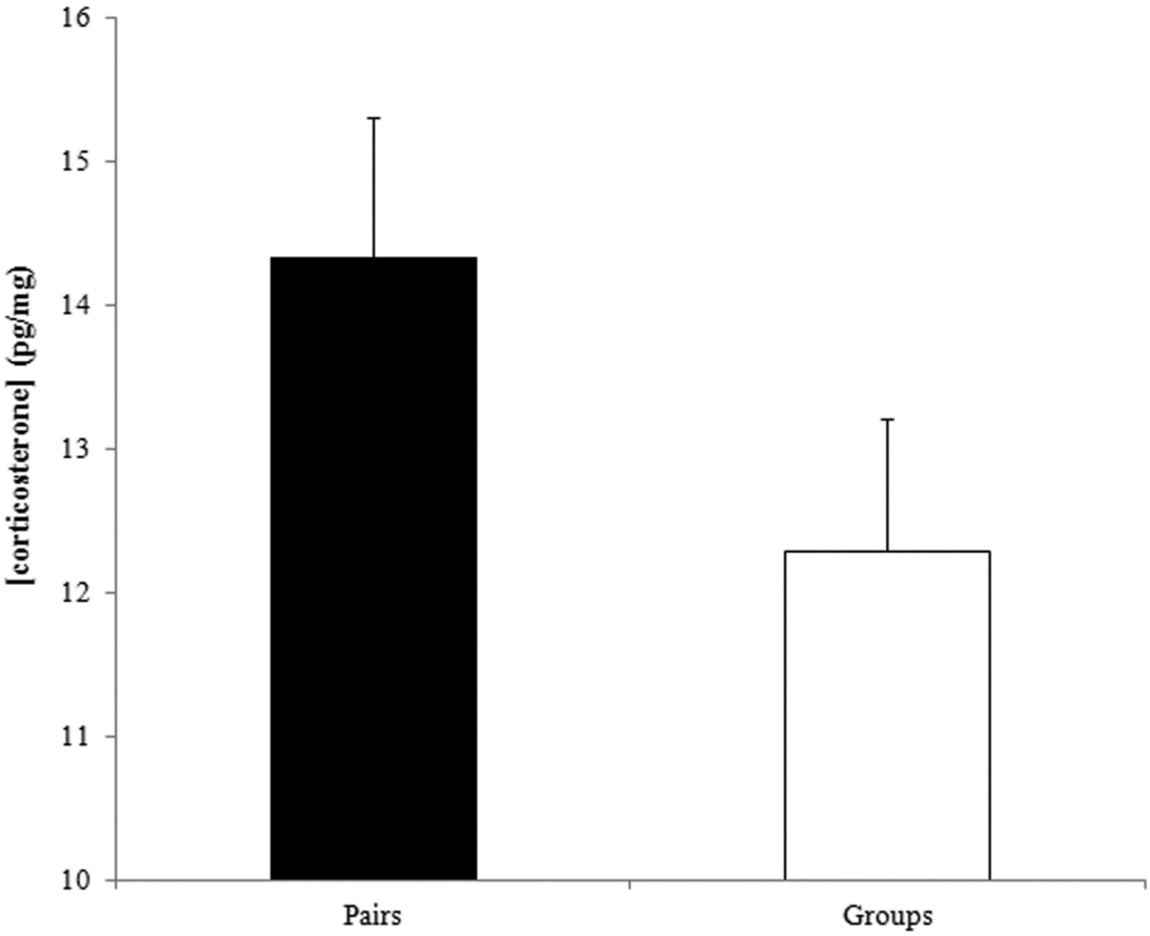

**Figure 4.** There was a significant decrease in first eggs yolk corticosterone levels (means and SE are shown) between clutches raised in pairs and clutches raised with helpers.

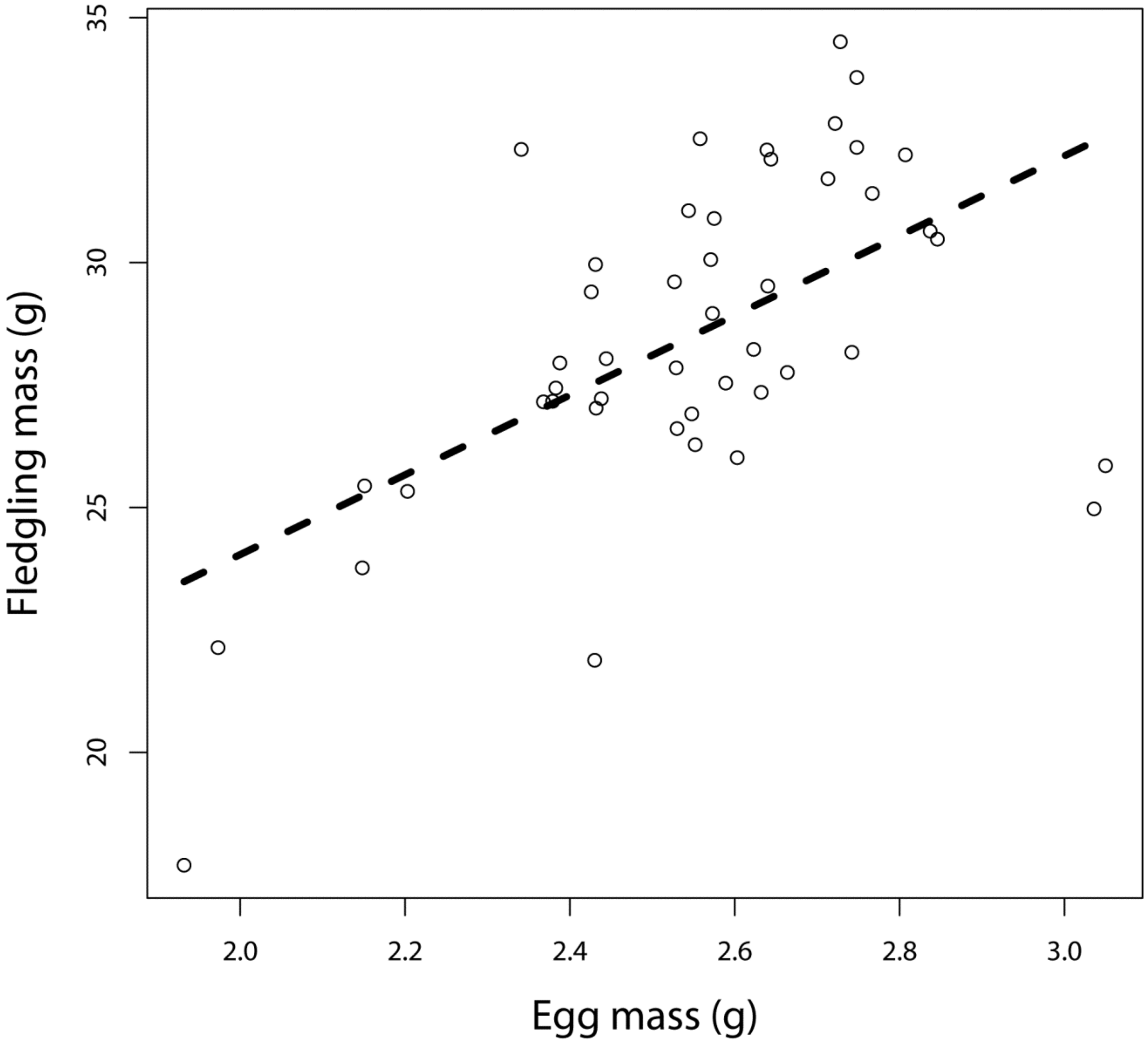

**Figure 5.** Fledging mass significantly increased in relation to egg mass.

# *Manuscript 2: Positive effect of communal roosting on nest temperature during winter and its potential impacts on breeding output in a cooperative breeder.*

*This manuscript in preparation will be completed with additional data from the current breeding season*

# Positive effect of communal roosting on nest temperature during winter and its potential impacts on breeding output in a cooperative breeder.

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**Running title**: thermoregulatory benefits of communal roosting in a cooperative breeder

## ABSTRACT

Physiological, morphological and behavioral adaptations have evolved to help coping with harsh thermal environments that can have strongly negative consequences on individual energetic expenses and thus ultimately on individual fitness. Communal huddling when temperatures are low is a major behavioral adaptation to harsh environment. Many cooperative breeders live in harsh or unpredictable environments and huddle together but whether it could represent an additional benefit of helpers have been overlooked. Also whether communal huddling has consequences on reproduction is actually unknown. We studied potential benefits of communal roosting in the sociable weaver *Philetairus socius* by using small temperature recorders and cameras. We found that the number of birds roosting together is strongly positively associated with the ambient nest temperature at night. Particularly, when calculating the theoretical temperature below which birds expense high energy in thermoregulation, it appears that birds spent less time below this critical temperature when roosting with more birds. Our data also show that roosting group size before breeding and breeding group size are positively correlated indicating a potential additional benefit of helpers on parents' fitness. Finally, preliminary data suggest a potential effect of communal roosting on female investment in reproduction (laying date and egg mass). Taken together these results suggest that roosting might have important proximal and evolutionary consequences that still deserve to be fully understand.

***Keywords:*** *communal roosting, huddling, thermoregulation, cooperative breeding, reproduction.*

## INTRODUCTION

Environmental variations such as temperature levels and fluctuations have strong influences on fitness acting on both survival and reproductive success (Newton and Brockie 1998). Hence, physiological, morphological and behavioral adaptations have evolved that help coping with harsh thermal environments, or even improve temperature conditions and reduce temperature fluctuations. For example in mammals and birds, endothermy allows a fine tuning of metabolic activities with a relative independence from the environmental temperature (Clarke and Pörtner 2010). However, maintaining a constant high body temperature is costly, especially under extreme temperatures, and considerable adaptations such as torpor, hibernation (Geiser 2004), nest building (Collias and Collias 1984, Hansell 2000) or huddling (Gilbert et al. 2010) enable endothermic organisms to minimize the costs of thermoregulation.

Communal huddling (i.e. roosting or nesting) is a widespread group behavior that reduces the body area exposed to cold and improves local ambient temperature with the number of individuals involved (Canals et al. 1989, Canals 1998, Gilbert et al. 2010). For example, the southern flying squirrel (*Glaucomys volans*) forms large social non-random, non kin nesting groups in winter that allow individuals to reduce winter daily energy expenditure by 26-33% (Stapp et al. 1991, Garroway et al. 2013). These energy savings are likely to affect individual fitness though survival or reproduction. Positive effects of communal huddling on survival rate have indeed been reported in several species (see Gilbert et al. 2010 for a review). By contrast, nothing is currently known about any effect of pre breeding communal huddling on endotherms reproduction (but see Rabosky et al. 2012 on a lizard species) even if ambient temperature levels and variation are known to affect reproductive output such as laying date (Schaper et al. 2012) or egg mass (Schaper and Visser 2013).

Cooperatively breeding species, where additional individuals called “helpers” assist the breeders by providing care to their offspring through extra food brought to the nest (Brown 1987, Emlen 1991), provide an interesting system to study this relationship between huddling group size, thermoregulation and reproductive investment. Communal roosting have been shown to have significant metabolic savings or reduced mass loss in numerous cooperatively breeding species such as Green Woodhoopoes *Phoeniculus purpureus* (Duplessis and Williams 1994), Speckeled Mousebirds *Colius striatus* (McKechnie and Lovegrove 2001) or Long-Tailed Tits *Aegithalos caudatus* (Hatchwell et al. 2009). Energetic saving during winter is likely to enhance individuals’ survival. On Alpine marmots (*Marmota marmota*), for instance, juvenile and adults’ survival were found to increase with hibernating group size (Arnold 1990, Allaine et al. 2000). Energetic savings might also have consequences for reproduction but potential thermoregulatory benefits of huddling group size remains poorly studied and any relationship between huddling group size and reproductive decisions has never been reported in cooperative and non-cooperative species.

It is especially interesting to study the relationships between roosting group size and temperature in a cooperatively breeding bird species as it is sometimes difficult to understand the benefits of cooperation in these species. The beneficial effects of helpers on reproduction are sometimes weak (Woxvold and Magrath 2005, Covas et al. 2008) or absent (Legge 2000, Eguchi et al. 2002) and one of the main proposed explanation for this low impact of cooperation is a parental “load lightening” corresponding to a lower chicks’ feeding (Hatchwell 1999, Kingma et al. 2010) or investment in eggs for females (Russell et al. 2007, Cockburn et al. 2008, Paquet et al. 2013) For cooperative species that use communal roosting, another potentially important benefit of helper presence may be a decrease in the costs of thermoregulation. This might either explain the differential investment in eggs (Schaper and Visser 2013) or might represent an additional mechanism by which breeders save energy, thereby contributing to increased breeder survival. Such a link between roosting and reproductive investment requires stability of the cooperative associations. Cooperatively breeding groups are usually stable within the breeding season, and pre-breeding stability, a prerequisite to explain a load lightening at the egg stage in presence of helpers, is usually assumed (Russell et al. 2007, Canestrari et al. 2011, Santos and Macedo 2011, Paquet et al. 2013) but has not been previously investigated.

We studied group stability, and the link between group size, roosting temperature, and reproduction in the sociable weaver *Philetairus socius*. This species is a colonial cooperative breeding bird that inhabits semi-arid habitats with very cold winters (the average minimum temperature in winter is 2.4°c since 1990). The sociable weavers represent an exceptional example of behavioral adaptations to face adverse thermal conditions. First sociable weavers build massive permanent communal nests that buffer against low temperatures at night during winter and against high temperatures during the day and in the summer (White et al. 1975, Bartholomew et al. 1976, van Dijk et al. 2013). Additionally, their nests contain “individual” chambers that are used not only for breeding but also for roosting during the whole year by one or several individuals (Maclean 1973b). Roosting groups’ size is likely to be linked with breeding group size and to provide thermoregulatory benefits but this has not been investigated.

Here, we firstly examine the relationship between the number of birds roosting in a chamber before the breeding season and the chambers’ ambient temperature. We were interested in determining if the differences in temperature may provide a thermoregulatory benefit for roosting birds, and hence we also investigate whether the birds were less exposed to temperatures below their theoretical lower critical temperature (Calder and King 1974) when roosting with more birds. Secondly, we studied the relationship between the pre-breeding roosting group size and the breeding group size that may strongly suggest an additional benefit of helpers' number for thermoregulation. Finally we investigate if pre-breeding roosting group size may influence reproductive success through laying date and egg mass.

## METHODS

### *Study species*

The sociable weaver is a colonial passerine endemic to the semi-arid acacia savannahs of southern Africa (Maclean 1973a, Mendelsohn and Anderson 1997). Sociable weavers build massive communal nests containing several independent nest chambers that are used for breeding and roosting throughout the year. They are facultative cooperative breeders, breeding in pairs or with up to five helpers (mean group size 2.43 birds for this study, however the proportion of birds breeding in groups varies from ca. 30-80% between years (Covas et al. 2006). Helpers are mainly offspring of one or both breeders (93%), although a small number of unrelated birds can also help (Covas et al. 2006).

### *Field methods*

Sociable weavers usually breed during the austral summer, starting between late September and mid-November. This study was conducted between 28th August and 1st October 2012. All nest chambers in our study colonies are marked with a numbered plastic tag. To measure temperature inside the nest chambers we started by placing temperature loggers (iButton®) inside the target chambers. I Buttons were placed on the top side of the chamber to record the chamber's internal ambient temperature, but avoiding direct contact with the birds roosting therein. In order to control for the outside temperature we also placed iButtons on the outside of the nest next to the chamber's entrance.

We then placed a HD video camera (HDR-CX250E, Sony) under the colonies that had temperature loggers. These cameras were placed before roosting at about 4 m from the nest entrance and focused on 1-5 chambers. The video cameras were picked up silently at least 30 min after sunset when all the birds were roosting and analyzed afterward to determine the number of birds that went roosting in each of chambers. 31 recordings were made at 10 different colonies giving a total of 32 roosting group sizes.

We used the iButtons' temperature measured during the night following the video recording (to the nearest 0.5°c, one recording every 5 minutes from 19:30 to 5:00).

To determine laying dates and the onset of reproduction, in 2012-2013 all nest chambers in these study colonies were inspected every 3 days. Two days after the first egg in a given nest was laid we weighed all eggs in that clutch to the nearest 0.001 g with a digital Pesola balance. Nest chambers were again checked the following day to weigh a possible fourth egg. We were able to determine the laying date of 27 chambers, the mean egg mass of 25 chambers and the clutch size of 23 chambers for which we previously identified the pre-breeding roosting group size.

Each individual was marked with a unique color ring combination before the breeding season (see Covas et al. (2002) for more details on the captures).To identify the individuals feeding at a given chamber and hence the number of helpers, we conducted a minimum of 1 hour daily observations for at least 3 consecutive days. Observers were situated in a hide placed at 3-5m from the colony. We were able to obtain the breeding group size for 21 chambers where we previously video recorded the number of birds roosting before reproduction.

### ***Statistical analyses***

Statistical analyses were performed using the software R (R Development Core Team, 2011). To study the potential effect of the number of birds roosting on the inside ambient temperature in the chambers we used linear models. The variable to explain was the average inside temperature and the two explanatory terms were the number of birds roosting and the average outside temperature. These two explanatory variables were not significantly correlated (Spearman rank correlation test: $\rho = 0.01$, $P = 0.96$).

In order to investigate if a higher number of birds roosting may reduce the energetic cost of thermoregulation, we calculated the theoretical lower critical temperature ($T_{lc}$) for sociable weavers using the following formulae: $T_{lc} = T_b - 6.98m^{0.266}$ (Scholander et al. 1950, Calder and King 1974). Using a body mass (m) of 27.4g (i.e. the average body mass of all birds captured this year N=420) and a body temperature ($T_b$) of 40°c we found a theoretical $T_{lc}$ of 23.16°c (below which a negative linear relationship between temperature and energetic expense should occur). We then calculated the proportion of time in the night when the inside ambient temperature was below 23°c (as the temperature was measured to the nearest 0.5°c). We then used this new variable (instead of the inside ambient temperature) as the response variable the number of birds and average outside temperature as explanatory variables.

To study the correlation between the number of birds roosting in a chamber before reproduction and the number of birds feeding at the nest during the reproduction we used a Spearman rank correlation test.

For the analyses of laying date and mean egg mass we used linear models and the following explanatory variables: roosting group size for the analysis of laying date, roosting group size and clutch size for the analyses of mean egg mass.

## RESULTS

The mean ambient temperature in roosting chambers varied from 13.96°c to 31.5°c and increased significantly with the outside temperature ($F_{1,18}$ = 84.51, P = 3.21 $10^{-8}$, estimate = 0.92±0.10) and the number of birds roosting ($F_{1,18}$ = 31.45, P = 2.54 $10^{-5}$, estimate = 2.02±0.36; Fig.1). The percentage of the night with an inside temperature below 23°c also decreased with the outside temperature ($F_{1,18}$ = 53.24, P = 8.86 $10^{-7}$, estimate = -0.07±0.01) and the number of birds roosting ($F_{1,18}$ = 11.06, P = 3.76 $10^{-3}$, estimate = -0.12±0.03, Fig.2).

The number of birds roosting prior to reproduction and the number of birds feeding during breeding were positively correlated ($\rho$ = 0.51, P = 0.016, ddl = 19; Fig.3).

The laying date was negatively associated with the number of birds roosting ($F_{1,25}$ = 7.07, P = 0.013, estimate = -6.90±2.60, Fig.4), with females laying earlier in chambers where more birds were roosting before breeding. Mean egg mass, by contrast, tended to decrease with the number of roosting birds ($F_{1,19}$ = 3.09, P = 0.095, estimate = 0.05±0.03, Fig.5) and clutch size ($F_{1,19}$ = 3.26, P = 0.087, estimate = 0.12±0.07) even if this was below significance.

## DISCUSSION

As expected we found that ambient chamber temperatures at night (corrected for the outside temperature) increased with the number of birds roosting. This is likely to be associated with energy savings as large roosting groups spent less time below the theoretical critical lower temperature level of $23^{\circ c}$. We also found that, although there were some changes between pre-breeding and breeding group these were positively correlated which confirms a certain predictability of breeding group size based on pre-breeding group size. Finally, we found that females laid earlier and tended to lay smaller eggs when breeding in chambers where more birds were roosting before breeding.

The strong relationship between the roosting group size and the inside ambient temperature at night suggests that it can be very advantageous for individuals to be part of a group. Interestingly the number of birds roosting in a chamber was not correlated with the outside temperature at night which suggests a social determination of roosting group size. These results coupled with the correlation between pre-breeding and breeding group sizes suggest a positive effect of helpers on adults' thermoregulation. Such positive effect is further supported by the results that weavers spent more time above the critical lower temperature when in larger groups. However the actual critical lower temperature has to be confirmed for weavers. It was calculated here from recognized theoretical expectations {Scholander, 1950 #34}{Calder, 1974 #33} but it might be lower than 23°c. For example on the close relative white-browed sparrow-weaver (*Plocepasser mahali*) the theoretical lower critical temperature is 21.4°c but measurements of metabolic rate showed an actual lower critical temperature of 13°c (Ferguson et al. 2002). Measuring the resting metabolic rate of sociable weavers at different temperatures could allow us to confirm and estimate the thermoregulatory benefit of communal roosting. Nonetheless, the outside temperatures experienced by the sociable weavers in winter can also be much lower than in the present study (temperatures below -5°c are relatively common while the minimal temperature recorded in the present study was 1°c).

To our knowledge, an effect of helpers on laying date has never been previously reported, although pre-breeding temperatures are known to influence laying date in many species as for instance great tits *Parus major* (Schaper et al. 2012) and, one reason being a faster gonadal growth as found for males song sparrows (*Melospiza melodia morphna*) (Perfito et al. 2005). We found that females laid earlier in chambers where pre-breeding roosting group size was higher. Indeed, females laid on average one month earlier in chambers were 6 birds were roosting compared to chambers were only one bird was roosting. The difference in laying date may allow females with helpers to have one more successful brood per year, which would contribute to a substantial increase in seasonal reproductive output. A previous study found indication that sociable weavers fledge more offspring per season when assisted by more birds, although the helpers effect on individual breeding attempts is limited (Covas et al. 2008). An earlier onset of breeding for females assisted by helpers could provide the mechanism for this effect, at least in part.

The relationship we found between laying date and roosting group size seems to be particularly due to the late laying date in the chambers where only one bird was roosting which could easily be explained by the fact that these birds still need to find a partner to breed. However, based on data of the whole breeding season, breeding groups of more than 2 birds were found to lay earlier than pairs alone (Mares et al. in prep.). Moreover, a negative relationship seem to occur between the chambers temperatures and the laying dates and this even not taking into account the chambers with one bird (see graph on supplementary material) but more data are needed to investigate this pattern.

Additionally to laying date we found a trend for a negative relation between the number of birds roosting before breeding and the average egg mass of the first laid clutches. This trend is in accordance with a previous result showing that sociable weaver females lay smaller eggs when breeding group size increases (Paquet et al. 2013). The lower investment in eggs in presence of helpers may be explained by a positive effect of egg mass on offspring fitness only under less favorable conditions (i.e. without helpers) (Fox et al. 1997, Christians 2002) and by a compensation thanks to the additional food provided by helpers (Russell et al. 2007). This implies that females can predict the future presence of helpers, and the results presented here show that the number of birds roosting before breeding and the numbers of birds feeding the chicks during breeding were positively correlated.

A better sample size is crucially needed for a better understanding of an effect of roosting temperature on reproductive output but a way through which females could adjust their egg mass according to the number of helpers may be the response to the ambient chamber temperature. For example, great tits lay bigger eggs under lower controlled temperatures when fed ad libitum (Schaper and Visser 2013). Interestingly not only sociable weavers but also carrion crows, superb fairy-wrens and even *Neolamprologus pulcher*, a cooperatively breeding cichlid, can roost or rest communally before breeding (Warham 1957, Wilmore 1979, Taborsky and Limberger 1981) and these species were all found to lay smaller eggs when assisted by helpers (Russell et al. 2007, Taborsky et al. 2007, Canestrari et al. 2011). Roosting or resting group's temperatures could be a proximal mechanism contributing to explain differential allocation in eggs according to helpers' presence. This relationship could be confounded by several factors; however, manipulating pre-breeding roosting temperature would be an easy way to test this hypothesis.

