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Maternal allocation strategies and offspring fitness in the cooperatively breeding sociable weaver: integrating climate, predation and helper effects

Rita Fortuna

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Integrating climate, predation and helper effects

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Tese de Doutoramento apresentada à
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Franck Theron
Alexandre Vaz
Rita Fortuna
Joel Prince

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Rita Fortuna
Programa Doutoral em Biodiversidade, Genética e Evolução
Departamento de Biologia
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Orientador
Rita Covas, Investigador Principal, CIBIO-InBIO, BIOPOLIS

Coorientador
Claire Doutrelant, Tenure Research Scientist, CEFE-CNRS, Univ Montpellier, France

Nota prévia

Na elaboração desta dissertação, e nos termos do número 2 do Artigo 4º do Regulamento Geral dos Terceiros Ciclos de Estudos da Universidade do Porto e do Artigo 31º do D.L. 74/2006, de 24 de Março, com a nova redação introduzida pelo D.L. 230/2009, de 14 de Setembro, foi efetuado o aproveitamento total de um conjunto coerente de trabalhos de investigação já publicados ou submetidos para publicação em revistas internacionais indexadas e com arbitragem científica, os quais integram alguns dos capítulos da presente tese. Tendo em conta que os referidos trabalhos foram realizados com a colaboração de outros autores, a candidata esclarece que, em todos eles, participou ativamente na sua conceção, na obtenção, análise e discussão de resultados, bem como na elaboração da sua forma publicada. Adicionalmente, a candidata foi coautora em dois artigos publicados em revistas internacionais não diretamente relacionados com o tema da tese. Esses artigos publicados em coautoria, não incluídos como capítulos da tese, estão detalhados no *Appendix A*.

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Abstract

Individuals are predicted to adopt flexible reproductive strategies in response to environmental factors that influence survival and reproductive success, such as climatic conditions, predation risk and social factors. Prenatal maternal allocation to offspring appears to be a flexible reproductive strategy with consequences for females' fitness, but also offspring growth, behaviour and ultimately survival. In birds, females can vary egg number, size, and content and often allocate more prenatal resources to reproduction in favourable climatic conditions and low predation risk. The effect of social factors has been studied in cooperative breeders i.e., where breeders have helpers that provide offspring care and, in several species, females were found to reduce egg size when breeding with more helpers. However, how social factors interact with remaining environmental effects is poorly known, and some longer-term findings suggest that females reduce egg size in good climatic conditions but lay larger eggs in adverse environments. Whether helper effects on maternal allocation are conditional on other environmental factors, such as predation risk, has not been tested, and helper effects on egg components are poorly understood. In addition, even though in many species helpers appear to increase reproductive success during rearing, it is unclear if helpers are associated with longer-term effects on offspring survival and can buffer adverse climatic effects on offspring survival during early-life.

The aims of this thesis were to investigate the effects of environmental factors – social group sizes, climatic conditions, predation risk – on maternal prenatal allocation strategies, explore the link between offspring begging behaviour and cooperative care rules, and test whether helpers modulate critical environmental effects on maternal allocation and offspring survival, in a cooperatively breeding species, the sociable weaver *Philetairus socius*.

The first three chapters focus on environmental effects on prenatal maternal allocation. First, an individual-based dataset collected over nine seasons was used to test how egg mass and clutch size varied with number of helpers, climatic conditions, and experimentally reduced nest predation risk. Second, variation in egg nutrients and hormones was measured in relation to number of helpers and egg laying order in two breeding seasons. Third, adult predation risk was manipulated to examine female allocation under increased risk and whether helpers buffer predator-induced effects on maternal allocation. These studies showed that clutch size was larger after more rainfall and reduced nest predation risk. In contrast, egg mass did not vary with environmental factors and was consistent within females, and egg hormonal content did not associate with helper number or predation risk. Yolk mass and lipid content were positively related to helper number, particularly for the last eggs of the clutch, and predator-exposed females laid eggs with lighter yolks.

The next chapter investigated how offspring begging behaviour, a trait suggested to be affected by prenatal maternal effects in this species, was associated with breeders' and helpers' feeding effort. Breeding males returned faster to feed the nestlings after higher begging rates, while mothers and helpers did not appear to respond to begging. This showed that females and males had different feeding responses to begging and suggests that females may influence the care provided by their partner via maternal effects. Regarding the helpers, it indicates that any indirect or direct fitness benefits obtained from helping are not maximised by responding to offspring demand.