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# FIGURES

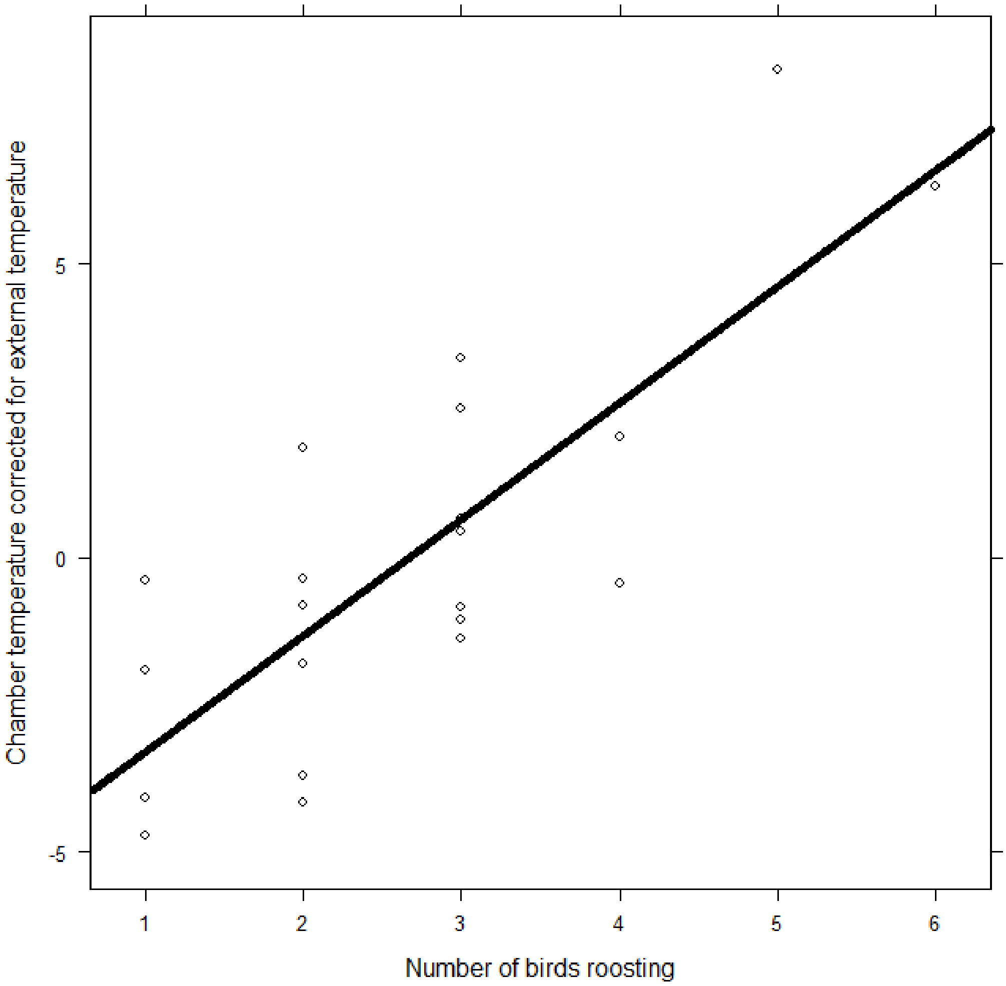


**Figure 2.** Relation between the residual mean ambient night chamber temperatures (i.e. controlled for the outside temperature) and the number of birds roosting.

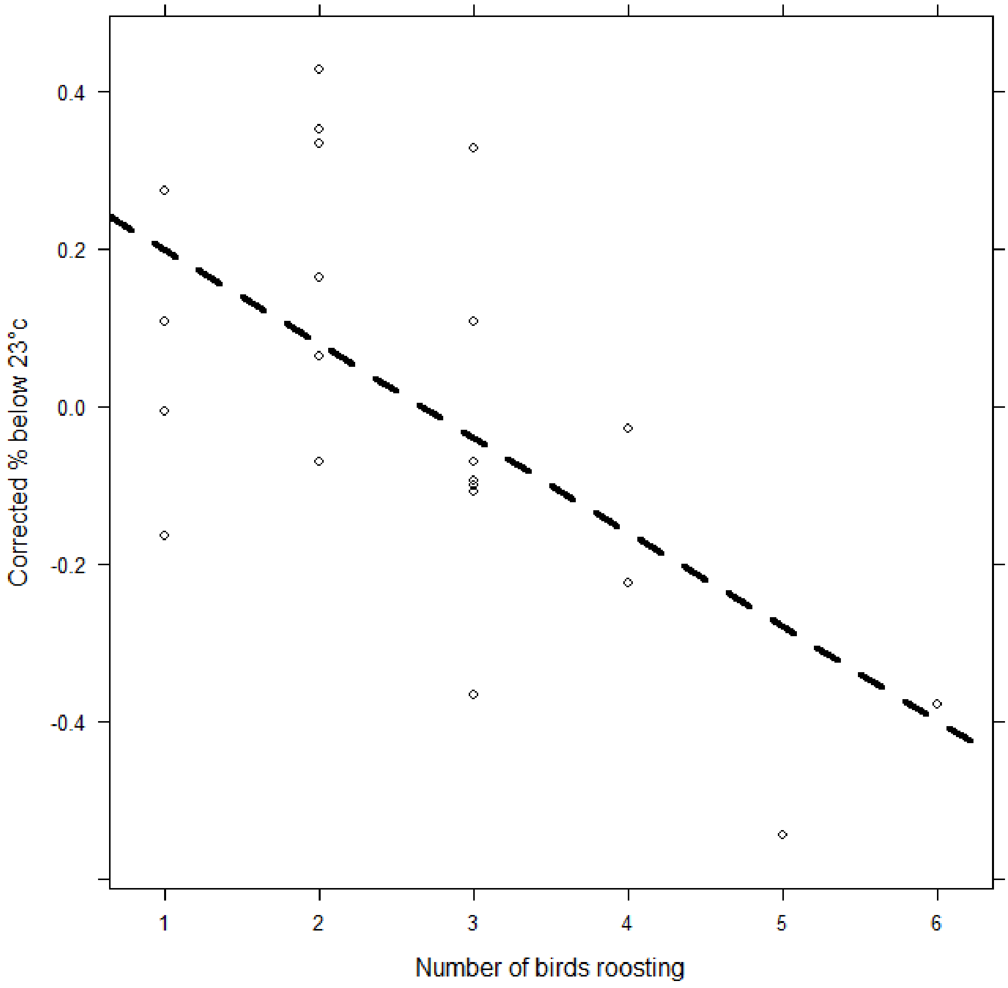


**Figure 3.** Percentage of the time when night ambient temperature in chambers was below 23°c (corrected for the outside temperature) in relation with the number of birds roosting.

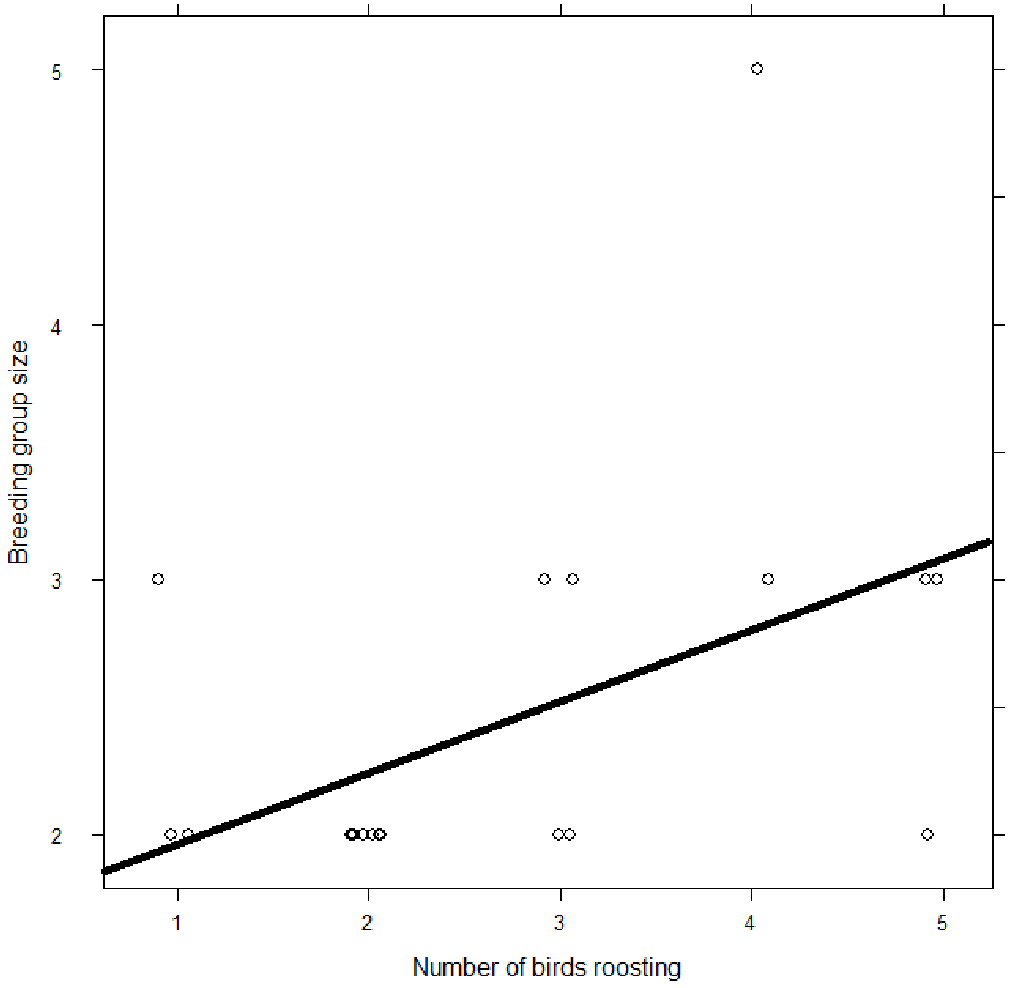


**Figure 4.** Positive correlation between the pre-breeding roosting group size and the breeding group size.

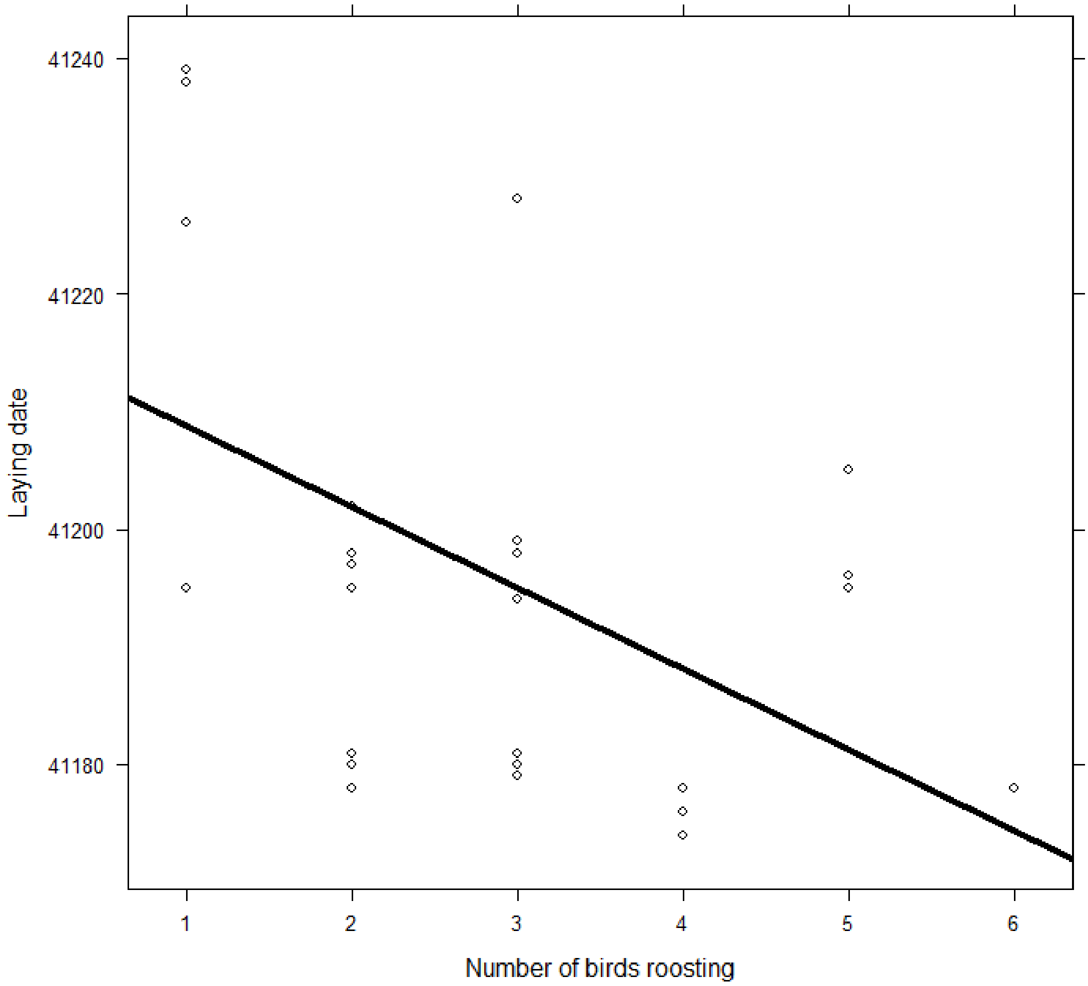


**Figure 5.** Negative relationship between the first laying dates and the number of birds roosting in chambers.

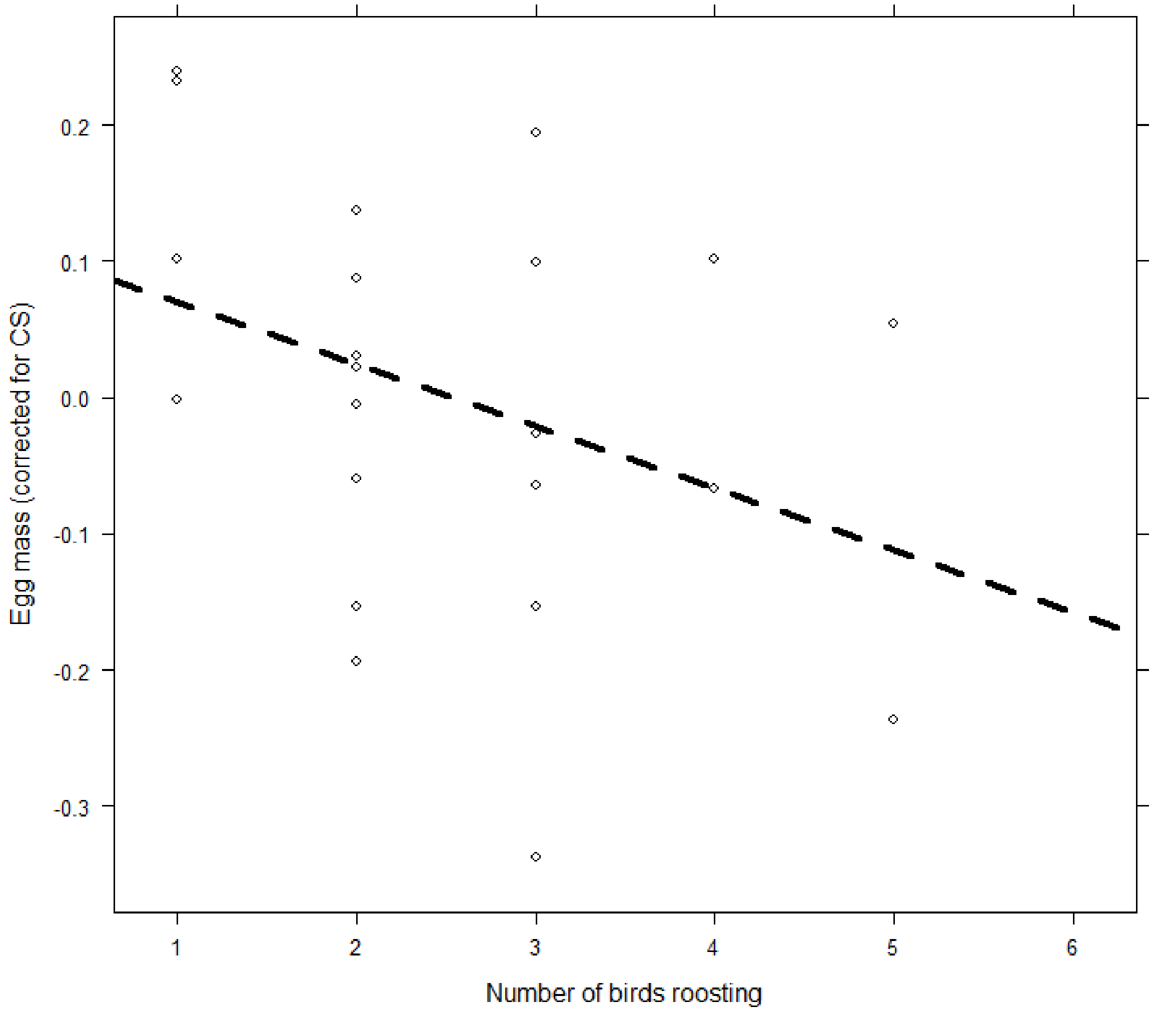
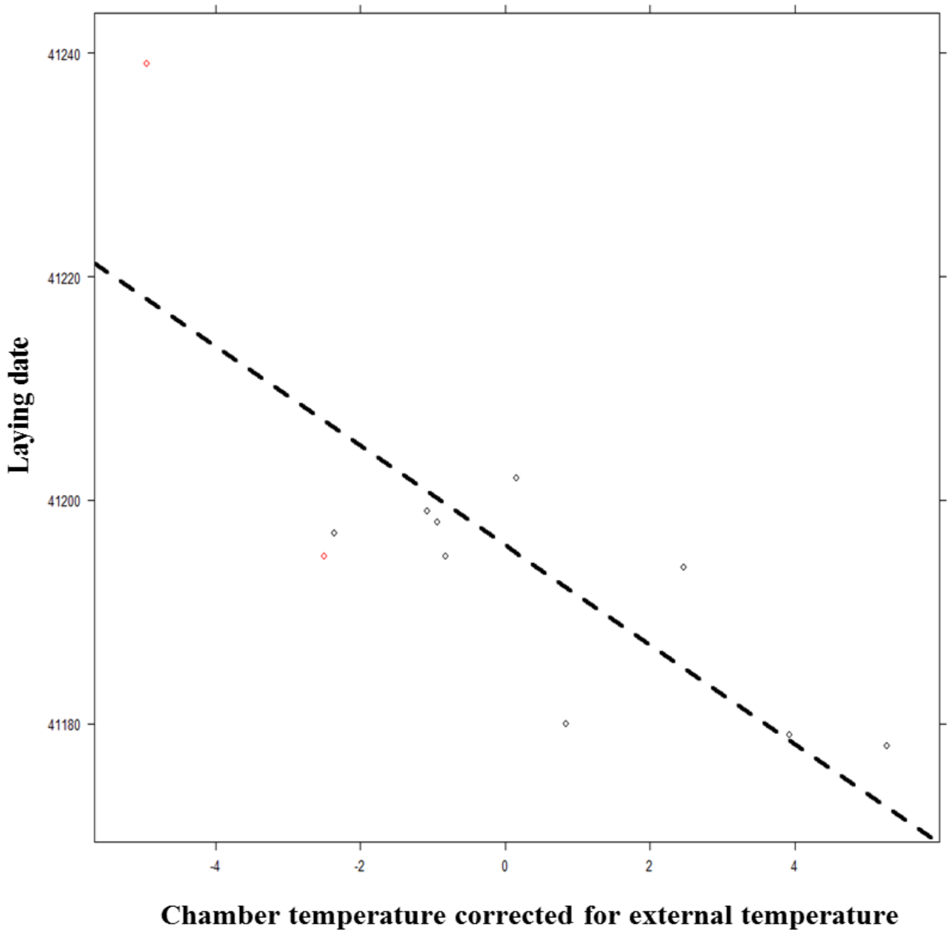


**Figure 6.** Egg mass corrected for clutch size in relation with the number of birds roosting.

## Supplementary material:



Laying dates in relation with the ambient chamber temperature at night (controlled for the outside temperature). Red dots indicate chamber where only one bird was roosting.

# *Manuscript 3: The presence of helpers is associated with increased female survival in the sociable weaver*

*In preparation*

# The presence of helpers is associated with increased female survival in the sociable weaver

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## ABSTRACT

Cooperatively breeding species are predicted to favor investment in own survival rather than current reproduction as they are typically long-lived. However the investigation of helper benefit for parent survival is surprisingly often neglected compared to reproductive success and also sexual differences in survival benefits of helping have been overlooked. Moreover all studies that reported a relationship between parents' survival and the presence of helpers didn't use Capture-Mark-Recaptures analyses (CMR) that allow accounting for the non-detection of alive individuals and avoid flawed results. By using CMR methods we investigated in the sociable weaver *Philetairus socius* if the presence of helpers was associated with an increase in survival probability for males and females' breeders. We found that females but not males without helpers had a substantially lower survival probability than other breeders. This result clearly indicates female-specific benefits and/or male specific costs of the presence of helpers that deserve to be further investigated in this species and other cooperative breeders.

***Keywords:*** *cooperative breeding, survival, CMR, helper, investment, sex-specific.*

## INTRODUCTION

Cooperative breeding is a mating system present in most animal taxa of the world (mammals, birds, fishes, insects) where supernumerary sexually mature individuals, named helpers, assist in raising the offspring of others, typically by bringing additional food to the young (Jennions and Macdonald 1994, Taborsky 1994, Choe and Crespi 1997, Cockburn 1998, Dickinson and Hatchwell 2004). While helping may provide direct benefits (Clutton-Brock et al. 2002, Richardson et al. 2002, Doutrelant and Covas 2007), helpers are often closely related to the parents (Griffin and West 2003) and hence gain indirect benefits by increasing the fitness of these close relatives (Hamilton 1964). This can occur by increasing parents' annual reproductive success and/or survival (Cockburn 1998, Hatchwell 1999, Khan and Walters 2002, Kingma et al. 2010). Cooperatively breeding species are typically long-lived and hence are predicted to favor investment in own survival as opposed to increased investment in current reproduction (Arnold and Owens 1998). This life-history strategy could explain why several studies failed to find a positive effect of helpers on reproductive success (as found in the rufous vanga Eguchi et al. 2002 and 12 other bird species reviewed in , Kingma et al. 2010).

Helpers' effects on breeders' survival have been relatively neglected compared to reproductive success. In particular, studies using Capture-Mark-Recapture (CMR) methods are extremely rare (but see McGowan et al. 2003). CMR is the only method currently available to account for the non-detection of individuals and thus to avoid flawed conclusions due to the fact that individuals are present but not detected (Gimenez et al. 2008). More studies of survival based on CMR methods are thus essential to determine the effect of helpers on adult survival.

Increased parental survival in presence of helpers can be due to the fact that parents save energy by reducing their investment in the current brood because helpers may compensate or even overcompensate this reduction (Hatchwell 1999, Russell et al. 2007, Canestrari et al. 2011). This strategy towards an increase of breeders' survival is especially likely when the probability to breed the following years is high, which can be due to high survival probability but also a high probability to maintain breeder status (Russell and Lummaa 2009).

The probability of breeding again in the following year may vary between sexes due to differences in life-history strategies between males and females. For instance, an improvement of male breeders' survival in presence of helpers was found to be associated with increased fidelity on a comparative study (Kingma et al. 2010). Additionally, in cooperatively breeding species, the magnitude of load-lightening and potential survival benefits may also differ between sexes. For example in long-tailed tits *Aegithalos caudatus*, males reduce more their food provisioning than females and males but not females are more likely to survive when helped to feed large broods (Meade et al. 2010). On the other hand in some species, females have been shown to reduce their investment in eggs when helped (Russell et al. 2007, Taborsky et al. 2007, Canestrari et al. 2011, Santos and Macedo 2011, Paquet et al. 2013). In these species, a higher effect of helpers is expected on female, rather than male, survival.

Here we test the hypothesis that helpers increase parental and mostly maternal survival on a colonial cooperatively breeding passerine, the sociable weaver *Philetairus socius*. Sociable weavers are socially and genetically monogamous (Covas et al. 2006), and both breeders incubate the eggs and feed the nestlings. Males feed at a higher rates than females (Doutrelant and Covas 2007) both breeding males and females reduce their provisioning effort at a similar rate when helped (Covas et al. 2008). We can thus expect a positive effect of helpers on both male and female survival. Additionally, females were found to lay lighter eggs when breeding with helpers (Paquet et al. 2013). In consequences, the presence of helpers may thus be more beneficial for females than males in term of survival probabilities.

## METHODS

### *Study species*

The sociable weaver is a passerine endemic to the semi-arid acacia savannahs of southern Africa (Maclean 1973a, Mendelsohn and Anderson 1997). Sociable weavers build massive communal nests containing several independent nest chambers that are used for breeding and roosting. They are facultative cooperative breeders, breeding in pairs or with up to five helpers (mean group size 3.15 birds, however the proportion of birds breeding in groups varies from ca. 30-80% between years; Covas et al. 2006). Helpers are mainly offspring of one or both breeders (93%), although a small number of unrelated birds can also help (Covas et al. 2006).

### *Field methods*

The work was conducted at Benfontein Nature Reserve in the Northern Cape Province of South Africa (28°52’ S, 24°50’E) under permission from the Northern Cape Department of Tourism, Environment and Conservation and under the approval of the Ethics Committee of the University of Cape Town. The study area covers approximately 15 $km^2$ of Kalahari sandveld, consisting of open savannah dominated by *Stipagrostis* grasses and the camelthorn tree, *Acacia erioloba*. The area is semiarid, experiencing low and unpredictable rainfall (average 431±127 mm per year; Weather Bureau, Pretoria). The study area contains about 30 sociable weaver colonies. This study was conducted on 23 of those colonies, although the number of colonies caught each year varied between 10 and 23. Colonies captures took place before the onset of the breeding season. The resident birds at each colony were captured by placing mistnets around the colony before dawn (i.e. when the birds are roosting inside) and then flushing the birds into the nets (Covas et al. 2002). Individuals were processed and released on the site of capture. All individuals were given a uniquely numbered aluminium ring and colour combination. In 1999, 2000, 2008, 2010 and 2011, we determined the breeding status (helped or not) of as many groups as possible. Then, from 2000-2005 and 2008-2013, we used capture-mark-recapture data to estimate survival.

We monitored breeding activity by inspecting all nest chambers in the study colonies were inspected every 3-4 days during the 5 breeding seasons (i.e. in 1999-2000, 2000-2001, 2008-2009, 2010-2011 and 2011-2012). These chambers were individually marked with a numbered plastic tag. To identify the individuals feeding at a given chamber and hence the presence of helpers, we conducted a minimum of 1 hour daily observations for at least 3 consecutive days (Covas et al. 2006, Doutrelant and Covas 2007). Observers were situated in a hide placed at 3-5m from the colony. We obtained data on breeding group composition for 168 breeders (85 females and 83 males). Of these, 97 bred with the assistance of helpers and 71 in pairs.

Rainfall closely influences food availability and the duration and success of the breeding season in sociable weavers (Maclean 1973b, Dean and Milton 2001, Covas et al. 2008) and can thus influence survival (Altwegg et al. 2013). To control for this factor we obtained seasonal rainfall from Kimberley airport (28°48’ S, 24°46’ E; ca. 10 km from the centre of the study site. Seasonal rainfall during the study period ranged from 251.5-875.9mm.

### *Molecular determination of the identity and sex of the parents*

Since sociable weavers are sexually monomorphic, sex had to be determined through molecular techniques. The breeders’ sex was determined by amplification of chromohelicase-DNA-binding genes located on the W and Z sex chromosomes using the P2 and P8 universal primers (Griffiths et al. 1998).

To determine whether a bird seen at a nest was a breeder or helper, we used microsatellite markers. For 1999-2000 and 2000-2001 we used the results of parentage analyses presented in Covas et al. 2006. For 2008-2009, 2010-2011 and 2011-2012, we determined parentage based on 17 microsatellites markers. For all captured adults and monitored offspring a blood sample was taken and total genomic DNA was extracted using a modified ammonium acetate precipitation method. The DNA content of the extractions was quantified using a Nanodrop ND8000 and then each sample was genotyped using 17 microsatellite loci for genotyping (PS1-GCSW15, GCSW47, INDIGO40, TG22-001, PS2-GCSW35, INDIGO41, Ppi2-Gga, TG01-148, WBSW9, PS3-GCSW13, INDIGO29, CAM1, CAM15, PS4-Ase18, GCSW31, GCSW57, TG07-022 Martinez et al. 1999, McRae and Amos 1999, Richardson et al. 2000, Sefc et al. 2001, McRae et al. 2005, Dawson et al. 2010, Dawson et al. 2013). These were grouped into four primer sets using a Qiagen Mastermix kit.

PCR product was sequenced using an ABI3730 capillary sequencer using the GeneScan™ 500 ROX™ Size Standard (Applied Biosystems), and results were analysed using Genemapper v3.7 software (Applied Biosystems). All of the scores were checked manually and adjusted wherever the genotype call was deemed to be in error.

The program CERVUS v3.0.3 (Tristan Marshal, Field Genetics Ltd) was used to quantify the number of alleles, the observed and expected heterozygosity and to check for null alleles. The program Genepop (http://genepop.curtin.edu.au) was used to test each locus for conformity to Hardy Weinberg equilibrium (HWE) and to check for Linkage Disequilibrium (LD) between loci.

The program Colony v2.0.3.5 (Jones and Wang 2010) was used to assign each chick a most likely mother and father through a likelihood approach. We used the genotypes of 181 offspring and used all genotyped male and female adult birds as parent candidates (529 females and 561 males). To simulate the chance that an unknown individual might be a parent the proportion of candidate mothers and fathers sampled was set at 75%. A rate of 1% marker typing error was set. Fathers and mothers were assigned when their output parentage probability was given as 1. As previously reported (Covas et al. 2006) we did not find any evidence of extra pair or extra group paternity in this study (100% of identified incubating males were found to be the father of the brood and 100% of genetically assigned fathers were seen feeding the nestlings).

### ***Statistical methods***

We tested for differences in survival between adults breeding in pairs alone versus pairs assisted by helpers using maximum likelihood statistics, following the general methods of Lebreton et al. (1992) and the program MARK (Cooch and White 1998, White and Burnham 1999). Individual capture histories were built for the 168 birds with known breeding group composition. When a breeding bird was studied over several years we used the breeding group type that the bird had in the first year in order to have the longest known capture recapture history after breeding for every bird.

The study colonies were subsequently captured every year (except in 2006 and 2007) and we recorded the presence/absence of a given individual in any of the colonies captured. By analyzing individual capture histories, it is possible to distinguish a probability of survival ($\Phi$) from a recapture probability (p), which is not the case when simply studying return (Gimenez et al. 2008). We first verified that our data set met the expectations of the Cormack-Jolly-Seber (CJS) assumptions (no trap-dependence and no transient effect), using program U-Care (Choquet et al. 2009). The test of goodness of fit on CJS indicated that this model offered a satisfactory fit to the data set allowing the use of CMR statistics (Goodness of fit test, global test, quadratic $\chi^2_{36} = 19.2472$, $p = 0.99$).

In these analyses we were mainly interested in the effect of helpers' presence on parent's survival the following year. However, a number of other factors could have affected survival and also had to be tested. To limit the number of parameters estimated simultaneously (Gregoire et al. 2004) we first tested the effect of year and sex on both global survival and recapture probability. We selected the best model, which here was **Φ(y)+p(t+s)** where survival probability varied between the first year (y: year following the known breeding status of the birds) and the subsequent years and the recapture probability varied with time (t: i.e. between years) and was lower for females than males (on average 0.59±0.12 for females against 0.70±0.10 for males).

We then tested the effects of several other variables of interest on the survival probability the specific year following the known breeding status of the birds (i.e. with/without helpers). These explanatory variables were: the presence of helpers, and also body mass and body mass$^2$, colony size and rainfall for the studied breeding season, which were all previously found to influence sociable weaver's survival (Covas et al. 2002, Altwegg et al. in press). In addition, we were interested in whether the effect of helper presence could interact with other factors, but we included only interactions that were considered biologically relevant a priori (Burnham and Anderson 2002). Specifically, we tested whether the presence of helpers could have an effect only under low rainfall conditions (Covas et al. 2008), or affect only one of the sexes (see introduction).

Since one of our main questions in this study was to determine whether the presence or the absence of helpers affects a specific sex, we also tested a posteriori for a difference between each specific parent category (for instance females with helpers) and the other individuals (for instance including females without helpers, males with helpers and males without helpers).

We tested hypotheses by comparing different models using the Akaike information criterion corrected for sample size ($AIC_c$). This method considers both the deviance and number of parameters (Akaike 1998). The model with the lowest $AIC_c$ is the best, whereas models that differ by $\Delta AIC_c < 2$ are considered to have equivalent support (Burnham and Anderson 2002). Additionally, in order to evaluate the significance of the effects of interest, likelihood ratio tests (LRT) were performed between nested models with a $\Delta AIC_c < 2$ (Lebreton et al. 1992).

## RESULTS

The two best selected models differ by 2 or less in $AIC_c$. These two models are model **1** (**Table 1** i.e. the null model) where survival only differed between the first year and the subsequent ones and the model **2** that show a positive effect of helpers' presence on survival probability to the following year (**Table 1**). This model **2** shows an estimated increase survival of 0.04 for parents with helpers compare to parents without helpers (**Figure 1**). The likelihood ratio test between model **1** and **2** showed no significant difference between these 2 models (LRT: p = 0.59). Thus we cannot exclude the hypothesis that helpers increase the survival probability of breeders.

When testing for specific differences in survival between a specific parent category and the other breeders (**Table 2**), the model with the lowest $AIC_c$ is the model where females without helpers have a lower survival than the other breeders (respectively 0.67 and 0.85, **Figure 2**). This model presents a lower $AIC_c$ than the previous best model (the null model, model **1**) where survival only differed between the first year and the subsequent ones ($\Delta AIC_c = 1.1752$). The LRT test between the two models is close to significance (p = 0.0678). Hence, our results suggest a lower survival of females without helpers. The third model testing specifically the survival of males in pairs compared to other categories (males with helpers and females with and without helpers) shows on the contrary, an increase, and not a decrease, for the survival probability of males in pairs compared to the other breeders. However this model differs of 2.1 from the best model (**Table 2**).

## DISCUSSION

The aim of this study was to investigate whether the presence of helpers is associated with an increase in parental survival and if mothers may benefit more than males from helpers presence. The results we found are in agreement with this hypothesis. First, our CMR models show that we cannot exclude the hypothesis that parental survival is higher in presence of helpers. More precisely, they show that this effect is due to the fact that females without helpers have a lower survival than the other categories of breeders (females with helpers, and males with and without helpers) suggesting that mothers do benefits more for the presence of helpers than males.

In our general model, which aimed to test the helpers effect on parental survival (**Table 1**) the two best models in terms of $AIC_c$ values did not differ by more than 2 so we cannot discriminate between these models. The model 1 did not include any explanatory variable on survival the year following the monitored breeding season. The second selected model included the effect of helpers' presence on breeder survival the subsequent year. Thus positive effects of helpers on breeders' survival cannot be excluded. Helper presence is the only effect present in the best models despite the fact that rainfall was found to affect survival in a previous study based on a larger sample size (Altwegg et al. 2013). Hence, helpers' effect might indeed be an important biological factor.

By looking more specifically at the effect of helpers on each class of breeders, we found that females without helpers seem to be much less likely to survive than females with helpers and males (0.67% against 0.85%) and that this model had a lower AICc than the null model (model 1) where survival just vary with time. The model including the interaction between sex and helper presence presented a higher $AIC_c$ than the presented models which is probably due to its high number of parameters and a lack of statistical power. However the fact that females without helpers have a lower survival than females with helpers and males clearly indicates sex-specific benefits of the presence of helpers due to more benefits and/or less costs associated with the presence of helpers for females. One potentially important reported benefit of the presence of helpers on females only is their lower investment in eggs when expected to be helped (Paquet et al. 2013). Similarly on superb fairy-wrens where females produce lighter eggs in presence of helpers (Russell et al. 2007), females but not males were also found to have a greater recapture rate in presence of helpers (Cockburn et al. 2008). The benefits of the reduction in egg investment in presence of helpers may be particularly high as sociable weaver females can lay up to 9 clutches in a single season (mainly as a result of nest predation Covas et al. 2008). However, as usual with correlative studies of cooperative breeders, the increased survival of females in the presence of helpers may due to better maternal quality or any other potential benefit of helpers linked with group augmentation (Kokko et al. 2001). Consequently a study of the direct relationship between egg mass and female survival is thus crucially needed in cooperative breeders to test the hypothesis that the higher female survival in presence of helpers is partly driven by egg mass reduction and thus energy saving during egg laying.

The apparent absence of helper effect on male survival is more surprising as breeding males feed at higher rates than the females and helpers (Doutrelant and Covas

2007) and reduce their provisioning rates in the presence of helpers (Covas et al. 2008). However, males may experience specific costs associated with the presence of helpers. In superb fairy-wrens the absence of helper effects for males was attributed to the costs of higher extra pair paternity rates associated with the number of helpers (Mulder et al. 1994, Dunn and Cockburn 1999, Cockburn et al. 2008). Extra-group paternity was found to be negatively correlated with males' survival on cooperatively breeding species (Kingma et al. 2010) but sociable weavers do not fit this trend as no evidence of extra-pair paternity was found in our population (Covas et al. 2006). The presence of helpers may be associated with other competition costs. For example Seychelles warblers (*Acrocephalus sechellensis*) had a lower survival probability when in larger groups, which may be the consequence of competition for resources (Brouwer et al. 2006). In sociable weavers, competition for resources is more likely at the colony level as all birds from a same colony usually forage communally (Maclean 1973b) and no effect of colony size was present in our best models. However, the presence of helpers might be associated with other potential costs for males, such as costs associated with social interactions. Sociable weavers colonies have ordered hierarchies and initial result indicate that, males engage frequently in aggressive interaction (M. Rat unpublished data), which may ultimately have survival consequences (Acker et al. in prep). Alternatively, males without helpers may tend to be younger individuals and hence have higher survival than older males. These suggestions, however, remain speculative and more data are needed to test these hypotheses..

In the null model (model 1, **Table 1**), the estimated survival probability of breeders (0.82) was interestingly higher than previously reported survival rates on sociable weavers (0.66 and 0.62 respectively in Covas et al. 2004; Altwegg et al. in press) suggesting a particularly high survival for breeders. If this may be also due to a statistical bias as breeders may disperse less than non-breeders due to their breeding position, but we controlled for the recapture rates and hence avoided this bias at least for short distance dispersal.

In this study also we found that the year of capture and sex best explained recaptures probability variations, females being less likely to be recaptured than males. As sociable weaver colonies have a significant level of genetic structure for males but not females (Covas et al. 2006) and as females disperse more frequently (Doutrelant et al. 2004) this result is probably due to the fact that females move between colonies more than males. Thus females are more likely to move away from the study colonies.

In conclusion, we found strong indication of a positive effect of helpers on females' but not males' survival by using capture-recapture analyses. This increase in survival is expected to considerably increase future females' breeding opportunities. It may be due to a reduced investment in reproduction and, in particular, by the lower investment in eggs in the presence of helpers, although direct tests of this hypothesis are needed.

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# TABLES

**Table 1.** Modeling the survival probability (Φ) and recapture probability (p) in relation to presence of helpers (h) and other covariates (s = sex, r = rainfall, c = colony size, m = mass, t= time). "y" corresponds to the discrimination between the year of interest and the following years. The two best models are in bold ($\Delta AIC_c<2$).

| **Model** | **$AIC_c$** | **$\Delta\ AIC_c$** | **$AIC_c$ weights** | **K** | **Deviance** |
|---|---|---|---|---|---|
| **1 Φ(y)+p(t+s)** | **743.8037** | **0** | **0.22539** | **14** | **714.71** |
| **2 Φ(y+h)+p(t+s)** | **745.6779** | **1.8742** | **0.08830** | **15** | **714.42** |
| Φ(y+s)+p(t+s) | 745.893 | 2.0893 | 0.07930 | 15 | 714.64 |
| Φ(y+r)+p(t+s) | 745.9504 | 2.1467 | 0.07706 | 15 | 714.69 |
| Φ(y+c)+p (t+s) | 745.9616 | 2.1579 | 0.07662 | 15 | 714.70 |
| Φ(y+m+$m^2$)+p(t+s) | 746.3272 | 2.5235 | 0.06382 | 16 | 712.90 |
| Φ(y+h+s)+p(t+s) | 747.759 | 3.9553 | 0.03119 | 16 | 714.33 |
| Φ(y+h+r)+p(t+s) | 747.8102 | 4.0065 | 0.03041 | 16 | 714.38 |
| Φ(y+c+h) +p(t+s) | 747.8476 | 4.0439 | 0.02984 | 16 | 714.42 |
| Φ(y+s+r)+p(t+s) | 748.0537 | 4.25 | 0.02692 | 16 | 714.63 |

**Table 2.** Models including a difference in survival for each breeder class (fp = females in pairs, mp = males in pairs, fh = females with helpers, mh = males with helpers) compared to the others. The two best models are in bold (ΔAICc<2).

| **Model** | **AIC$_c$** | **Δ AIC$_c$** | **AIC$_c$ weights** | **K** | **Deviance** |
|---|---|---|---|---|---|
| **Φ(y+fp)+p(t+s)** | **742.6285** | **0** | **0.38078** | **15** | **711.37** |
| **Φ(y)+p(t+s)** | **743.8037** | **1.1752** | **0.21158** | **14** | **714.71** |
| Φ(y+mp)+p(t+s) | 744.7337 | 2.1052 | 0.1329 | 15 | 713.48 |
| Φ(y+fh)+p(t+s) | 745.0054 | 2.3769 | 0.11602 | 15 | 713.75 |
| Φ(y+h)+p(t+s) | 745.6779 | 3.0494 | 0.08289 | 15 | 714.42 |
| Φ(y+mh)+p(t+s) | 745.8559 | 3.2274 | 0.07583 | 15 | 714.60 |

# FIGURES

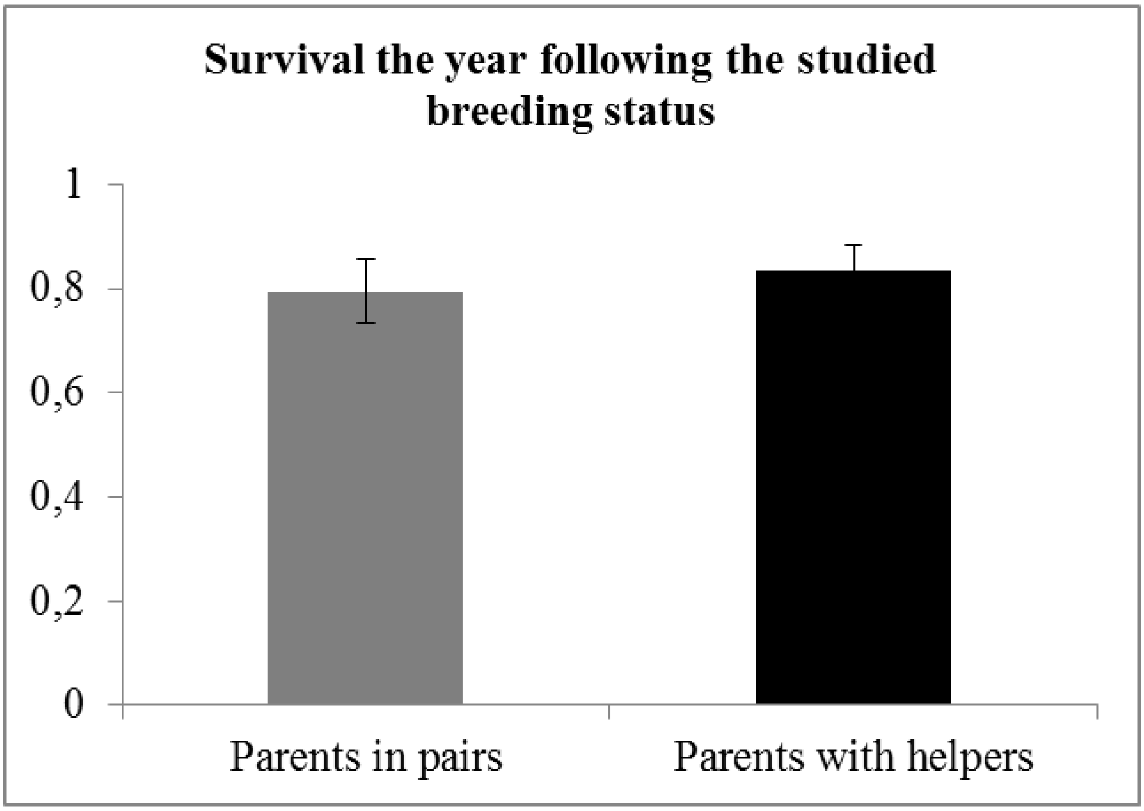

**Figure 7.** Survival probability of the parents in pairs versus with helpers from the model Φ(y+h)+p(t+s) (**Table 1**).

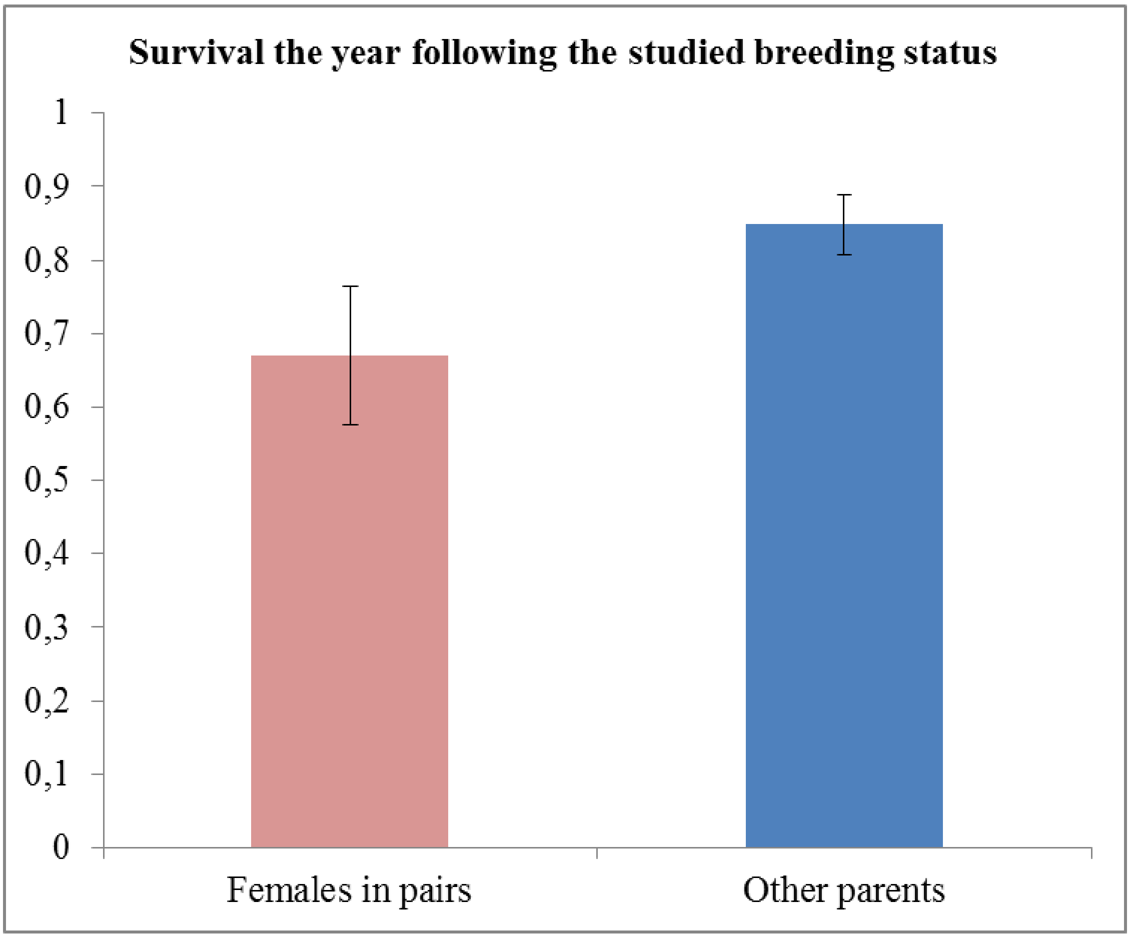

**Figure 8.** Survival probability of the breeding females in pairs versus the other parents from the model Φ(y+fp)+p(t+s) (**Table 2**).