In the last chapter, a seven-year capture-mark-recapture dataset was used to estimate long-term effects of being raised with more helpers and how this interacts with rainfall and temperature conditions during the breeding and winter periods. Results showed that female offspring had higher first-year survival when raised with more helpers in low rainfall conditions. There was thus some indication that the number of helpers modulates the association between climatic conditions and offspring first-year survival, but this was limited to rainfall and to female offspring.

Overall, the findings in this thesis showed that some maternal allocation measures can vary with climate, adult and offspring predation risk and number of helpers, but interactive effects of helpers and remaining environmental factors on maternal allocation were not supported. Moreover, these results contradicted the expected and commonly found load-lightening pattern across cooperative breeders and encourage a reassessment of helper effects on maternal allocation by exploring alternative pathways for flexible allocation, such as variation in egg nutrients. Exciting future questions arise on whether maternal effects and offspring phenotype influence the care provided by other individuals, and how prenatal maternal care and postnatal helper care combine to affect offspring survival in multidimensional and dynamic environments.

Keywords:
begging, climate, cooperative breeding, differential allocation, egg content, helpers, load-lightening, maternal allocation, offspring survival, predation risk, reproductive strategies, sociable weaver

Resumo

Os indivíduos devem adotar estratégias reprodutivas flexíveis em resposta a fatores ambientais que influenciam a sua sobrevivência e sucesso reprodutivo, como condições climáticas, risco de predação e fatores sociais. A alocação materna pré-natal à prole parece ser uma estratégia reprodutiva flexível e com consequências para a aptidão evolutiva das fêmeas, mas também para o crescimento, comportamento e sobrevivência da prole. Nas aves, as fêmeas podem variar o número de ovos, o tamanho e o conteúdo e, muitas vezes, alocam mais recursos para a reprodução em condições climáticas favoráveis e sob baixo risco de predação. O efeito dos fatores sociais tem sido estudado em sistemas de cria cooperativa, onde os reprodutores têm ajudantes que cuidam da prole, e em várias espécies verificou-se que as fêmeas produziram ovos mais pequenos, quando tinham mais ajudantes. No entanto, é ainda pouco conhecido de que maneira este fator social pode interagir com outros efeitos ambientais, e algumas descobertas de estudos de longo termo sugerem que as fêmeas reduzem o tamanho dos ovos quando sujeitas a condições climáticas favoráveis, mas produzem ovos maiores em ambientes adversos. Além disso, não há ainda investigações que procurem perceber se os efeitos dos ajudantes na alocação materna podem ser condicionados por outros fatores ambientais, como o risco de predação, bem como qual o efeito dos ajudantes no conteúdo dos ovos. Embora em muitas espécies os ajudantes pareçam aumentar a sobrevivência da prole durante a criação, não está ainda claro se a presença de ajudantes está associada a efeitos de longo prazo na sobrevivência da prole, bem como se estes podem mitigar efeitos climáticos adversos durante o início de vida.

Os objetivos desta tese passaram por investigar os efeitos de fatores ambientais – tamanho de grupos sociais, condições climáticas, risco de predação – nas estratégias de alocação pré-natal materna, bem como explorar a ligação entre o comportamento de solicitação de comida pelas crias e as regras de cuidado cooperativo e, por último, testar se os ajudantes moderam os efeitos ambientais que influenciam a sobrevivência da prole, numa espécie de cria cooperativa, o tecelão sociável *Philetairus socius*.

Os três primeiros capítulos focam-se nos efeitos ambientais na alocação materna pré-natal. Primeiro, foram analisados dados individuais coletados ao longo de nove épocas de reprodução para testar como a massa dos ovos e o tamanho da ninhada variaram com o número de ajudantes, condições climáticas e o risco de predação de ninhos, tendo este sido experimentalmente reduzido. Em segundo lugar, a variação nos nutrientes e hormonas dos ovos foi medida em relação ao número de ajudantes e a

ordem de postura dos ovos, em duas estações reprodutivas. Por último, o risco de predação de adultos foi manipulado para examinar efeitos na alocação materna e averiguar se os ajudantes mitigaram os efeitos negativos induzidos pela perceção de predadores na alocação materna. Estes estudos mostraram que o tamanho da ninhada foi maior após períodos com mais chuva e risco de predação do ninho reduzido. Em contraste, a massa dos ovos não variou com fatores ambientais e foi consistente nas fêmeas, e o conteúdo hormonal dos ovos não se associou com o número de ajudantes ou risco de predação. Por outro lado, a massa da gema e o teor em lipídios pareceram positivamente relacionados com o número de ajudantes, sobretudo para os últimos ovos da ninhada, e as fêmeas expostas ao predador produziram ovos com gemas mais leves.