# *Manuscript 4: Prenatal influence on begging behavior: a cross fostering experiment in a cooperatively breeding species*

*In preparation*

# Prenatal influence on begging behavior: a cross fostering experiment in a cooperatively breeding species

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## ABSTRACT

Parent-offspring conflicts occur when offspring ask for more investment, than it is optimal for parents to supply. Females may modulate parent-offspring conflicts by depositing different amounts of hormones into eggs thereby acting on young begging behavior notably depending on expected breeding conditions. Cooperatively breeding species represent a fascinating system to study maternal control of begging behavior because the presence of helpers creates predictable rearing environment for their nestlings. However to date whether prenatal environment affects begging behavior has not been studied in cooperative breeders. We investigated with a cross fostering experiment in a cooperative breeder, the sociable weaver, whether begging behavior is influenced by prenatal environment. We measured begging vocalizations at two nestling stages, early after hatching at day 4 and in the middle of their growth at day 9. We found an effect of both nests of origin and of foster nests. As predicted if prenatal environment influences begging chicks originally from groups with more birds beg less early after hatchling. Chicks fed by more foster birds also beg at a lower rate in accordance with the fact that they receive more food and are therefore more satiated. This shows that both prenatal and postnatal environment are important in determining nestling begging behavior and that mothers may control to some extent the behavior of their young.

***Keywords:*** *begging behavior, cooperative breeding, maternal effects, helpers, cross fostering, parents-offspring conflicts, family conflicts.*

## INTRODUCTION

Individuals modulate their investment in the current reproduction according to the current and the expected breeding conditions (Sheldon 2000, Benton et al. 2005). These differential parental allocation strategies are likely to induce parent-offspring conflicts of interests as parents and offspring may not have the same short and long term interests (Trivers 1974, Lessells and Parker 1999). For instance it is in the offspring's interest to receive more investment than it is optimal for parents to supply at each breeding attempt.

An obvious and widespread manifestation of parent-offspring conflict can be seen through begging-provisioning rates interactions when parents adjust their provisioning of resources in response to conspicuous offspring begging displays and offspring adjust their begging behavior in response to the amount of resources received from the parents (Kilner and Johnstone 1997, Smiseth et al. 2008). Begging behaviors are commonly observed in species with parental care and can be visual, chemical or acoustic (Kilner and Johnstone 1997, Mas and Kolliker 2008) and at least two solutions have supposed to evolve to mediate parents offspring conflicts. A resolution of conflicts is possible if begging behavior is costly and can thus act as a honest signal of offspring needs that parents use to fine tune their parental investment (Godfray 1995, Kilner and Johnstone 1997). Additionally, interactions between offspring begging and adult provisioning may be under maternal hormonal control.

There is growing evidence that maternal hormones, such as testosterone and corticosterone, are involved in the regulation of begging behavior, especially on birds, at least early after hatching (Schwabl 1996, Saino et al. 2002, Smiseth et al. 2011). It is well known that maternal allocation of hormones into eggs depends on pre-breeding and/or expected breeding conditions (Saino et al. 2002, Mazuc et al. 2003, Sandell et al.

2007). More specifically, by depositing different amounts of hormones into eggs females may modulate parent-offspring conflicts by acting on young begging behavior (Schwabl 1996) and then on their own (Tschirren and Richner 2008) and/or their partner’s food provisioning (Moreno-Rueda 2007, Muller et al. 2007). For example in the Budgerigar *Melopsittacus undulatus* males, but not females, increased feeding to broods that begged more (Stamps et al. 1985).

Cooperatively breeding species represent a fascinating system to study maternal control of begging behavior and family conflicts. In such breeding systems the breeding groups involve parents and current offspring but also helpers that are often kin (related to one or both parents). Helpers are supernumerary individuals that assist the breeders by providing care to their offspring, particularly though additional food provisioned to the nest (Brown 1987, Emlen 1991). In the presence of helpers, parents can either maintain their provisioning effort, in which case helper care is additive, but they can also reduce their provisioning effort, which is partially or fully compensated by the care of helpers (see Hatchwell 1999 for a review). When assisted by helpers, females may also adjust their investment in eggs. Specifically, recent result have shown that females may invest less by producing smaller eggs when they have helpers (Russell et al. 2007, Canestrari et al. 2011, Santos and Macedo 2011, Paquet et al. 2013). There is thus a clear potential for family conflicts in these systems and whether females may manipulate begging behavior to their own interest have never been investigated so far.

Interestingly, the only study that investigated hormone allocation variations in relation to the presence of helpers, has shown that sociable weaver (*Philetairus socius*) females deposit less testosterone and corticosterone in their eggs when they expected to have helpers at the nest (Paquet et al. 2013). By doing so, mothers could induce the reduction of their own provisioning investment which can be compensated by helpers.

Indeed, because both hormones are known to enhance begging behavior in several species (Smiseth et al. 2011), it is possible that mothers influence begging behavior of their offspring by this way, reducing it in presence of helpers and explaining in return why parents feed less in the presence of helpers.

In order to test the possibility of maternal manipulation of their offspring need we used a cross fostering experiment in the sociable weaver. Cross fostering is a powerful method to disentangle prenatal from postnatal needs that are directly influenced by the provisioning and the number of the careers. As begging rate may vary with offspring need we expected chicks' begging rate to be lower when actually fed by more birds. However in addition, as eggs were found to contain less testosterone and corticosterone in presence of helpers (Paquet et al. 2013) and as both hormones are known to enhance begging behavior (see Smiseth et al. 2011 for a review) we also expected an effect of the nests of origin on the begging rate. More precisely, eggs laid in nests without helpers are expected to produce nestlings with higher begging rates than eggs laid in nests with helpers. As hormonal maternal effects may affect chicks' begging behavior only during early developmental stages (Schwabl 1996, Saino et al. 2006) we expected the potential influence of original group size on chicks' begging to be stronger or only detectable early after hatching . Here we recorded chicks at day 4 and 9 and so we expected a stronger effect at day 4.

## METHODS

### *Study species*

The sociable weaver is a colonial passerine endemic to the semi-arid acacia savannahs of southern Africa (Maclean 1973a, Mendelsohn and Anderson 1997). Sociable weavers are facultative cooperative breeders, breeding in pairs or with up to five helpers (in this study, we had 0-3 helpers, mean group size 2.72 birds). The helpers are usually related to one or both breeders. In this species, the overall frequency of food delivery was found to increase with the number of helpers in the sociable weaver (Covas et al. 2008) and males have been found to feed more than females (Doutrelant and Covas 2007). At the egg stage, feeding group size is supposed to be already fixed because chicks from the previous year help their parents for one or two years before breeding themself (Covas et al. 2006) and another study shows that pre breeding roosting group size and breeding group size are well correlated (Paquet et al. in prep).

### *Field methods*

Our aim was to swap synchronous clutches with and without helpers which implies determining laying dates and clutch sizes for as many nests as possible. In sociable weaver the onset and duration of reproduction is unpredictable, depending on rainfall which is erratic in this semi-arid region of the world. To determinate the onset of reproduction 15 study colonies were inspected every 3 days from September 2012 to march 2013 (approximately 400 individually marked chambers). As soon as an egg was found in a colony, chambers were inspected every day to determine the clutch size and the laying date of a maximum of pairs. Sociable weavers lay one egg per day, usually 3-4 eggs per clutch (Covas et al. 2008). When 2 clutches in the same colony were of the same size and laid synchronously or within one day interval, the totality of eggs in these clutches were swapped on the day after the last egg was laid. A total of 28 clutches were swapped. However, due to high level of snake predation (up to 80%: Covas et al. 2008), only 9 swapped pairs (i.e. 18 cross-fostered broods) reached fledging age and thus constitute our sample size.

The sociable weavers nestling period is 21-24 days (Maclean 1973b). Chicks were weighted on days 4 and 9 after the hatching date of the first chick (hereafter day 4 and day 9 ). At these times we recorded acoustic begging of the cross-fostered chicks for 6 hours with a tie-clip microphone (Olympus ME15, frequency range = 15-12000 Hz) clipped at the entrance of the chamber and connected to an Olympus WS-750M recorder. Calls were recorded at 44.1 kHz in uncompressed PCM format for further analyses. Due to technical problems in the field we were only able to record begging of 17 of the 18 broods at day 4 and 15 at day 9.

To identify group size, before the onset of breeding, we first captured and marked all the individuals roosting in the colony with a unique color ring combination (see Covas et al. (2002) for more details on the captures). To identify the individuals feeding at a given cross-fostered chamber and hence the breeding group size, we then conducted 1 or 2 hours of daily observations for at least 3 different occasions (min = 3, max = 25, average = 9.5 during the whole season). Observers were located under a hide placed at 3-5 m from the colony. We were able to identify the breeding group size of the 18 cross-fostered chambers that reached fledging corresponding to nine pairs and nine groups (of 3, 4 and 5 birds).

### ***Begging analyses***

Begging spectrograms were analyzed and measured using the Syrinx sound analysis program (John Burt, www.syrinxpc.com). For each recording we visually isolated 10 feeding events easily identifiable through the calls emitted by the parents when entering the chamber immediately followed by the initiation of the chicks' begging calls (Figure1). Feeding events where chicks were begging intensively for 10 seconds or more (mean duration of the selected begging events: 11.29 sec at day 4 and 11.88 sec at day 9 respectively) were analyzed. We measured the begging rate as the average number of calls emitted from one chick (the loudest and most easily distinguishable in the spectrogram) per second during intensive begging (Figure 1). we choose to study this component of begging behavior since it was found to be linked to the chicks' needs

(Price and Ydenberg 1995) and to the eggs or chicks' hormones (see Smiseth et al. 2011 for a review).

As the time spent measuring the chicks and setting up the microphones prevented parents from feeding the chicks we checked for any potential effect of the time lap between the start of the recording and the feeding event on the begging rate at day 4 and 9 and did not find any effect (both P values >0.43).

***Statistical analyses***

The main purpose of these analyses was to study the effect of the original and foster breeding group size on the begging rate of the chicks at day 4 and day 9. These two sets of analyses were conducted by using linear mixed models with the package nlme in R (R Development Core Team, 2011). The two final models were obtained by sequentially eliminating explanatory variables showing P values >0.1 using a backwards stepwise approach. The minimal models provided the P values of significant terms whereas P values for non-significant terms were obtained by reintroducing each non-significant variable into the minimal model (Crawley 2002).

In order to take into account the non-independence of the 10 begging events recorded per breeding chamber we fitted the random factor 'nest chamber' nested in a 'colony' factor. The random chamber effect was highly significant for both begging rates at day 4 and day 9 (Likelihood ratio LR = 36.46, $P < 0.001$ and LR = 38.51, $P < 0.001$ respectively) indicating a strong begging rate repeatability within chambers. For the analyses of begging rate at both day 4 and day 9 we fitted original and foster group size as two explanatory variables. Begging duration was added as a co-variable to control for any potential correlation with begging rate. The date (Julian day) and the time of the day of the begging events were also added as co-variables as they may impact feeding and begging behavior, notably through the effect of temperature

(Ricklefs and Hainsworth 1968, du Plessis et al. 2012). Finally, the mean brood weight and the brood size at day 4 and day 9 were included as fixed terms to study potential begging rate variations with chicks' condition and competition at day 4 and day 9 respectively. Begging rates at day 4 and day 9 were not significantly correlated (Pearson correlation coefficient r = 0.107, P = 0.21) suggesting that they can be influenced by different factors.

## RESULTS

### *Begging rate at day 4*

Begging rate at day 4 was influenced by both original and foster brood size. It decreased significantly with the number of foster birds feeding the chicks (i.e. foster group size, Figure 2, Table 1) but also was influenced by the original group size (i.e. the group at laying before cross fostering, Figure 3, Table 1). Eggs laid in nests without helpers produced nestlings with higher begging rates than eggs laid in nests with helpers (Figure 4). There was a significant negative effect of the date and an effect of the time of day, but these effects were considerably low (see estimates Table 1). No effects of brood weight, number of chicks or begging duration were found (Table 1).

### *Begging rate at day 9*

Begging rate at day 9 also decreased significantly with the number of birds feeding (Figure 5, Table 2) but was not influenced by the size of group of origin (table 2). It decreased with the duration of the begging event but was not affected by date, time, mean brood weight or the number of chicks (Table 2).

## DISSCUSSION

We investigated for the first time in a cooperative breeder whether begging behavior may be influenced by prenatal environment. As predicted the nest of origin influenced the begging rate of the chicks early in life, the number of helpers of the breeding group of origin being negatively related to chicks begging rate at day 4. As expected, we also found an effect of the rearing environment: chicks begged less when the rearing group size is higher. This shows that both prenatal and postnatal environment are important in determining nestling begging behavior and that mothers may control to some extent the behavior of their young.

In sociable weavers (Covas et al. 2008), as found in several other cooperatively breeding species (Hatchwell 1999), the number of helpers caused a significant increase on the total food provided to nestlings. The fact that chicks begged at a lower rate when fed by more carers (i.e. foster group size) is consistent with the fact that begging rate may act as a signal of offspring need for food, the nestlings begging less in foster groups with helpers because they have more food and are more satiated. The fact that begging is a signal of need has been shown in many species. For example an experimental study showed that begging performance of magpie chicks (*Pica pica*) was strongly influenced by the food intake of nestlings (Redondo and Castro 1992) or on bell miners, *Manorina melanophrys*, the increase in food delivery induced by begging playbacks caused nestlings to reduce their own begging (McDonald et al. 2009).

Most interestingly we also found that the begging rate of the chicks at day 4 decreased with the number of carers of their nest of origin and this independently of the number of birds that actually fed them. This clearly indicates a prenatal effect on offspring begging early in the development which can be due to several factors. First, a sex ratio difference between broods with and without helpers may lead to a difference in begging behavior. Here we did not have access to the sex of the nestlings but in sociable weavers groups with helpers were previously found to produce more males than pairs (Doutrelant et al. 2004). However when sex differences in begging are reported, males are found to beg more intensively than females nestlings in passerine birds (von Engelhardt et al. 2006, Bonisoli-Alquati et al. 2011) so we would expect groups with helpers to beg more and not less intensively as reported in our study. Secondly this may be due to a difference in parental quality that is likely to affect offspring phenotype, for instance body size. Here we controlled our analyses for nestling body mass and did not find an effect of body condition on chicks' begging. Third it can be due to maternal effects and possibly the lower amount of yolk testosterone and/or corticosterone as has been found in eggs with helpers in this species (Paquet et al. 2013). Concurring with this hypothesis, the effect of prenatal group size was no longer found at day 9 which may be explained by the fact that it was beyond the developmental stage when maternal hormones affect begging (Schwabl 1996, Smiseth et al. 2011).

To conclude, our results show that prenatal environment influences the begging behavior of nestlings. More data are needed to show that prenatal effect is due maternal manipulations but the fact that eggs with helpers have different hormonal contents (Paquet et al. 2013) and chicks different begging behaviors (this study) suggest this is a likely possibility. Another interesting step would be to study breeding males, females and helpers' individual responses to begging variations and yolk hormones. Indeed, males and females' responses to begging behavior may differ (Kilner 2002, MacGregor and Cockburn 2002, Muller et al. 2007, English et al. 2008) and in cooperative breeding species this mechanism can be particularly likely and advantageous as not only one but several individuals can be manipulated. Moreover, maternal manipulation of helpers' provisioning effort is expected to be more beneficial for females when helpers are unrelated to them and thus when they do not pay kin-related costs. Cooperatively breeding species thus represent perfect candidate systems in which to further study conflicts between female, offspring and the other carers depending on their relatedness, the number of carers and maternal allocation in eggs hormones.

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# TABLES

**Table 3.** Factors affecting offspring early begging rate (at day 4)

| Explanatory terms | Estimate | SE | F | df | P |
|---|---|---|---|---|---|
| **intercept** | **554.143** | **105.967** | | | |
| **Group size during feeding** | **-0.357** | **0.049** | **53.095** | **10** | **$< 1\ 10^{-5}$** |
| **Group size of the nest of origin** | **-0.312** | **0.0523** | **35.717** | **10** | **0.0001** |
| **Date** | **-0.013** | **0.0026** | **26.922** | **10** | **0.0004** |
| **Time** | **$< 1\ 10^{-5}$** | **$< 1\ 10^{-5}$** | **10.827** | **152** | **0.0012** |
| Mean brood weight | | | 0.502 | 9 | 0.4966 |
| Number of chicks | | | 1.517 | 9 | 0.2493 |
| Begging duration | | | 2.855 | 151 | *0.0932* |

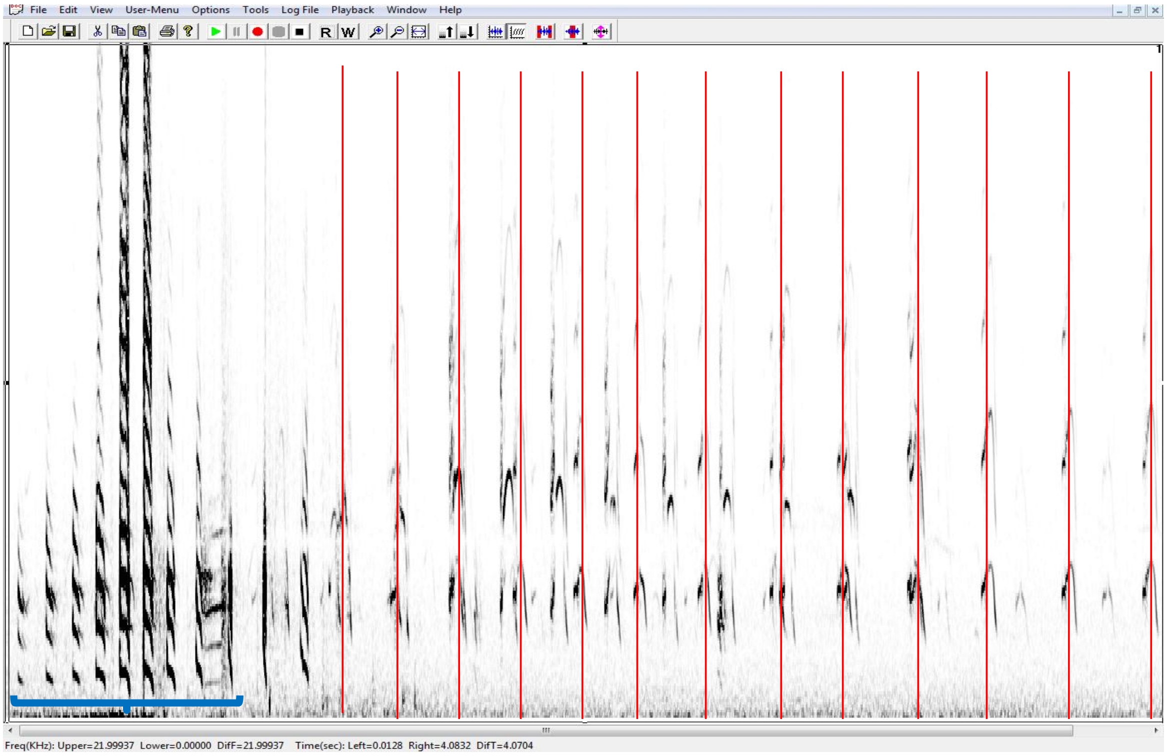
Estimates and SE are given for significant (bold characters) explanatory terms included in the minimal model.

**Table 4.** Factors affecting later begging rate (at day 9)

| Explanatory terms | Estimate | SE | F | df | P |
|---|---|---|---|---|---|
| **intercept** | **6.228** | **0.283** | | | |
| **Group size during feeding** | **-0.254** | **0.0973** | **6.801** | **10** | **0.0261** |
| **Begging duration** | **-0.037** | **0.00593** | **38.914** | **134** | **$< 1\ 10^{-5}$** |
| Group size of the nest of origin | | | 0.843 | 9 | 0.3825 |
| Date | | | 2.879 | 9 | 0.124 |
| Time | | | 0.329 | 133 | 0.567 |
| Mean brood weight | | | 0.4636 | 9 | 0.5131 |
| Number of chicks | | | 2.351 | 9 | 0.160 |

Estimates and SE are given for significant (bold characters) explanatory terms included in the minimal model.

# FIGURES



Freq(KHz): Upper=21.99937 Lower=0.00000 DifF=21.99937 Time(sec): Left=0.0128 Right=4.0832 DifT=4.0704

**Figure 1. Spectrogram of the beginning of an analyzed begging event.** The sum of the begging calls emitted by a single chick (red lines) was divided by the duration of the intense begging following the entrance of an adult feeder (adult entrance calls in the blue bracket) to obtain the begging rate.

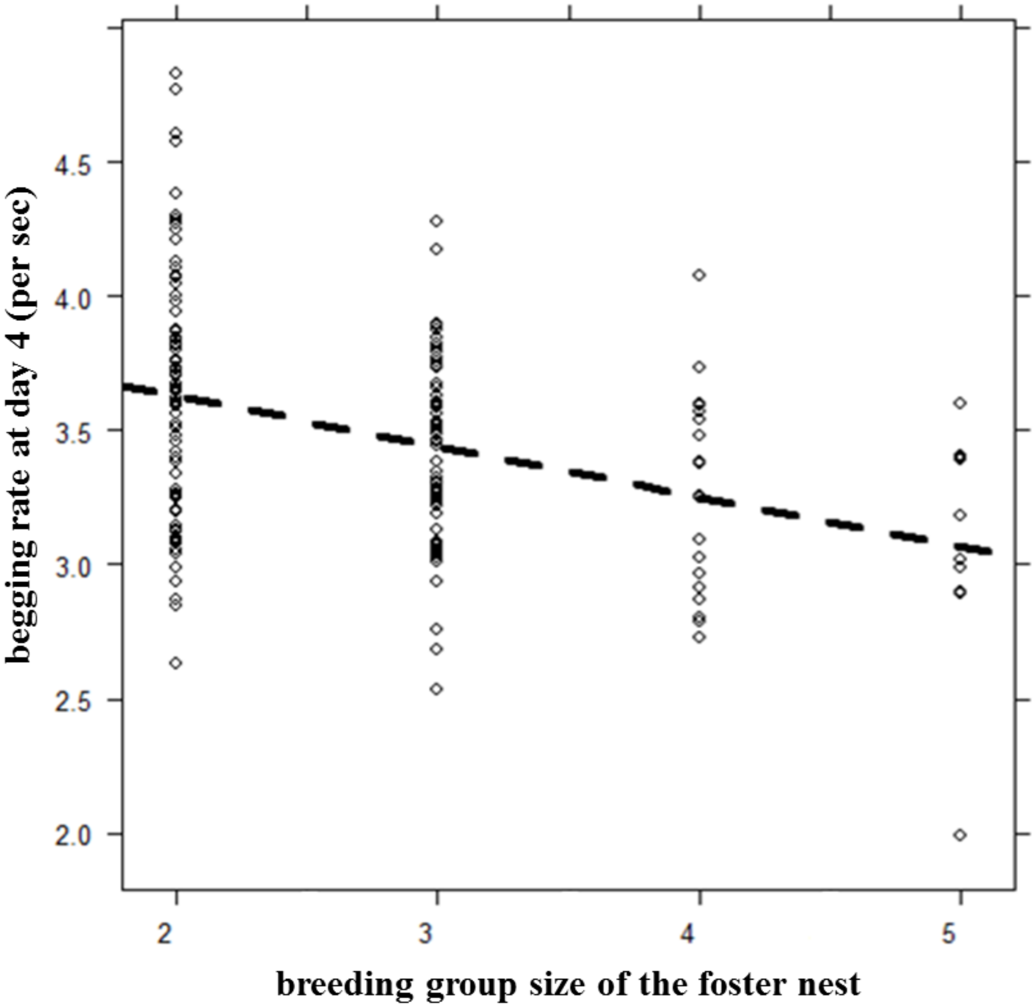


**Figure 2. Relationship between offspring begging rate at day 4 and number of adult birds feeding the foster nest.** The dashed line indicates the predicted values.

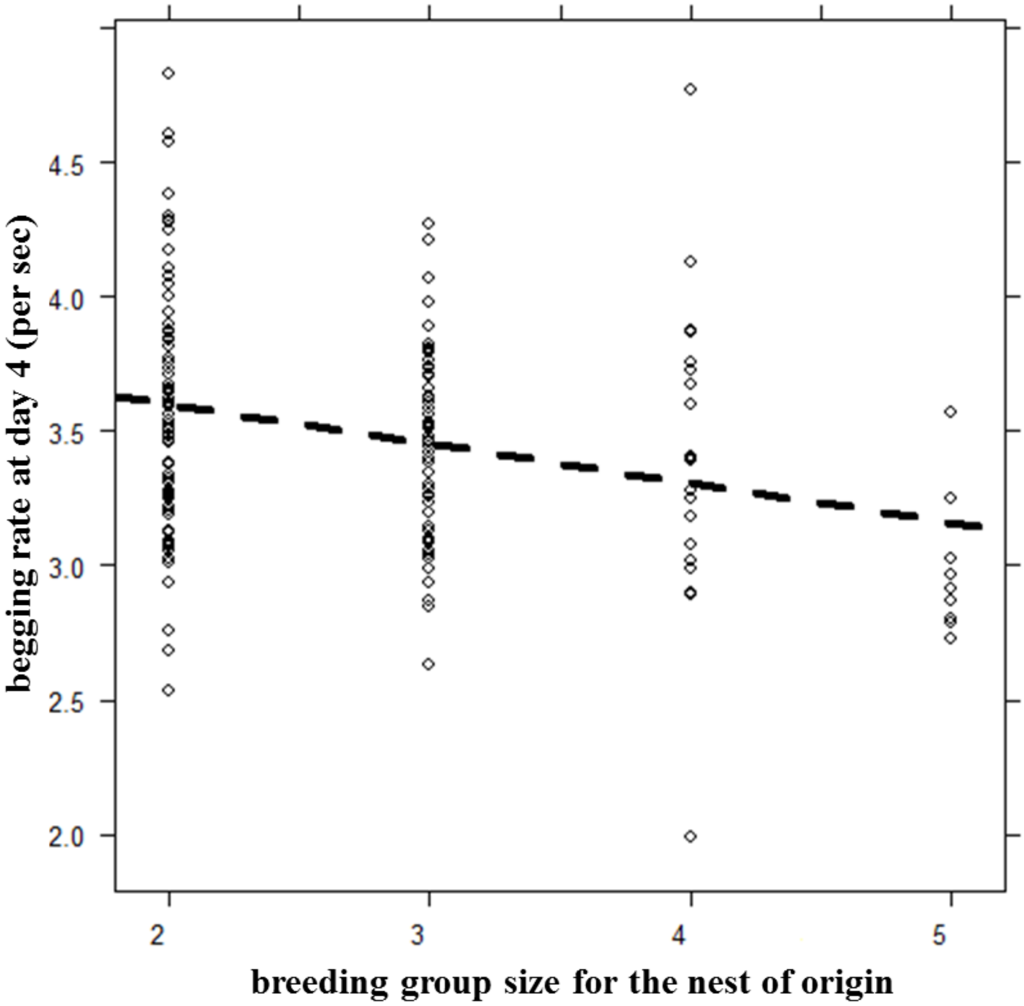


**Figure 3. Offspring begging rate at day 4 decreased with the breeding group size of the nest of origin (before cross fostering).** The line indicates the predicted values.

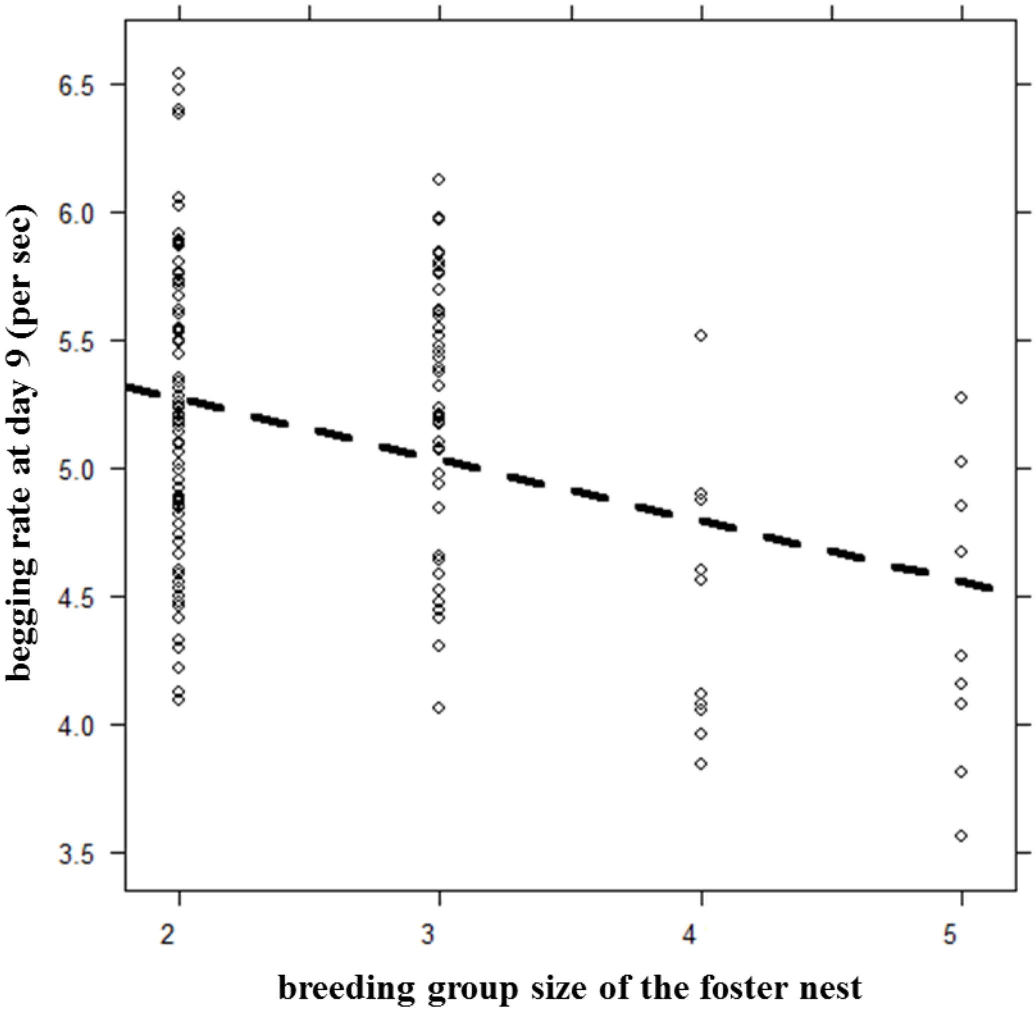


**Figure 4. Relationship between offspring begging rate at day 9 and number of adult birds feeding the foster nest.** The line indicates the predicted values.

# *Manuscript 5: The effect of helpers on the post-fledging period of a cooperatively breeding bird, the sociable weaver*

*MASTER THESIS OF LARA BROOM*

***In Biodiversity Genetic and Evolution at the CIBIO, Portugal***

***Co supervised with Rita Covas and Claire Doutrelant***

## ABSTRACT

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 fledglings 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:*** *cooperative breeding, capture-mark-recapture, post-fledging survival, helpers.*

## INTRODUCTION

Cooperative behavior 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 (S. A. West, Griffin, & Gardner, 2007; S. A. West, Griffin, Gardner, & Diggle, 2006). In higher orders of biological organization cooperation exists in various ways – some animals cooperate in the detection and/or defense 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, & 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 behavior 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 behavior 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 behavior 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 & Hamilton, 1981).

A specific case of cooperative behavior is cooperative breeding. This happens in some species of vertebrates, mainly insects, birds and mammals (Clutton-brock, 2002; Cornwallis et al., 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 & West, 2002). Several studies have found that helping behavior 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 (Doutrelant, Dalecky, & Covas, 2011; Wright, McDonald, te Marvelde, Kazem, & Bishop, 2010). 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 (Doerr & Doerr, 2007; Hodge, 2005; Woxvold & Magrath, 2005).

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 (N. J. Raihani & 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, Young, Spong, Jordan, & B, 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 (N. J. Raihani & 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 (Cheng & Martin, 2012; Martin, 1995). In agreement with this study, a recent comparative study showed that cooperative species tend to fledge their young earlier (A R Ridley & 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 (Covas, Plessis, & Doutrelant, 2008; Hatchwell, 1999) 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, S.A. 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 (Nichola J Raihani & Ridley, 2008). A similar behaviour was observed for the cooperatively breeding apostlebirds (Woxvold & 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., 2007). 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 (Covas et al., 2011; McGowan, Hatchwell, & Woodburn, 2003; Sankamethawee, Gale, & Hardesty, 2009). 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 et al., 2009); in one study done on long tailed tits, there was a positive effect (McGowan et al., 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 behavior 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.

To determine whether lower juvenile survival in the presence of helpers is due to a higher mortality or to increased dispersal, we first 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 investigated whether the presence of helpers affected the duration of the nestling period, and 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 G.L., 1973e). They build a very large communal nest (the colony), which is made of *Stipagrostis* grasses, and is built most commonly on Acacia trees (Mendelsohn J.M., Anderson M.D. 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, Dalecky, Caizergues, & Doutrelant, 2006; Covas et al., 2008). Both sexes can help, but helpers older than 1 year are normally all males (Doutrelant et al., 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 G.L., 1973e, Covas et al., 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 G.L., 1973a).

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 et al., 2011). These studies suggest that both direct and indirect (kin selected) fitness benefits are important to maintain the helping behavior 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 unfavorable conditions, such as large group size or low rainfall (Covas et al., 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 aluminum ring and a unique color 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 et al., 2008).

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 every day 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 every day 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 G.L., 1973e) 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 color 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 a maximum of 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 time points. During the study new chicks would fledge and so in each occasion we would observe new juveniles, and also record their presence. A maximum of 12 colonies were observed in the same occasion. 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 analyses*

Using the individual capture histories it is possible to estimate survival parameters via maximum likelihood methods (Jean-Dominique Lebreton , Kenneth P . Burnham , Jean Clobert, 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.

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 also tested the interactions between each covariate and the effect of helper presence/absence. Rain was defined as the total amount of rain that occurred on the previous 30 days to day 17 (Covas et al., 2008; Dean & Milton, 2001).

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 et al., 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 modeled 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.

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, we use instead Phi(1age)p(t+c) as our base model. We did not test any of the variables mentioned in the period following 30 days.

**Table 1:** Modeling 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)** | 1048,0113 | 14,5656 | 0,00011 | 0,00070 | 12 | 1023,38 |
| 2.Phi(age)p(t) | 1051,9443 | 18,4986 | 0,00002 | 0,00010 | 16 | 1018,84 |
| 3.Phi(t)p(t) | 1057,5022 | 24,0565 | 0,00000 | 0,00000 | 16 | 1024,40 |
| 4.Phi(age)p(age) | 1059,6073 | 26,1616 | 0,00000 | 0,00000 | 16 | 1026,50 |
| 5.Phi(t)p(.) | 1064,0523 | 30,6066 | 0,00000 | 0,00000 | 8 | 1047,76 |
| 6.Phi(.)p(t) | 1068,8353 | 35,3896 | 0,00000 | 0,00000 | 11 | 1046,30 |
| 7.Phi(.)p(.) | 1090,9193 | 57,4736 | 0,00000 | 0,00000 | 2 | 1086,90 |

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

**Table 2:** Modeling 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)** | 1040,72 | 7,27 | 0,00428 | 0,02630 | 13 | 1013,99 |
| 2.Phi(2age)p(t+h+c) | 1042,72 | 9,27 | 0,00157 | 0,00960 | 14 | 1013,87 |
| 3.Phi(2age)p(t+h) | 1047,90 | 14,45 | 0,00012 | 0,00070 | 13 | 1021,17 |
| 4.Phi(2age)p(t) | 1048,01 | 14,56 | 0,00011 | 0,00070 | 12 | 1023,38 |

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

## Fledgling period analysis

The aim of this analysis was to investigate if juveniles with helpers fledged earlier than juveniles without helpers. 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). Fledging in this species usually occurs when the juveniles are 21-25 days old. 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 analyzed 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 center 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 analyze 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, G. P. and M. J. Keough, 2002). For these analyses we conducted linear mixed models using the package nlme in R (R Core Team 2013) using). 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).

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.

**Table 3:** Modeling 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.

Rainfall was present in 6 models and had always a positive effect on survival probability (Fig. 4). Colony size was present in 4 models and had always a negative effect on survival (Fig. 3). Group size was present in 2 models, and had always a negative effect on survival (Fig. 2). Finally, helpers 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).

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).

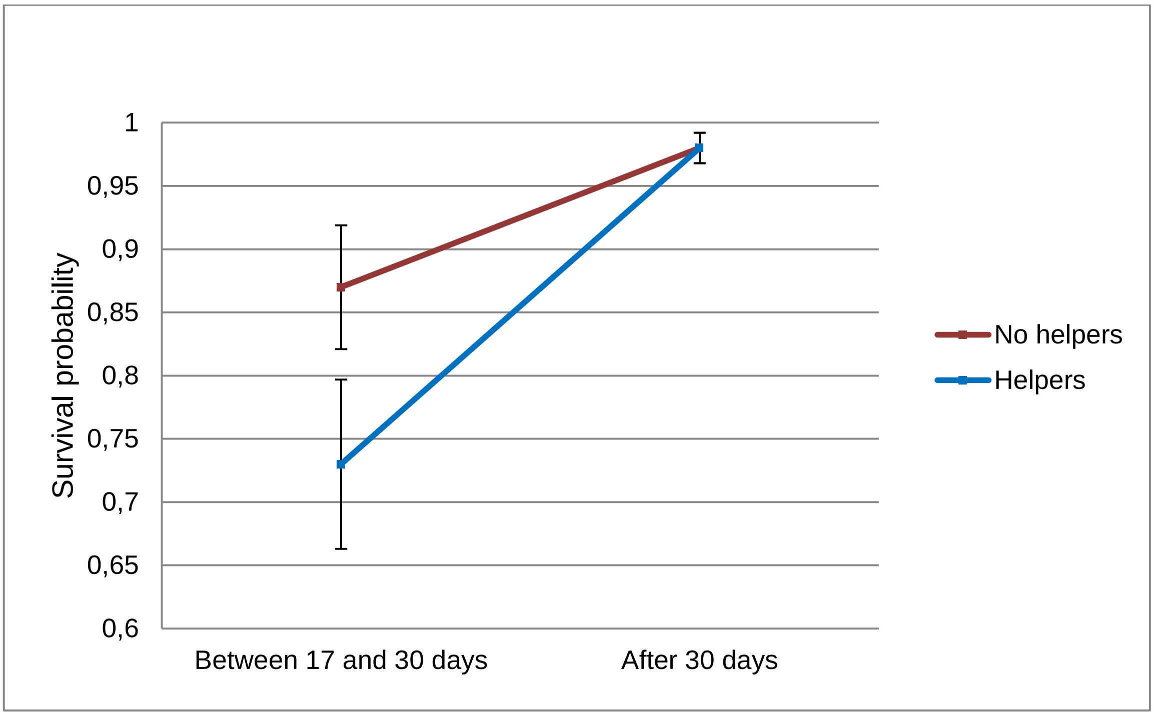


**Figure 1:** Survival probability between 17 to 30 days and after 30 days of juveniles raised in groups (triangles) versus juveniles raised in pairs (squares). Estimates taken from the model Phi(1age+h+R)p(t). Standard errors are given.