O capítulo seguinte investigou como o comportamento de solicitação das crias, que parece ser influenciado por efeitos maternos pré-natais nesta espécie, se associou com o esforço alimentar de pais e ajudantes. Os machos reprodutores retornaram mais rápido para alimentar as crias após taxas de solicitação mais elevadas, mas as mães e ajudantes não pareceram responder a este comportamento. Vimos assim que fêmeas e machos tiveram diferentes respostas à solicitação de comida pelas crias, o que sugere que as fêmeas podem influenciar o cuidado prestado pelo parceiro por meio de efeitos maternos. Em relação aos ajudantes, estes resultados indicam que quaisquer benefícios de aptidão evolutiva, indiretos ou diretos, obtidos com a ajuda no ninho não são maximizados pela resposta à solicitação da prole.

No último capítulo, foi usado um conjunto de sete anos de dados de captura-marca-recaptura para estimar os efeitos de longo prazo de ser criado com mais ajudantes e como isso interage com as condições de chuva e temperatura durante os períodos de reprodução e de inverno. Os resultados mostraram que as crias fêmea tiveram maior sobrevivência no seu primeiro ano, quando criadas com mais ajudantes e em condições de baixa pluviosidade. Há, portanto, alguma indicação de que o número de ajudantes modera a associação entre as condições climáticas e a sobrevivência da prole no primeiro ano de vida, ainda que os efeitos tenham sido notórios apenas em relação à chuva e às crias fêmea.

No geral, os resultados desta tese mostraram que algumas medidas de alocação materna podem variar com o clima, com o risco de predação de adultos e de crias e com o número de ajudantes, apesar de não terem sido detetados efeitos de mitigação dos ajudantes na alocação materna. Estes resultados contradizem ainda o esperado efeito de produção de ovos mais pequenos, comumente encontrado em espécies de cria cooperativa, e incentivam uma reavaliação dos efeitos dos ajudantes na alocação

materna, explorando caminhos alternativos para alocação flexível, como variação nos nutrientes dos ovos. Surgem ainda questões empolgantes para o futuro, nomeadamente acerca de como os efeitos maternos e o fenótipo da prole influenciam o cuidado prestado por outros indivíduos, e de que maneira o cuidado materno pré-natal e o cuidado pós-natal se combinam para afetar a sobrevivência da prole em ambientes multidimensionais e dinâmicos.

Palavras-chave: ajudantes, alocação diferencial, alocação maternal, clima, conteúdo dos ovos, cria cooperativa, estratégias de reprodução, risco de predação, sobrevivência das crias, solicitação de comida, tecelão sociável

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List of abbreviations

AIC	Akaike Information Criterion
CHN	Carbon-Hydrogen-Nitrogen
CI	Confidence Interval
CLM	Cumulative Link Model
CLMM	Cumulative Link Mixed Model
CMR	Capture-mark-recapture
CV	Coefficient of variation
DHEA	Dehydroepiandrosterone
DHEA-S	Dehydroepiandrosterone sulfate
DI	Deionized
DIC	Deviance Information Criteria
DOI	Digital Object Identifier
ELISA	Enzyme-linked immunoassay
FFT	Fast Fourier Transformation
GLM	General Linear Model
GLMM	General Linear Mixed Model
GS	Group size
HD	High-Definition
HPD	Highest Posterior Density
HPLC	High Performance Liquid Chromatography
ID	Identity
JAGS	Just Another Gibbs Sampler
LMM	Linear Mixed Model
LRT	Likelihood-Ratio Test
MCMC	Markov chain Monte Carlo
ML	Maximum Likelihood
OD	Optic Density
OR	Odds Ratio
PCM	Pulse-code modulation
REML	Restricted Maximum Likelihood
RIA	Radioimmunoassay
SAWS	South African Weather Service
SD	Standard deviation
SE	Standard error
US	United States of America
UV	Ultraviolet