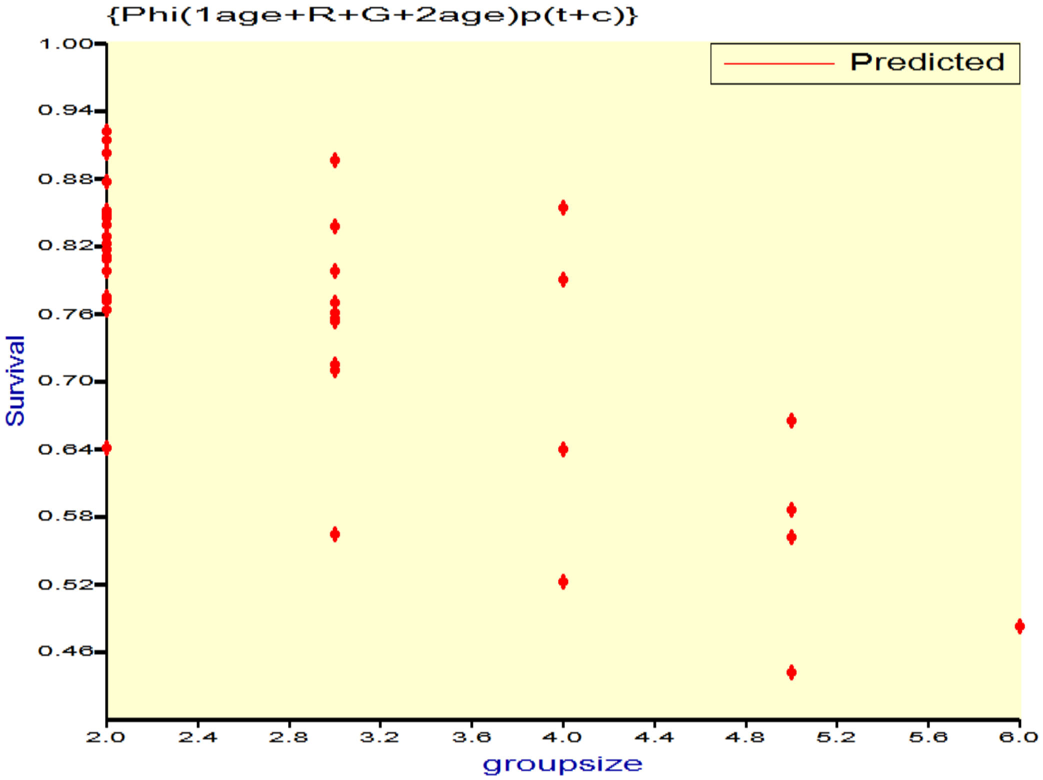


**Figure 2:** Survival probability in relation to group size from the model Phi(1age+R+G)p(t+c).

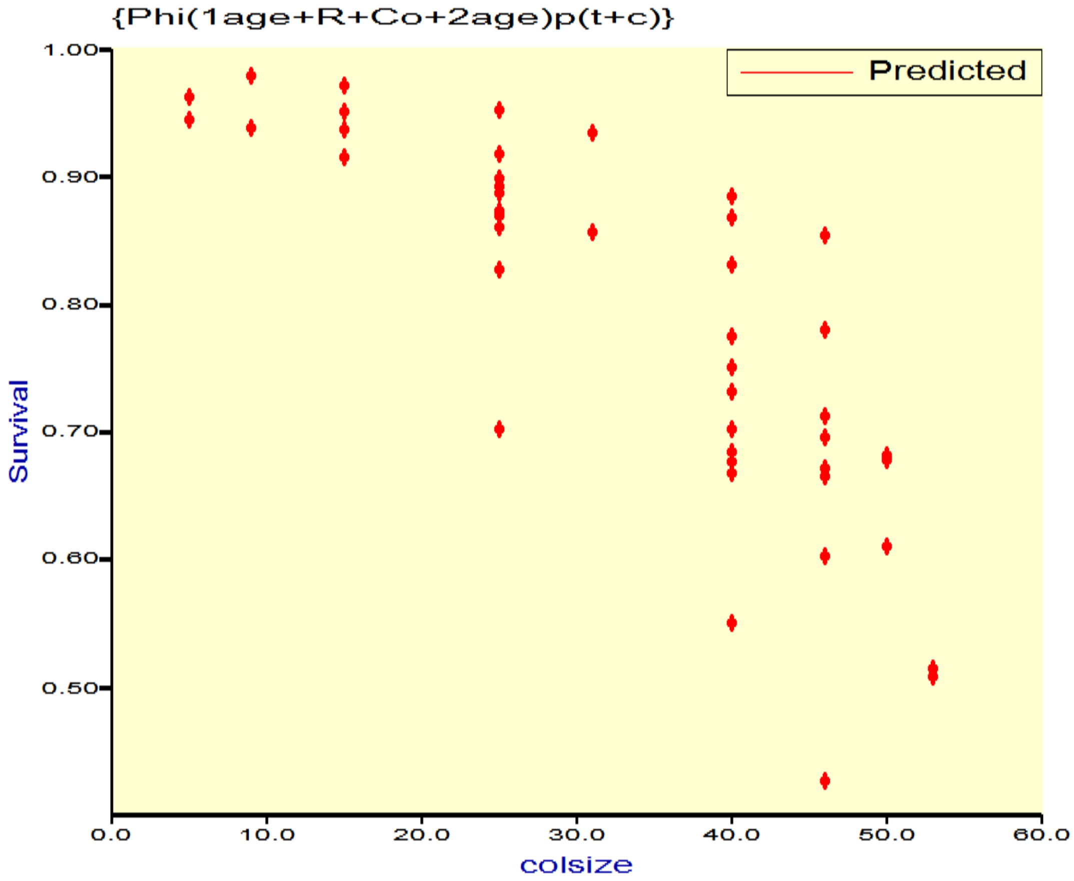


**Figure 3:** Survival probability in relation to colony size from the model Phi(1age+R+Co)p(t+c).

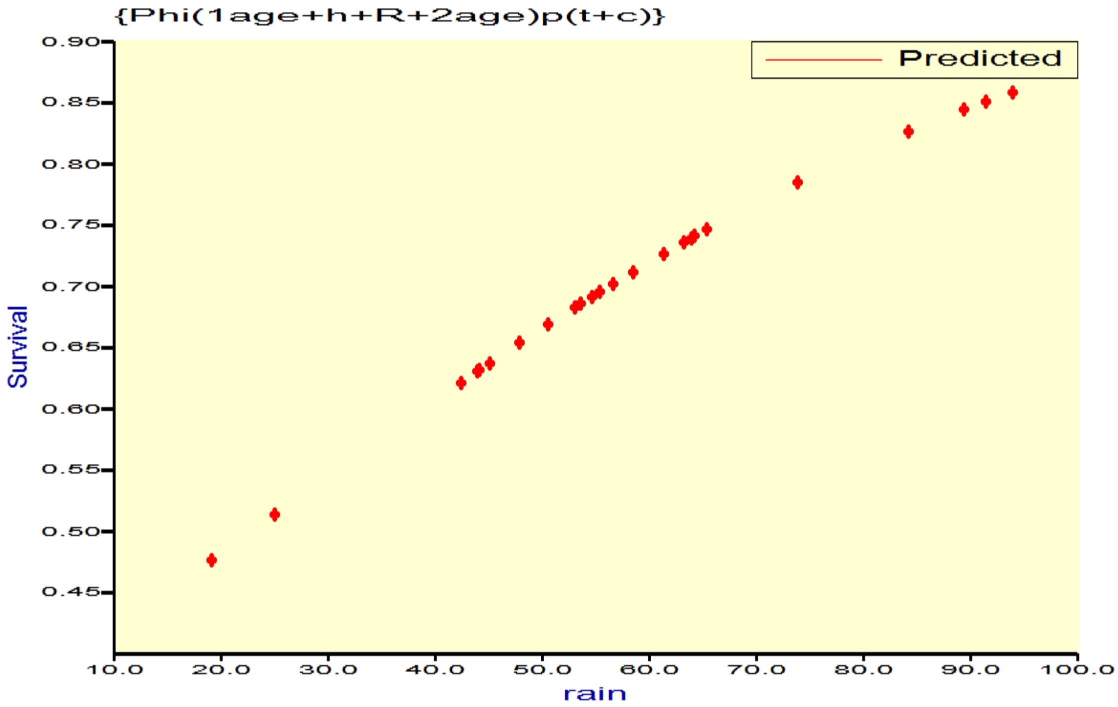


**Figure 4:** Survival probability in relation to rainfall (mm) from the model Phi(1age+h+R)p(t+c).

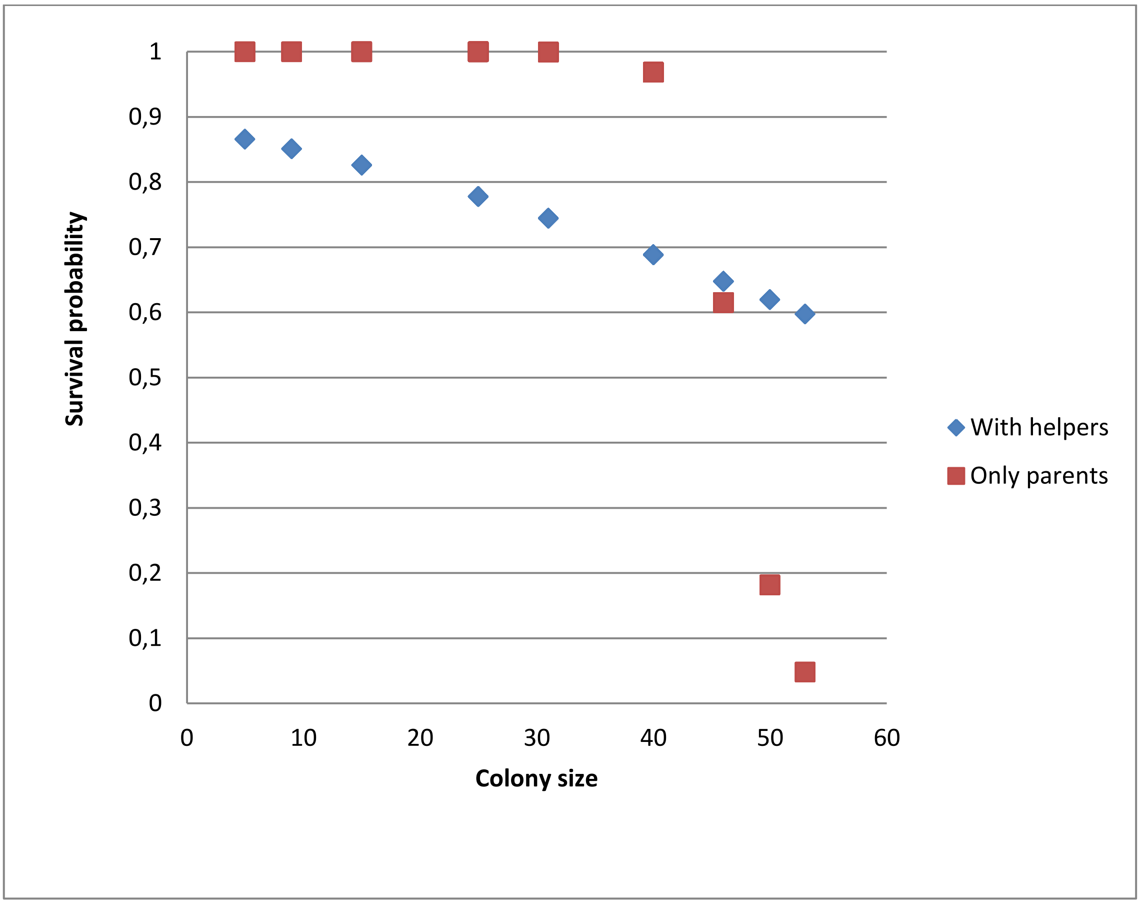


**Figure 5:** Survival probability in relation to colony size for juveniles raised with and without helpers from the model Phi(1age+h*Co)p(t). For larger colonies (> 45 inds), 13 juveniles were raised without helpers, and 28 were raised with helpers.

### *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:** LMM showing the terms associated with the temperature inside the nest during the day. The significance of each term when it was dropped from the model is presented.

| | numDF | denDF | F-value | p-value | Value | Std.Error |
|---|---|---|---|---|---|---|
| Intercept | 1 | 104 | 1604,3922 | <.0001 | -3632,164 | 1296,7324 |
| **Day** | 1 | 104 | 33.951 | <.0001 | -0.39 | 0.0818 |
| **Average Ambient temperature** | 1 | 104 | 57.268 | <.0001 | 0.443 | 0.0577 |
| **Number of fledglings** | 1 | 104 | 4.651 | 0.0333 | 0.532 | 0.234 |
| **Laying date** | 1 | 18 | 7.962 | 0.0113 | 0.089 | 0.0315 |
| **Group type** | 1 | 17 | 3.399 | 0.0827 | | |
| **Parents** | | | | | -0.602 | 0.4568 |
| Day x group type | 1 | 103 | 0.576 | 0.4495 | | |
| <u>Model 2</u> | | | | | | |
| Group size | 1 | 17 | 1.703 | 0.2093 | | |
| Day x group size | 1 | 103 | 0.857 | 0.3566 | | |

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

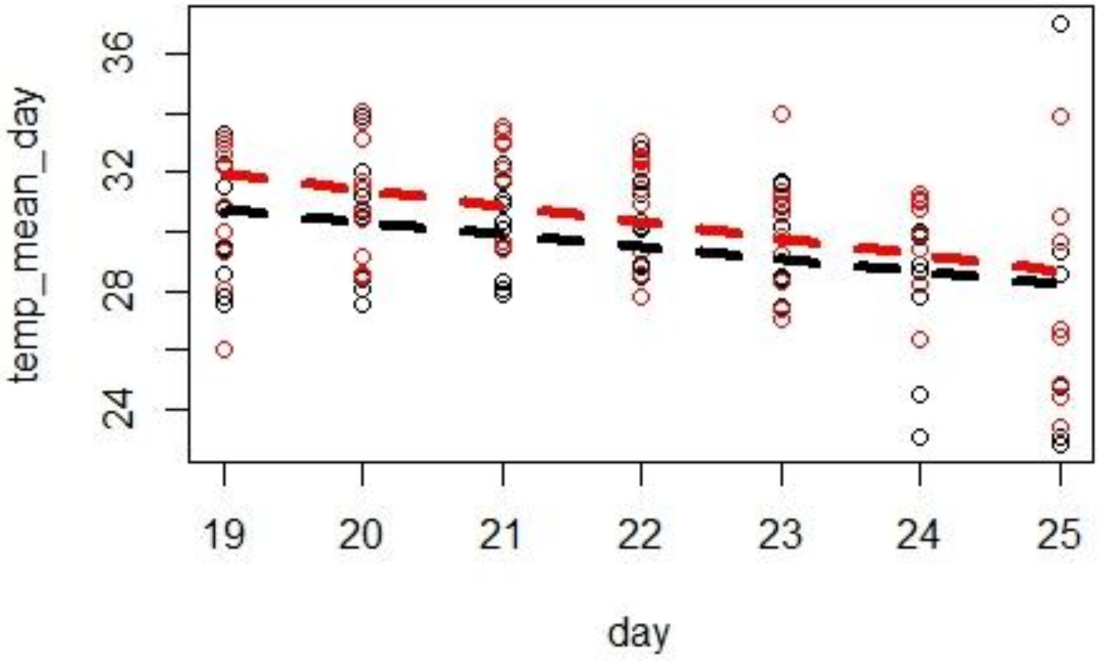


**Figure 6:** Daytime temperature for nests with only parents (black line) and with parents and helpers (red line), measured from day 19 to 25.

### *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 6:** Factors tested for an effect on the inter-nesting interval. The significance of each term when it was dropped from the model is presented. Analyses based on group size and group type were conducted separately.

| | numDF | denDF | F-value | p-value |
|---|---|---|---|---|
| Group type | 1 | 20 | 193.150 | 0.1799 |
| Number 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 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 |
| **Number Group size x 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. 2013, in press, 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 analyzed annual survival on this species, and found that fledglings raised in groups had lower survival probability in their first year (Covas et al., 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 & 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 et al., 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 (A R Ridley & 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 (Nichola J Raihani & Ridley, 2008). In sociable weavers, parents are known to lower their feeding rates, during the nestling stages, when they have helpers (Covas et al., 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 (Nichola J Raihani & 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 et al., 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 (A R Ridley & 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 & Martin, 2012). In species with high nest predation, like the sociable weaver (where ca 70% of all clutches are lost to predation; Covas et al., 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 (A. R. Ridley & 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, Griesser, & Sheffield, 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., 2007). This is not the case in sociable weavers, since dispersal does not take place so early in life, however, we cannot 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. 2013, in press). This is in accordance with the fact that insect availability increases with rain, which is the main food source of sociable weavers (Maclean G.L., 1973e). 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 et al., 2008). Another capture-mark-recapture study done on the cooperatively breeding Seychelles warbler found that survival decreased with increasing group size (Brouwer, Richardson, Eikenaar, & Komdeur, 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, 2000). 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 (Legge, 2000). The same thing happens in other cooperatively breeding species: long-tailed tits (Meade, Nam, Beckerman, & Hatchwell, 2010), rufous vanga in Madagascar (Eguchi, 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, S. C. 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 et al., 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 et al., 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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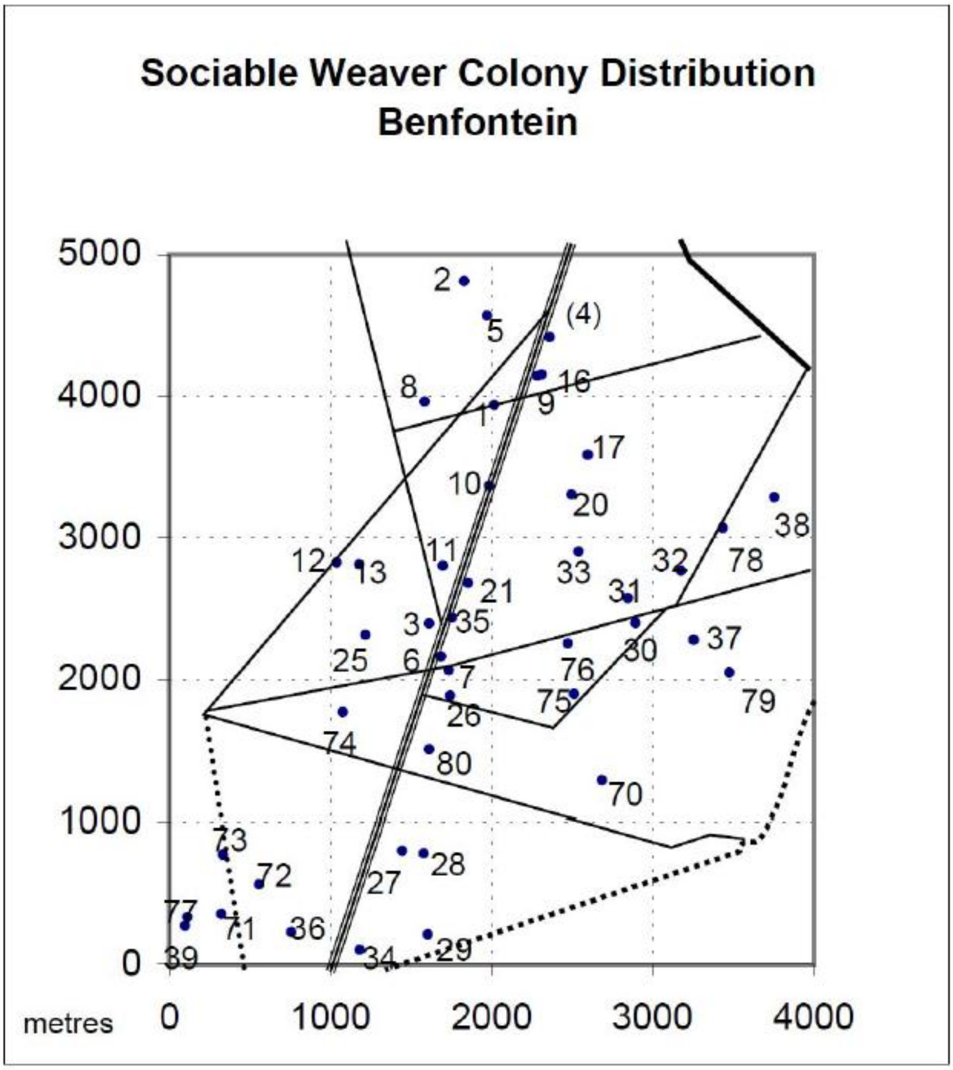
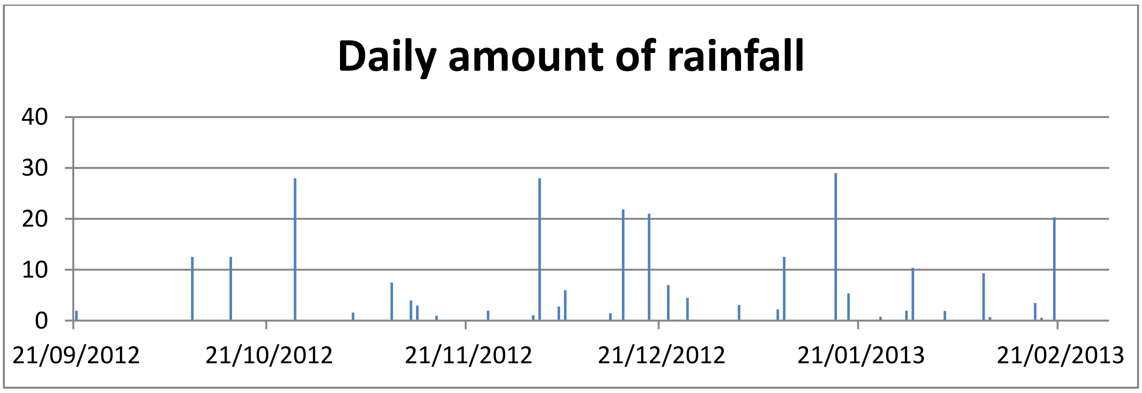
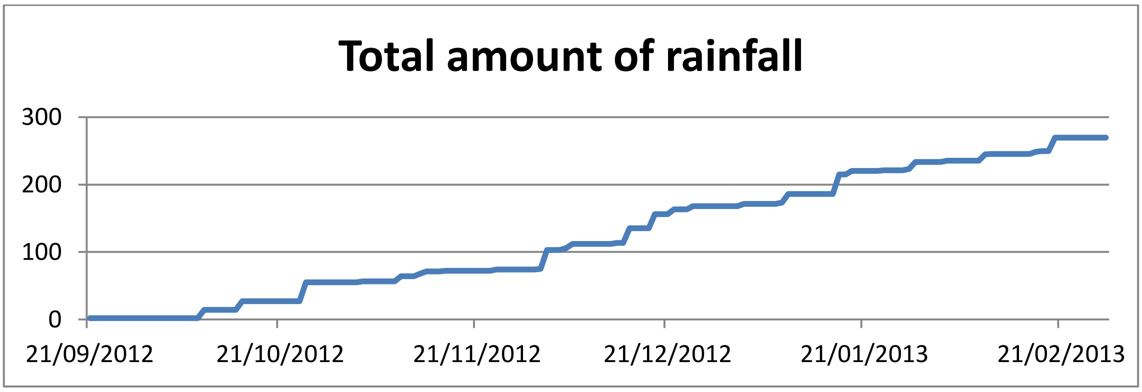
# ANNEXES MANUSCRIPT 5

**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).

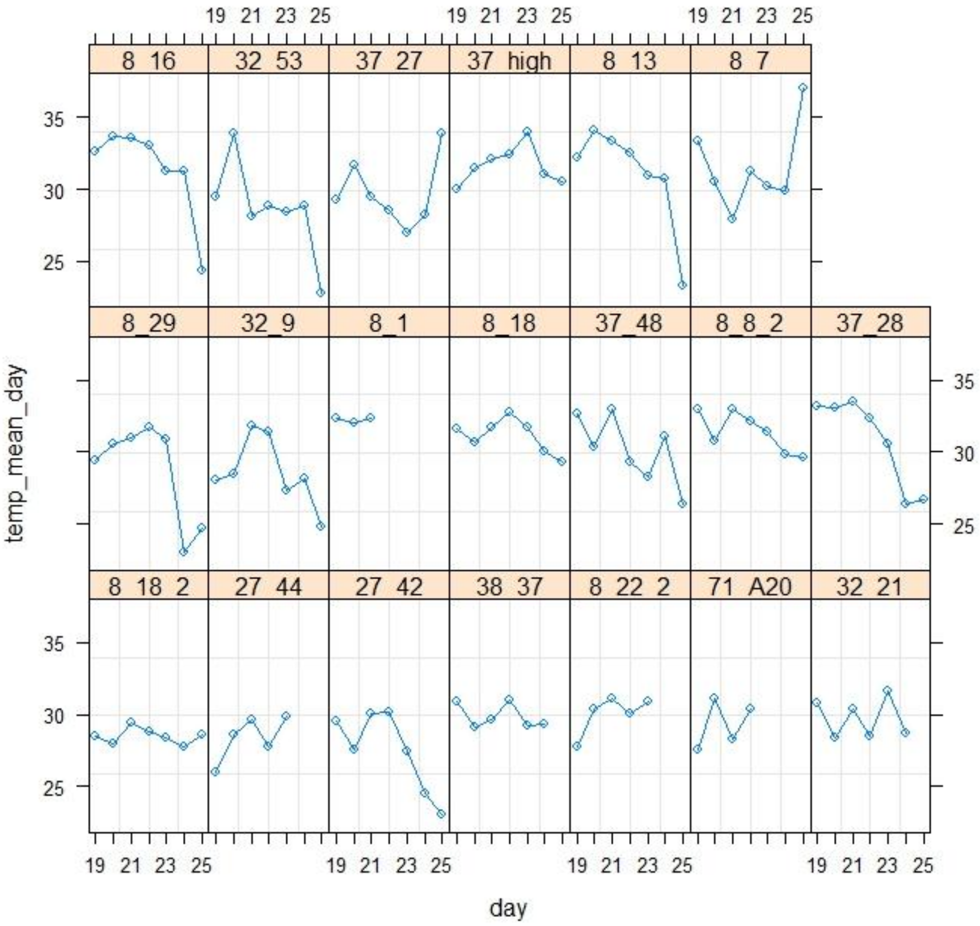




**Annex 3:** Number of individuals known to be present at the colonies analyzed. Colony sizes were deducted from the captures before the breeding season.

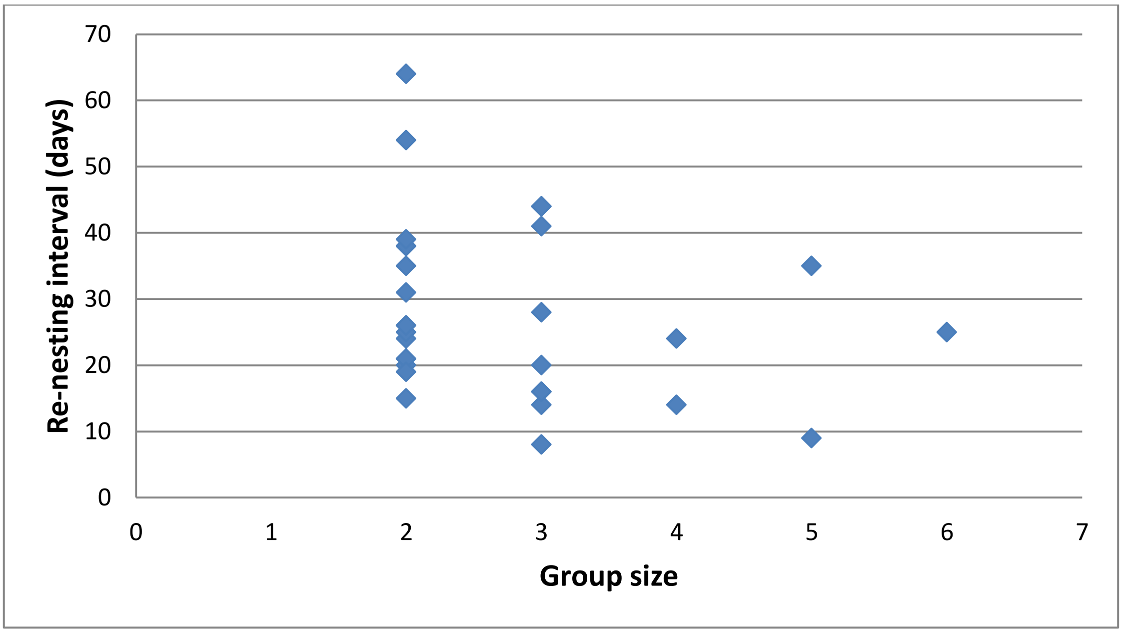
| Colony ID | Colony size (Number of individuals) |
|---|---|
| **2** | 15 |
| **6** | 5 |
| **8** | 40 |
| **11** | 31 |
| **20** | 25 |
| **27** | 15 |
| **31** | 50 |
| **32** | 25 |
| **37** | 46 |
| **38** | 53 |
| **39** | 9 |
| **71** | 9 |

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

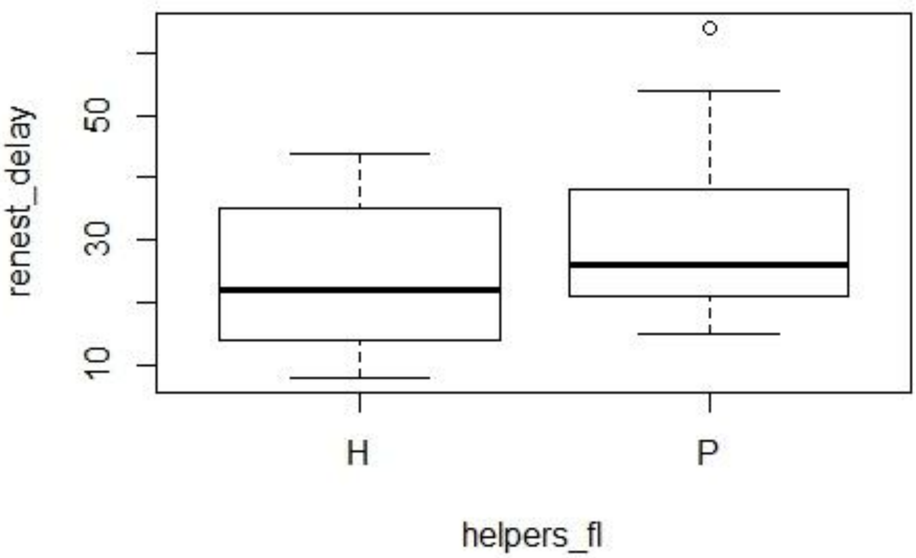


Legend: Identification of colony _ Identification of the nest

**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, 2age: 2-age classes, Co: colony size, h: helper effect, R: rainfall, G: group size, G: group type, B: brood size, C: chick order; W: day 17 weight, S: snake protection.

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

| | | | | | |
|---|---|---|---|---|---|
| **Phi(1age+R+B+2age)p(t+c)** | 1037.509 | 4.0636 | 0.01624 | 0.1311 | 15 | 1006.536 |
| **Phi(2age*h)p(t+c)** | 1038.094 | 4.6486 | 0.01212 | 0.0979 | 15 | 1007.121 |
| **Phi(1age+G+2age)p(t+c)** | 1038.149 | 4.7035 | 0.01179 | 0.0952 | 14 | 1009.299 |
| **Phi(2age+h+c)p(t+c)** | 1038.253 | 4.8068 | 0.0112 | 0.0904 | 15 | 1007.279 |
| Phi(2age+G)p(t+c) | 1038.456 | 5.0099 | 0.01012 | 0.0817 | 14 | 1009.605 |
| **Phi(1age+h*B+2age)p(t+c)** | 1038.552 | 5.1062 | 0.00964 | 0.0778 | 16 | 1005.446 |
| **Phi(1age+h+Co+B+2age)p(t+c)** | 1038.657 | 5.2112 | 0.00915 | 0.0739 | 16 | 1005.551 |
| **Phi(1age+h+Co+Gd+2age)p(t+c)** | 1038.792 | 5.3459 | 0.00855 | 0.069 | 16 | 1005.686 |
| **Phi(1age+Co+B+2age)p(t+c)** | 1038.812 | 5.3658 | 0.00847 | 0.0684 | 15 | 1007.838 |
| **Phi(1age+h*C+2age)p(t+c)** | 1038.996 | 5.5507 | 0.00772 | 0.0623 | 16 | 1005.891 |
| **Phi(1age+h*R+h*B+2age)p(t+c)** | 1039.108 | 5.6625 | 0.0073 | 0.0589 | 18 | 1001.712 |
| **Phi(1age+h+W+2age)p(t+c)** | 1039.163 | 5.717 | 0.0071 | 0.0573 | 15 | 1008.189 |
| **Phi(1age+h+C+2age)p(t+c)** | 1039.21 | 5.7645 | 0.00694 | 0.056 | 15 | 1008.237 |
| **Phi(2age+h)p(t+c)** | 1039.274 | 5.8279 | 0.00672 | 0.0543 | 14 | 1010.423 |
| **Phi(1age+h+S+2age)p(t+c)** | 1039.282 | 5.8367 | 0.00669 | 0.054 | 15 | 1008.309 |
| **Phi(1age+h+B+2age)p(t+c)** | 1039.336 | 5.8902 | 0.00651 | 0.0526 | 15 | 1008.362 |
| Phi(2age+c)p(t+h+c) | 1039.536 | 6.0906 | 0.00589 | 0.0476 | 15 | 1008.563 |
| **Phi(2age+h+c)p(t+h+c)** | 1040.02 | 6.5744 | 0.00463 | 0.0374 | 16 | 1006.914 |
| **Phi(1age+W+G+2age)p(t+c)** | 1040.18 | 6.7344 | 0.00427 | 0.0345 | 15 | 1009.207 |
| **Phi(2age+h*co)p(t+c)** | 1040.187 | 6.7415 | 0.00426 | 0.0344 | 16 | 1007.082 |
| **Phi(1age+C+G+2age)p(t+c)** | 1040.225 | 6.7795 | 0.00418 | 0.0338 | 15 | 1009.252 |
| **Phi(1age+B+G+2age)p(t+c)** | 1040.237 | 6.7909 | 0.00415 | 0.0335 | 15 | 1009.263 |
| **Phi(1age+S+G+2age)p(t+c)** | 1040.265 | 6.819 | 0.00409 | 0.033 | 15 | 1009.291 |
| **Phi(2age+G+h)p(t+c)** | 1040.411 | 6.9648 | 0.00381 | 0.0308 | 15 | 1009.437 |

| | | | | | | |
|---|---|---|---|---|---|---|
| **Phi(2age+h)p(t+h+c)** | 1040.48 | 7.0345 | 0.00368 | 0.0297 | 15 | 1009.507 |
| Phi(2age)p(t+c) | 1040.722 | 7.276 | 0.00326 | 0.0263 | 13 | 1013.986 |
| **Phi(1age+h*S+2age)p(t+c)** | 1041.056 | 7.6104 | 0.00276 | 0.0223 | 16 | 1007.95 |
| **Phi(1age+h*W+2age)p(t+c)** | 1041.224 | 7.7782 | 0.00253 | 0.0204 | 16 | 1008.118 |
| **Phi(1age+h+B+W+2age)p(t+c)** | 1041.265 | 7.8194 | 0.00248 | 0.02 | 16 | 1008.159 |
| **Phi(1age+h+C+B+2age)p(t+c)** | 1041.302 | 7.8567 | 0.00244 | 0.0197 | 16 | 1008.197 |
| **Phi(2age+h+S)p(t+c)** | 1041.378 | 7.9323 | 0.00235 | 0.019 | 15 | 1010.404 |
| **Phi(1age+h*B+h*C+2age)p(t+c)** | 1041.471 | 8.0256 | 0.00224 | 0.0181 | 18 | 1004.075 |
| **Phi(1age+Ch+2age)p(t+c)** | 1042.428 | 8.9822 | 0.00139 | 0.0112 | 14 | 1013.578 |
| Phi(2age)p(t+h+c) | 1042.722 | 9.2767 | 0.0012 | 0.0097 | 14 | 1013.872 |
| **Phi(1age+S+2age)p(t+c)** | 1042.83 | 9.3847 | 0.00114 | 0.0092 | 14 | 1013.98 |
| **Phi(1age+B+2age)p(t+c)** | 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+c)** | 1043.461 | 10.0152 | 0.00083 | 0.0067 | 16 | 1010.355 |
| **Phi(t+c)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(3age)p(t) | 1048.011 | 14.5656 | 0.00009 | 0.0007 | 12 | 1023.382 |
| Phi(2age+c)p(t+h) | 1049.499 | 16.0537 | 0.00004 | 0.0003 | 14 | 1020.649 |

|  |  |  |  |  |  |  |
|---|---|---|---|---|---|---|
| Phi(2age+c)p(t) | 1049.877 | 16.4309 | 0.00003 | 0.0002 | 13 | 1023.141 |
| **Phi(2age+h+c)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+c)** | 1052.335 | 18.8895 | 0.00001 | 0.0001 | 8 | 1036.047 |
| **Phi(1age+2age)p(1age+R+h+c)** | 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(g*t)p(.) | 1067.985 | 34.5397 | 0 | 0 | 13 | 1041.25 |
| Phi(.)p(t) | 1068.835 | 35.3896 | 0 | 0 | 11 | 1046.304 |
| Phi(g)p(t) | 1070.843 | 37.3969 | 0 | 0 | 12 | 1046.214 |
| Phi(age)p(.) | 1072.468 | 39.022 | 0 | 0 | 7 | 1058.244 |
| Phi(g*t)p(t) | 1072.564 | 39.1178 | 0 | 0 | 26 | 1017.651 |
| Phi(t)p(g*t) | 1073.877 | 40.4312 | 0 | 0 | 27 | 1016.733 |
| Phi(g*t)p(g*t) | 1077.86 | 44.4143 | 0 | 0 | 32 | 1009.423 |
| Phi(.)p(g*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+c)** | 1260.967 | 227.5216 | 0 | 0 | 15 | 1229.994 |

# ANNEX: The thermoregulatory benefits of the communal nest of sociable weavers *Philetairus socius* are spatially structured within nests

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# The thermoregulatory benefits of the communal nest of sociable weavers *Philetairus socius* are spatially structured within nests

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## ABSTRACT

Structures built by animals, such as nests, mounds and burrows, are often the product of cooperative investment by more than one individual. Such structures may be viewed as a public good, since all individuals that occupy them share the benefits they provide. However, access to the benefits generated by the structure may vary among individuals and is likely to be an important determinant of social organisation. Here we use the massive, communal nests of sociable weavers, *Philetairus socius*, to investigate whether their thermoregulatory function varies in relation to the size of communal nests, and the position of individual nest chambers within the communal structure. We then examine whether this spatial variation in thermoregulatory function predicts the social organisation of colonies. First, we show that the sociable weavers' communal nests buffer variation in ambient temperature, and reduce temperature variability within nest chambers. The extent of this buffering effect depends significantly on the position of nest chambers within the communal structure, and on the depth to which chambers are embedded within the nest mass. We detected no effect of nest volume on thermoregulatory benefits, suggesting that there are likely to be additional, non-thermoregulatory benefits leading to communal nests. Finally, our results indicate that there may be competition for access to the benefits of the public good, since older birds occupied the chambers with the highest thermoregulatory benefits, where breeding activity was also more common. We discuss how the spatial structure of the benefits of the public good might influence social organisation in the unique communal lifestyle of sociable weavers.

## INTRODUCTION

The function of physical structures built by animals to control their environment is often poorly understood and the extent to which such structures approach their adaptive optima is rarely investigated (Hansell 2005). Nests, burrows or mounds may provide thermoregulatory benefits (Reid et al. 2002), reduce the risk of predation for adults (Jackson 2000, Hölzl et al. 2009) or their offspring (Siedelmann 1999, Kleindorfer 2007, Prokop and Trnka 2011), or, in the case of bowers, they may act as signals to conspecifics (Humphries and Ruxton 1999, Olsson et al. 2009). In birds, parents and offspring benefit from well-insulated nests, slowing egg-cooling rates when the parents are not attending the clutch and thus reducing the parents' energetic costs of reheating the eggs to incubation temperatures (Collias and Collias 1984, Drent 1975, Reid et al. 2000). Nestling growth rates and offspring survival may also be influenced by nest microclimate (Martin and Schwabl 2008, Nord and Nilsson 2011). However, the extent to which animals may build nest structures to enhance thermoregulatory benefits is likely to be influenced by the time and energy costs of nest construction (McGowan et al. 2004, Mainwaring and Hartley 2009, Olsson et al. 2009, Moreno et al. 2010), as well as various interacting environmental factors, such as climate and predation risk (Spottiswoode 2007, Edelman 2011, Prokop and Trnka 2011).

An interesting characteristic of many of these physical structures built by animals is that they may be viewed as a public good. The benefits that are derived from the nest are shared among all of a nest's occupants, whereas the costs of construction of nests or burrows are borne only by the individuals that contribute to it. Therefore, when multiple individuals contribute to the construction of a communal nest, as in mound-building mice *Mus spicilegus* (Garza et al. 1997) or monk parakeets *Myiopsitta monachus* (Navarro et al. 1995; see also Manning et al. 1992, Ford and Johnson 2007, Bollazzi and Roces 2010), each individual would obtain the highest overall payoffs by not paying the costs of construction, but gaining the benefits of the communal structure. This type of conflict between individuals over investment in a public good is rife in nature (e.g. Hardin 1968, Arnqvist and Rowe 2005, MacLean and Gudelj 2006, McGowan et al. 2006, West et al. 2006, Gutierrez et al. 2011), and may eventually lead to the breakdown of cooperation in a process described by the tragedy of the commons (Hardin 1968). How such conflicts between individuals over investment in the communal good are resolved, depends on the costs and benefits of the public good, their spatial and temporal distribution, as well as on the social structure and dominance hierarchies within the community (Rankin et al. 2007).

Here, we examine spatial variation in the benefits of the massive communal nest of the sociable weaver *Philetairus socius* and the effects of this variation on social organisation. The nests of the sociable weavers are one of the largest nests known among birds, and both sexes invest in its building and maintenance (Collias and Collias 1978). The nest structure consists of nest chambers embedded within a communal thatch overarching the nest chambers. The nest chambers are used not only for breeding, but also for roosting throughout the year, which means that the potential thermoregulatory benefits extend beyond the breeding phase. Once constructed, the nest may exist for many decades and be used by many generations (Collias and Collias 1964). This communal structure provides an excellent model system to address questions concerning the function of the nest as a public good and the variation in the benefits that individuals derive from that public good. Two previous studies directly addressed the potential benefits of the sociable weaver’s nest, showing that it buffers against low temperatures at night, especially during winter, and against high temperatures during the day, especially in the summer (White et al. 1975, Bartholomew et al. 1976). Although these studies revealed the heat retaining capacities of the thatch and the nest chambers, their focus was on how the ecology of the sociable weaver may be affected by the ameliorating effects of their communal nests. Furthermore, birds were allowed to enter the nest chambers in which temperature was recorded, and temperature was measured in very few chambers in one or two nests. In order to understand the social organisation of sociable weaver colonies and the benefits of contributing to the communal structure it is necessary to determine whether the thermoregulatory benefits of a communal nest vary between colonies of different sizes and between nest chambers at different positions within colonies. Measurements of such benefits should be recorded without birds present in the nest.

The objective of this study was to measure the temperature inside multiple nest chambers within colonies of different volumes to investigate whether: (i) the volume of the nest predicts its thermoregulatory properties, (ii) the thermoregulatory properties vary within colonies depending on the position of the nest chamber, and (iii) the thermoregulatory benefits of nest chambers predict social organisation at colonies. We expected: (i) the benefits to increase with increasing volume of the thatch, and (ii) towards the centre of the nest where the size of the thatch is likely to be largest; and (iii) that the chambers that provide the largest buffer against the ambient temperatures would be occupied by better competitors and would have a higher probability of breeding activity. Here we use the age of an individual as a proxy for its competitive abilities, the rationale being that male sociable weavers are philopatric to their natal colonies (Brown et al. 2003, Doutrelant et al. 2004) and older birds are therefore likely to be better able to obtain the best nest chambers due to their experience and prior occupancy at a given colony.

## METHODS

### Study species and field site

The sociable weaver is a colonial, cooperatively breeding passerine endemic to the semi-arid *Acacia* savannahs of southern Africa that are associated with the Kalahari ecosystem (Spottiswoode 2005). These weavers live in colonies varying in size from five to over 300 individuals that are built communally by the colony members. The colony structure consists of thatched *Stipagrostis* grasses forming a large structure into which the individual nest chambers are embedded. In addition to being used for breeding, the nest chambers are used for roosting throughout the year by family groups or, more rarely, by single individuals (Maclean 1973; RC, CD and MP pers. obs.). The colonies are typically built on *Acacia* trees, although other tree species and man-made structures, such as telephone poles, can also be used (Maclean 1973).

The study was conducted between 8 September and 5 December 2010 and between 23 September and 22 December 2011 at Benfontein Game Farm, Kimberley, South Africa (28°52’ S, 24°50’E). This study area, containing approximately 30 colonies of sociable weavers, covers about 15km$^2$ of Kalahari sandveld, consisting of open savannah dominated by *Stipagrostis* grasses and camelthorn trees, *Acacia erioloba*. In this study we included data from 20 colonies.

**Temperature logging**

We logged the ambient temperature and the temperature inside the nest chambers at 20 colonies using a flexible thermistor PB-5006-3M probe, which was inserted into the nest chamber to a constant depth (to the centre of the nest chamber) and was connected to a TinyTag Plus 2 TGP-4510 data logger (Gemini Data Loggers Ltd., Chichester, UK) recording data every 30s. The temperature probe was inserted into nest chambers at three different positions at each colony: T1 – a nest chamber near the edge of the communal nest (mean distance to nearest edge ± SD: 12.8 ± 3.8cm, n = 18 colonies), T2 – a nest chamber at intermediate distance from the edge of the communal nest (26.5 ± 8.5cm, n = 13), and T3 – a nest chamber near the centre of the communal nest (55.5 ± 14.7cm, n = 20).

After inserting the temperature probe, we sealed off the entrance to the nest chamber using chicken wire and a single layer of mosquito netting. This allowed the normal airflow in and out of the chambers, but prevented birds from entering the chambers, which would disturb our measurements of the physical thermoregulatory conditions inside the chamber. The ambient temperature was logged near the thatch on the branch supporting the communal nest in the shade and at a similar height from the ground as the communal nest. The temperature inside the three chambers and the ambient temperature were measured simultaneously for a continuous period of 78hr 14min 32s ± 14hr 7min 18s per nest (mean ± SD). All temperature measurements were conducted before and during the early phase of the breeding season when the sociable weavers may regularly switch between nest chambers for roosting (REvD and MP, unpublished data). None of the monitored chambers contained eggs or nestlings. Thus, disturbance to roosting or breeding activity was likely to be minimal. The depth of the nest chamber where we inserted the temperature probe was measured as a straight line from the outer rim of the entrance tunnel alongside the lip at the base of the nest chamber to the ceiling of the nest chamber using a ruler.

**Communal nest volume**

A digital photograph was taken from each of four sides of the nest, each at a 90° angle to each other, at a fixed distance (10m) using a Panasonic Lumix TZ-7 camera. A 1m ruler with 10cm markings was held against the nest side that was photographed. The digital images were then imported into Adobe Photoshop (v. 7.0) to estimate the length, width and height of the nest, using our ruler to calibrate our measurements and the ‘measure tool’ in Adobe Photoshop to take the measurements. The length (or width) and height were taken across the centre of the visible side of the thatch on the photograph. To account for the irregularity of the nest shape to some extent, we estimated height of the thatch as the mean of the height measured on each of the four photographs (percentage of variation in measurements relative to the largest measurement per nest: 23.2 ± 14.1% (mean ± SD)), length as the mean of the length measured on the two photographs of the two longest sides of the thatch (9.5 ± 9.8%), and width as the mean of the length of the two shortest sides (13.6 ± 9.6%). The volume (in $m^3$) of the communal nest was then estimated as length x width x height.

**Nest chamber assignment**

The birds of the 20 colonies that we monitored were trapped using mist nets positioned around the nests at dawn, and were ringed with one numbered, metal ring and three colour rings (Covas et al. 2011). We labelled all nest chambers with an individually numbered tag. Individuals were assigned to nest chambers when they were seen building or roosting inside nest chambers at 15 colonies in 2010 and at 14 colonies in 2011 in observations conducted throughout the day (between 06:16 and 18:50 SAST). These observations were performed from a hide positioned beneath the nest for an average of 33h 53min ± 24h 56min per nest. The hide was placed initially at about 10m from the colony to accustom the birds to the hide and avoid disturbance. After at least 12h the hide was moved closer to the nest so that the nest chambers could be observed. When an individual used multiple nest chambers (n = 175 individuals out of a total of n = 432 individuals used 2.9 ± 1.2 (mean ± SD) nest chambers), we included the chamber that was used most frequently in the analyses concerning how age is related to the position of the nest chamber in the nest. For each individual we had 4.7 ± 7.9 (mean ± SD) observations.

Using a long-term dataset on the population of sociable weavers we studied (which has been regularly ringed since 1993), we then searched for birds whose exact age was known, i.e.

sociable weavers in the database that were first ringed as nestlings. When two individuals of known age used the same chamber at equal frequency, we randomly selected an individual to include in the analyses (n = 6 nest chambers; at four out of these six chambers the individuals had the same age). For each individual of known age we had 2.7 ± 2.1 observations.

We used photographs taken from the underside of the communal nest, so that a 1m ruler, the labelled nest chambers and their position were visible to measure the distance between the nest chambers and the nearest edge of the communal nest. For the nests where we assigned individuals to nest chambers in 2010, we also determined in which chambers, and at which position, a breeding attempt was observed (n = 75 nest chambers in 13 communal nests) between 9 September 2010 and 6 April 2011. A 'breeding attempt' was defined as eggs were laid. All nest chambers of 14 nests were checked for breeding activity approximately every three days during this period. For graphical purposes in figures 2 and 4 and for the analysis concerning likelihood of breeding activity we classified the position of the nest chambers following the criteria described above (T1 < 16.6 cm, 16.6 cm ≤ T2 < 35.0 cm, and T3 ≥ 35.0 cm).

**Statistical analyses**

The volume of the communal nest ($m^3$) (or nest segment if a colony consisted of two or three separate nest structures) and the number of birds in each colony (or nest structure) were highly correlated ($r = 0.880$, $df = 19$, $p < 0.001$). We therefore include only the volume in the models we present.

We used Linear Mixed Models (LMM) with restricted maximum likelihood implemented using the package nlme in R (R Development Core Team, 2011) to account for the pseudoreplication introduced by the statistical non-independence of multiple temperature measurements at a given position of a nest chamber (i.e. near the edge, in the centre or in between those positions) and of nest chambers within colonies. Position (where appropriate) and colony ID were entered as random factors with position nested within colony.

To determine whether communal nest volume or nest chamber position has thermoregulatory consequences, we used the temperature buffer ΔT, defined as the absolute difference between the ambient temperature and the temperature measured inside the nest chambers, as a response variable. We used the distance between the nest chamber and the nearest edge of the communal nest as the independent variable representing nest chamber position. Ambient temperature (°C) and nest volume ($m^3$) were entered as additional covariates. ΔT was square-root-transformed prior to the analyses concerning the spatial variation in temperature benefits to achieve a normal distribution of the errors. In order to accommodate the serial autocorrelation in our data due to diurnal effects, we used the mean values per hour for ΔT and for the ambient temperature in our LMMs and applied a moving average model as the class of autocorrelation structure (AIC = 2707.12, likelihood ratio = 3822.60, $p < 0.001$).

To test whether temperature variability changed towards the centre of the nest, we ran a separate LMM with the standard deviation of chamber temperature ($T_{SD}$) per position (i.e. T1, T2, and T3) per colony as the response variable. $T_{SD}$ was log-transformed to achieve a normal error structure prior to analyses. To investigate whether the change in temperature buffer or variability may depend on the depth of the nest chambers, we ran an LMM with depth of the nest chambers in response to the distance to the nearest edge of the nest chamber and to communal nest volume, including colony ID as a random effect. In order to analyse how the depth of a nest chamber predicts its thermoregulatory capacities, in a separate LMM we used the means of ΔT per nest chamber as the response variable with the depth of the nest chamber, the communal nest volume and the ambient temperature as covariates, while colony ID was entered as a random effect.

To investigate whether the position of the nest chamber predicted the age of its occupants, we used a LMM with maximum likelihood and occupant's age as the response variable, the nest chamber's distance from the nearest edge and volume of the communal nest as covariates, and colony ID as a random factor. If an individual of known age used more than one nest chamber (n = 12 individuals using 3.0 ± 1.3 nest chambers) we used the average distance between the nest chambers and the nearest edge of the nest in the analysis. Five out of these 12 individuals used 3.2 ± 1.3 nest chambers that were of the same distance category (i.e T1, T2 or T3). Age was log-transformed prior to analysis. To investigate whether the position of the nest chamber predicted the likelihood of a breeding attempt we calculated the proportion of nest chambers per position (i.e. T1, T2 and T3, using the criteria mentioned above) where a breeding attempt had been observed. This proportion of nest chambers was then square-root transformed and included as the response variable in an LMM with restricted maximum likelihood with position of the nest chamber as the fixed effect, and colony ID as the random factor.

## RESULTS

### Nest size

The ambient temperature at the colonies during observations ranged from 1.4°C at night to 42.4 °C during the day (median = 20.8 °C), while the temperature inside nest chambers ranged from 4.4 to 36.2 °C (median = 22.3 °C). ΔT ranged from 0.0 to 13.1 °C (median = 2.6 °C). Temperature was logged inside 51 nest chambers (18 at T1, 13 at T2, and 20 at T3) at 20 colonies, ranging in size from 0.7 $m^3$ to 10.0 $m^3$ and from 7 to 65 active nest chambers.

The thermoregulatory capacity of the sociable weaver's nest was not associated with the volume of the communal nest (Fig. 1, Table 1a), although ΔT was smallest at the nest with the smallest volume.

### Spatial variation of temperature buffer

ΔT increased significantly towards the centre of the colony (Fig. 2a, Table 1a), so that ΔT increased on average by 0.47 °C from position T1 to position T2 and by 0.57 °C from T1 to T3. These results remained unchanged when T3 or T1 were excluded from these analyses: ΔT increased significantly with the distance from the nearest edge from T1 to T2 (0.013 ± 0.005, df = 11, t = 2.447, p = 0.032) and from T2 to T3 (0.005 ± 0.002, df = 12, t = 2.633, $P$ = 0.022). Not only did ΔT increase towards the centre of the colony, but the temperature inside the chambers also became less variable (Fig. 2b, Table 1b), so that standard deviation of ΔT decreased on average by 0.73 °C from position T1 to position T2 and by 0.59 °C from T1 to T3. The low effect estimates of these results are probably a consequence of the relatively large spread of the data surrounding the observed increase in ΔT towards the centre of the colony.

The depth of the nest chambers was not predicted by the volume of the communal nest (Table 1c), but increased significantly towards the centre of the communal nest (Fig. 2c; Table 1c). Accordingly, ΔT increased (Fig. 3; Table 2a), and $T_{SD}$ decreased with the depth of the chamber (Table 2b). Volume appeared to be negatively associated with ΔT in this model, but the effect estimate of this result is extremely low. We did not find a significant interaction between depth of the chamber and the distance from nearest edge (df = 25, t = -0.148, p = 0.884; random effect 'Colony': p = 0.999).

### Social organisation and spatially structured benefits

We knew the exact age (1-12 years (range), 4.1 ± 2.7 (mean ± SD) years) for 46 individuals with an identified nest chamber. Older individuals occupied nest chambers near the centre of the colony, while nest chambers near the colony edge were occupied by younger birds (Fig. 4a, Table 3a). Using our observations of breeding attempts between September 2010 and April 2011, we found that breeding was more likely to take place in nest chambers near the centre of the communal nest (Table 3b; Fig. 4b).

## DISCUSSION

Our study shows that the sociable weaver's unique communal nest is an effective temperature buffer. The communal structure acts as a buffer against the cold temperatures at night (this is likely to be especially important during winter when temperatures may drop well below 0 °C at night with temperatures of -5 °C or lower being relatively common) and against high temperatures during the day (during the summer temperatures regularly reach more than 40 °C; www.climate-charts.com). Developing sociable weaver offspring may benefit from higher temperatures inside chambers at night during the breeding period between September and March. Although relatively little is known about the effect of temperature on the development of eggs and nestlings, stable temperatures inside the nest chambers are likely to be beneficial (Martin and Schwabl 2008, Nord and Nilsson 2011). The temperature buffer may also mitigate the energetic demand on parents to maintain a stable temperature during the incubation and nestling phase (Collias and Collias 1984, Drent 1975, Reid et al. 2000, Kosztolányi et al. 2009, Dawson et al. 2011).

Interestingly, our study also shows spatial variation in the thermoregulatory benefits of the nest. These benefits increased towards the centre of the communal nest and with the depth to which the nest chamber is embedded into the thatch. Our data further suggest that this variation has consequences for the social organisation within colonies: we showed that the position of the nest chamber within the communal nest predicted the age of the occupant, and that breeding was more likely to take place towards the centre of the colony. We also found that ΔT did not increase with increasing communal nest volume overall, although there did appear to be some decrease in thermoregulatory benefits for the smallest nests.

Any absolute thermoregulatory benefit of nesting in a communal nest appears to be small, given that there was a median difference of only 2.6 °C in recorded nest chamber temperature compared to ambient temperature. Nonetheless, a small difference in temperature is likely to be significant for a small bird like the sociable weaver (mean body mass = 26.9 g) that not only breeds but also roosts in the nest chambers throughout the year (see Ferguson et al. 2002). In contrast to White et al. (1975), who concluded that the insulative effectiveness (and heat input of the occupants) of the communal nest increases with size, our results suggests that there is no general thermoregulatory benefit of larger colony size. The proportion of high quality nest chambers away from edges of nests is higher in larger colonies, which could provide a benefit of communal living, but against that benefit are likely to be increasing costs of nest predation, parasite infection and brood reduction (Spottiswoode 2007). Furthermore, the risk of the nest becoming too heavy for the supporting tree (eventually resulting in branches breaking and the nest falling out of the tree) increases with nest size (REvD, pers. obs., White et al. 1975).

Given minimal thermoregulatory benefits of larger colonies, there may be benefits other than thermoregulation from living in larger communities. Larger groups are potentially more successful at finding food (Ward and Zahavi 1973, Alonzo and Sheldon 2010, King et al. 2011) or reducing predation risk through enhanced vigilance (Harrison and Whitehouse 2011, Hirsch 2011). In addition, there is significant kin structure among males between communal nests of sociable weavers and they are facultative cooperative breeders in which helpers are generally related to the breeders they assist (Covas et al. 2006). Thus, thatch building may be a kin-selected behaviour (Hamilton 1964) if investment in the communal nest benefits relatives living within the same colony. For example, contributions to building may depend on an individual’s relatedness to other colony members and the spatial arrangement of any relatives in the communal structure.

Alternatively, the benefits of investing in nest construction may be selfish, rather than altruistic, with thatch building acting as a handicap signal (Zahavi 1995). For example, if thatch-building behaviour is costly, it may indicate the dominance status or parental quality of individuals and hence be used in mate choice (Zahavi 1995, Soler et al. 1998, Szentirmai et al. 2005, Berg et al. 2006, Schaedelin and Taborsky 2010, Sanz and Garcia-Navas 2011). A role of individual quality in the social organisation of sociable weaver nests is suggested by our findings that older birds occupied better quality nest chambers, and that breeding was more likely to take place in these chambers. We note that the fact that breeding was more likely in central chambers could be due to either the individual quality of the occupants or a direct consequence of the thermoregulatory characteristics of these chambers, or both. Further analyses are required to tease apart these effects.

Our observation that older individuals occupied the best quality nest chambers suggests competition for access to the best positions within the communal nest. Predation risk is unlikely to provide a satisfactory explanation for such competition for central chambers. Nest predators, mostly snakes (Cape cobras *Naja nivea* and boomslangs *Dispholidus typus*), cause an average of 75% of offspring mortality (Covas 2002). Snakes typically take all offspring present at a colony during a single foraging bout, although some nests do survive such events (Spottiswoode 2007). Whether offspring in central nest chambers, or in chambers that are more deeply embedded into the thatch, are more likely to survive such predation events remains to be investigated. Nevertheless, the relationship between nest chamber position and occupants' age and probability of breeding suggests that spatially structured benefits of the public good could strongly influence social organisation of sociable weavers. Similarly, in a study of long-tailed tits (*Aegithalos caudatus*) the benefits of roosting communally vary with position within the roost (Hatchwell et al. 2009) and access to the best positions is related to an individual's dominance status within the flock (McGowan et al. 2006).

It would be interesting to determine whether thatch building is costly and to investigate which individuals contribute to the public good most in order to substantiate the above propositions that thatch building may be a selfish behaviour associated with gaining access to breeding opportunities or that it may be a kin-selected behaviour. Addressing the costs of communal investment and the question of who should bear these costs will help us to explain how cooperation may be maintained in sociable weavers.

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## TABLES

**Table 1**. (a) $\Delta T$ (°C), (b) $T_{SD}$, and (c) the depth of sociable weaver nest chambers in relation to the volume of the communal nest and the distance between the nest chamber and the nearest edge of the communal nest. The random terms 'Colony' and 'Position' had a significant effect in model (a) (likelihood ratio 'Colony': 191.90, $p < 0.001$; likelihood ratio 'Position': 111.92, $p < 0.001$), while the random effects in the models (b) and (c) were non-significant ($p > 0.113$); n = 20 colonies.

| (a) $\Delta T$ | | | | |
|---|---|---|---|---|
| Fixed effects | Model effect estimate ± SE | df | t | p |
| Distance from edge | 0.007 ± 0.002 | 30 | 4.733 | <0.001 |
| Volume | -0.004 ± 0.015 | 18 | -0.299 | 0.769 |
| Ambient temperature | -0.010 ± 0.002 | 4098 | -5.459 | <0.001 |
| (b) $T_{SD}$ | | | | |
| Distance from edge | -0.004 ± 0.001 | 29 | -3.562 | 0.001 |
| Volume | <1.0x10$^{-7}$ ± 1.0x10$^{-7}$ | 18 | 1.518 | 0.146 |
| Ambient temperature | -0.041 ± 0.013 | 29 | -3.160 | 0.004 |
| (c) nest chamber depth | | | | |
| Distance from edge | 0.438 ± 0.197 | 31 | 2.220 | 0.034 |
| Volume | 1.0x10$^{-6}$ ± 2.0x10$^{-6}$ | 18 | 1.413 | 0.175 |

**Table 2.** Temperature inside sociable weaver nest chambers as a function of the depth of the nest chamber. (a) ΔT (°C) and (b) $T_{SD}$ (°C). The random term 'Colony' was not significant in model (a) (p =0.999), but had a significant effect in (b) (likelihood ratio: 4.77, p =0.029).

| (a) *ΔT* | Model effect estimate ± SE | df | t | p |
|---|---|---|---|---|
| Depth | 0.153 ± 0.032 | 27 | 4.758 | <0.001 |
| Volume | $-1.0\times10^{-7} \pm <1.0\times10^{-7}$ | 18 | -2.720 | 0.014 |
| Ambient temperature | 0.136 ± 0.043 | 27 | 3.184 | 0.004 |
| (b) $T_{SD}$ | | | | |
| Depth | -0.124 ± 0.036 | 27 | -3.398 | 0.002 |
| Volume | $<1.0\times10^{-7} \pm 1.0\times10^{-7}$ | 18 | 1.819 | 0.086 |
| Ambient temperature | -0.205 ± 0.066 | 27 | -3.120 | 0.004 |

**Table 3.** (a) Age and (b) the proportion of nest chambers where a breeding attempt was observed as a function of the position of the nest chamber in the communal nest of sociable weavers. The random term 'Colony' was not significant in models (a) and (b) (p =0.999). Position T1 is used as the reference category (intercept) in (b).

| (a) | Model effect estimate ± SE | df | t | p |
|---|---|---|---|---|
| Distance from edge | 0.016 ± 0.006 | 27 | 2.577 | 0.016 |
| Volume | $<1.0 \times 10^{-7} \pm 0.5 \times 10^{-7}$ | 27 | -0.740 | 0.465 |
| (b) | | | | |
| Intercept | 0.122 ± 0.140 | 24 | 0.871 | 0.392 |
| T2 | 0.376 ± 0.135 | 24 | 2.796 | 0.010 |
| T3 | 0.313 ± 0.135 | 24 | 2.330 | 0.029 |
| Volume | 0.019 ± 0.019 | 11 | 0.968 | 0.354 |

# FIGURES

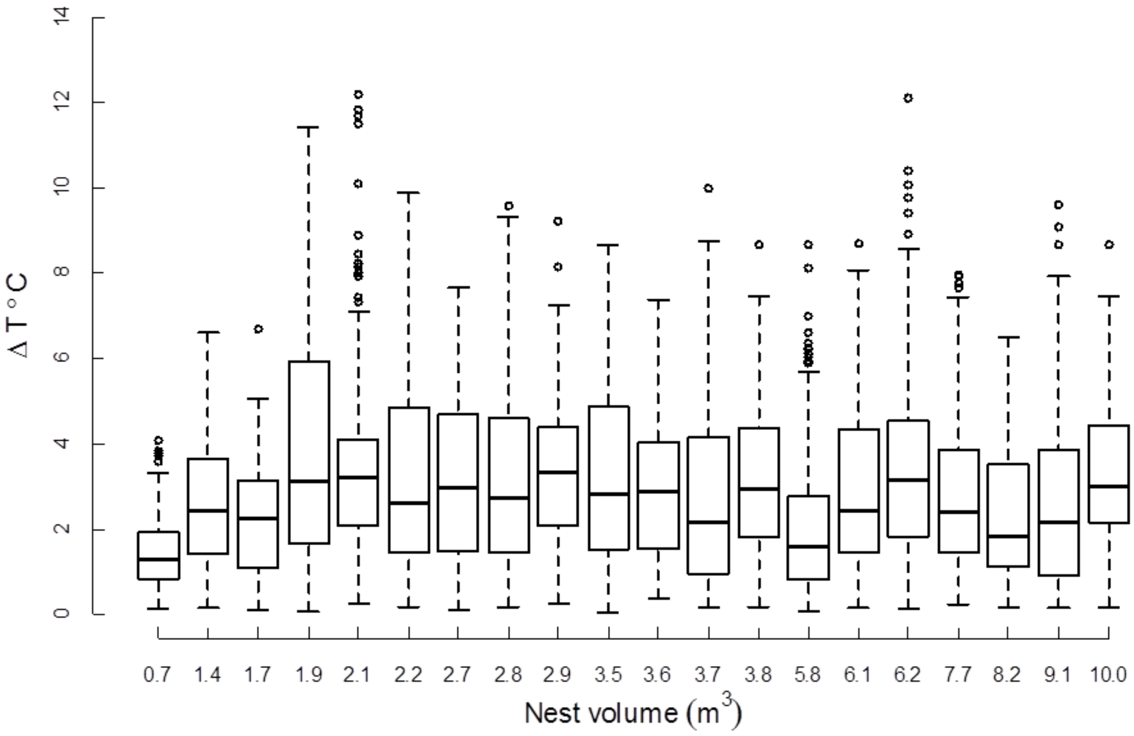
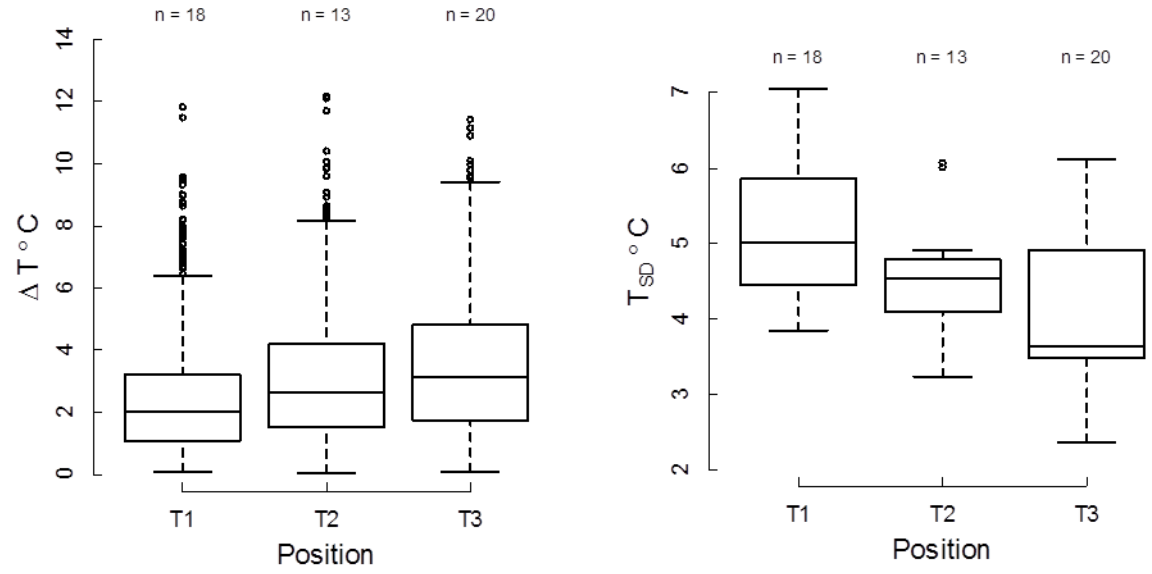


**Figure 1.** Temperature buffer, ΔT (°C), as a function of the volume of the communal nest of sociable weavers. Boxplots indicate the median, the interquartile range, the maximum and minimum values excluding outliers, and outliers; n = 20 colonies.

(b)



(c)

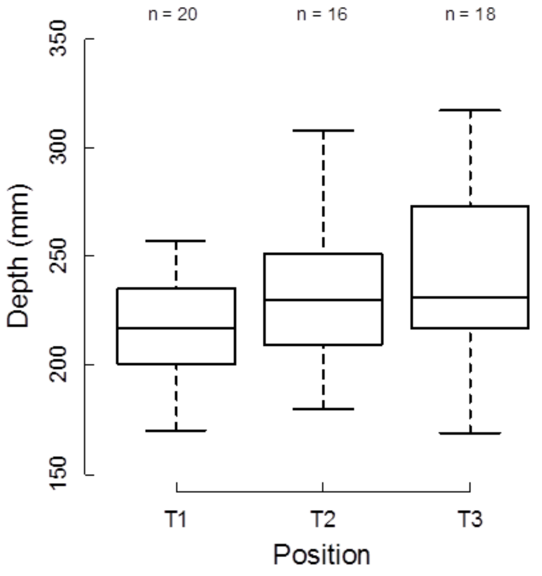


**Figure 2.** (a) The temperature buffer, ΔT (°C); (b) standard deviation of ΔT, $T_{SD}$ (°C); and (c) the depth of the nest chamber as a function of the chambers' position in the communal nests of sociable weavers. T1, T2 and T3 correspond to positions near the edge of the communal nest (T1), near the centre of the communal nest (T3), and in between those two positions (T2; see text for mean ± SD distance from the nearest edge for each position) and are used here for graphical purposes; n is the number of colonies.

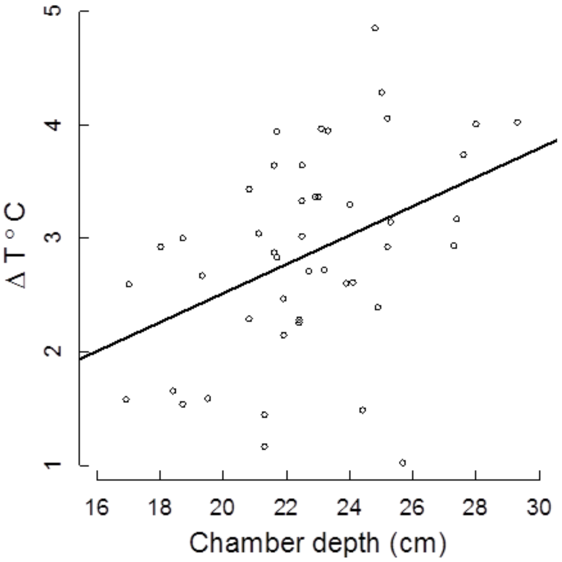


**Figure 3.** Temperature buffer, ΔT °C, inside sociable weaver nest chambers as a function of their depth.

(b)

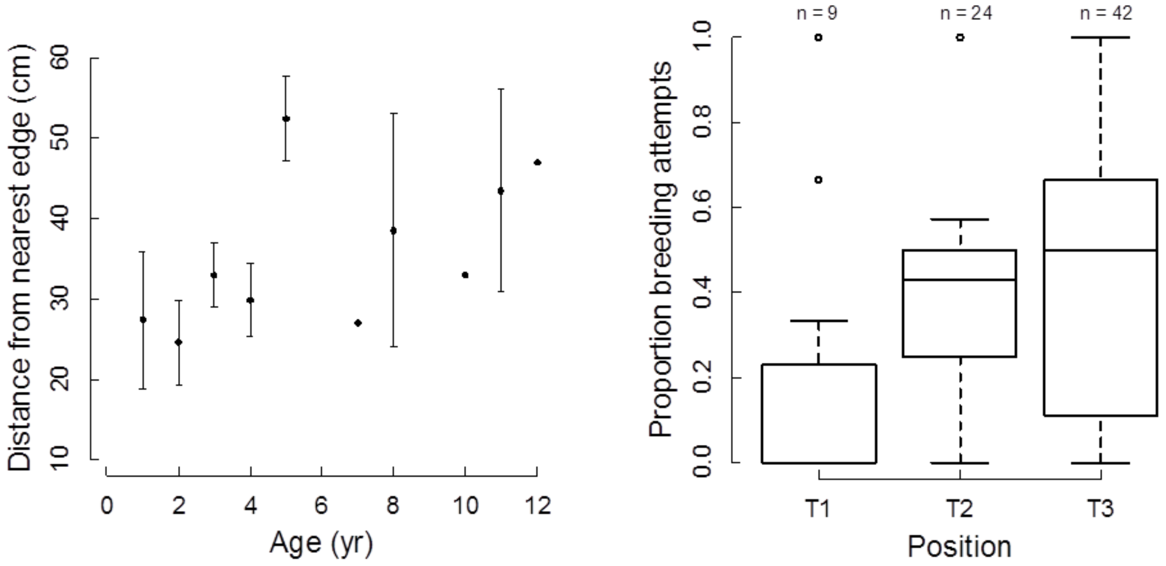


**Figure 4.** (a) The age of the individuals versus the distance between their nest chamber and the nearest edge of the communal nest (mean ± SE; n = 46 individuals) and (b) the proportion of nest chambers where a breeding attempt was observed as a function of the position of the nest chamber. T1, T2 and T3 correspond to positions near the edge of the communal nest (T1), near the centre of the communal nest (T3), and in between those two positions (T2; see text for mean ± SD distance from the nearest edge for each position) and are used here for graphical purposes; n is the number of nest chambers.

## Maternal effects and life history trade-offs in a cooperative breeder, the sociable weaver (*Philetairus socius*)

Maximizing of the number copies of genes that are transmitted to the next generations involves a series of tradeoffs. In cooperatively breeding species some sexually mature individuals do not breed but instead help other individuals to raise their offspring. These helpers are particularly interesting in a life history context as they create a predictably favorable breeding environment and their presence can thus influence evolutionary trade-offs. A major evolutionary trade-off that is often neglected in studies on cooperative breeding is maternal allocation, notably through maternal effects that are epigenetic modifications of offspring phenotype. Here we investigate whether there are maternal effects induced by the presence of helpers and their possible consequences on females and their offspring in a colonial cooperative breeder of southern Africa, the sociable weaver *Philetairus socius*. Our results show that females lay smaller eggs in the presence of helpers and in addition these eggs have lower corticosterone and testosterone concentrations. Our results also show a higher survival probability of females breeding in groups, which may be partially due to their lower investment in eggs. In addition, a study of roosting chamber temperatures in relation to group size suggests further benefits for parents and helpers, particularly through lower costs of thermoregulation that could also allow energy savings for survival. To start understanding the consequences of helpers presence and differential maternal allocation for offspring we conducted a cross fostering experiment. Our results show that eggs produced by females breeding in larger groups produce chicks that beg at a lower rate, showing that maternal effects may influence chicks' behavior. Finally, we investigated post-fledging survival through capture-recapture analyses and, surprisingly, found that fledglings have a lower survival probability when raised with helpers. Taken together, these results demonstrate the importance of studying maternal effects on cooperative breeders and open several research prospects on family conflicts and life history trade-offs according to the presence of helpers.

***Keywords:*** *cooperative breeding, life history trade-offs, maternal effects, hormones, birds*

## Effets maternels et compromis évolutifs chez une espèce à reproduction coopérative, le Républicain social (*Philetairus socius*)

Maximiser le nombre de copies de gènes transmises aux générations suivantes implique une série de compromis. Chez les espèces à reproduction coopérative, des individus ne se reproduisent pas mais participent aux soins des jeunes d'autres individus reproducteurs. Ces assistants sont particulièrement intéressants dans le contexte des traits d'histoire de vie car ils forment un environnement prédictible favorable pour la reproduction, et leur présence peut aussi influencer les compromis évolutifs chez les reproducteurs. Un compromis évolutif majeur mais sous-étudié dans le cadre de la reproduction coopérative est l'allocation maternelle notamment via des effets maternels qui sont des modifications épigénétiques du phénotype de la descendance. Nous avons étudié l'existence d'effets maternels associés à la présence d'assistants et leurs possibles conséquences sur les femelles et leurs descendants chez un oiseau colonial et coopératif du sud de l'Afrique, le Républicain social *Philetairus socius*. Nos résultats montrent que les femelles pondent des œufs plus légers en présence d'assistants et que ces œufs sont moins concentrés en corticostérone et testostérone. Nos résultats montent aussi une plus grande probabilité de survie pour les femelles se reproduisant en groupe pouvant être en partie due à leur plus faible investissement dans les œufs. De plus, l'étude de la température dans les nids en fonction de la taille des groupes a permis de suggérer d'autres bénéfices pour les parents et assistants, en particulier via une réduction des coûts de thermorégulation qui pourrait aussi permettre de garder de l'énergie pour la survie. Pour comprendre les conséquences de la présence d'assistants et de l'allocation différentielle pour les poussins, une expérience d'adoption croisée a été réalisée. Elle a révélé que les œufs pondus par les femelles avec plus d'assistants produisent des poussins qui quémandent moins, montrant que des effets maternels pourraient influencer le comportement des poussins. Enfin nous avons étudié la survie des poussins après l'envol à l'aide d'analyses de captures recaptures et avons trouvé de manière surprenante que les poussins à l'envol ont une probabilité de survie plus faible lorsqu'ils sont élevés présence d'assistants. Ces résultats dans leur ensemble démontrent l'importance d'étudier les effets maternels chez les espèces coopératives et ouvrent de nombreuses perspectives de recherche sur les conflits familiaux et de compromis évolutifs associés à la présence d'assistants.

***Mots clés :*** *reproduction coopérative, compromis évolutifs, effets maternels, hormones, oiseaux*

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