Chapter 1

General Introduction

Reproductive strategies and environmental complexity

Exploring the causes and consequences of the phenotypic variation we observe in nature, and specifically why certain phenotypes more successfully survive and reproduce, is essential to understand and predict natural selection processes (Darwin, 1859; West-Eberhard, 2003). To maximise reproductive success over a lifetime, individuals should balance investment in current reproduction against survival and future breeding opportunities (Roff, 1993; Stearns, 1992). These life-history trade-offs may be resolved by adopting flexible reproductive strategies in response to environmental conditions, depending on how these affect survival and/or offspring value (Erikstad et al., 1998; Stearns, 1992). Environmental effects on reproductive investment, breeding success, and survival may however be challenging to understand and predict, as natural environments are dynamic, multidimensional and can act directly and indirectly on individuals.

Environmental conditions vary within seasons, between seasons and across generations (Jones et al., 2001). In fluctuating environments, phenotypic plasticity – the ability of a genotype to produce different phenotypes – may allow individuals to adjust reproductive investment to their current environment (Scheiner, 1993; Schlichting & Pigliucci, 1998). When an environmental factor is variable and predictable enough, there is potential for phenotypic plasticity in relation to this environmental factor to be favoured by selection (Berrigan, 2004; Burgess & Marshall, 2014; Taborsky, 2017). Examples of plastic reproductive strategies in relation to environmental conditions have been described across taxa. For instance, female bighorn sheep *Ovis canadensis* were found to reduce energy expenditure in reproduction to favour their own mass gain over their lambs, when breeding under lower resource availability (Festa-Bianchet & Jorgenson, 1998). Song sparrows *Melospiza melodia* that experienced experimentally increased perceived predation risk reduced the number of eggs laid and nest feeding visits (Zanette et al., 2011). Saving energy by investing less or even suspending reproduction when resources are scarce, or offspring fitness value is low, may have fitness advantages if it allows individuals to invest more in reproduction in the future when breeding conditions improve (Roff, 1993; Stearns, 1992; Williams, 1966). Hence, the potential for individuals to flexibly respond to environmental cues needs to be considered when studying reproductive strategies and their fitness outcome. This may however be difficult to achieve, as it requires repeated observations of the same individuals under contrasting environmental conditions throughout their reproductive lifetime.

One other challenging aspect in the study of environmental effects is that, in nature, what defines a good or an adverse environment is usually not one environmental variable but several ecological, climatic, and social variables that may, independently or in interaction, affect reproductive success and survival. Ideally, when studying how individuals adjust reproductive strategies to their environment, one should take this complexity into account, but in practice this can bring enormous challenges, as it requires 1) knowing which environmental variables are relevant for each species' life-history and how to measure them in a meaningful way, 2) manipulations of several variables simultaneously in experimental studies, or 3) substantial variation in these environmental factors in observational studies.

Lastly, the study of environmental effects on phenotypic variation has been expanded by the idea that environments can act directly on the phenotype of an individual, or indirectly when environmental effects on one individual affect the phenotypic development of another one. A classic example of these "indirect environmental effects" are maternal effects i.e., when environmental effects experienced by the mother affect the phenotype of her offspring over and above the direct effect of the transmitted genes (Bernardo, 1996a; Mousseau & Fox, 1998). The quality of the first environment experienced by offspring depends almost exclusively on their mother, specifically on how her breeding environment affects the quality and quantity of resources she allocates to reproduction (Lindström, 1999; Mousseau & Fox, 1998). This maternal allocation may in turn influence offspring phenotype and survival (Lindström, 1999; Metcalfe & Monaghan, 2001; Mousseau & Fox, 1998). Studies in insect species illustrate well these co-dependencies showing, for example, that in a species of beetle (*Statos limbatus*) females flexibly lay larger eggs in poor-quality host plants, and that larvae from large eggs survive better in this poor-quality environment (Fox et al., 1997; Fox & Mousseau, 1996). Maternal effects are viewed as an important source of offspring phenotypic variation in animal populations, especially early in an individuals' life (Badyaev, 2008; Lindström, 1999; Moore et al., 2019). This highlights the importance of studying how environments influence the allocation of resources towards

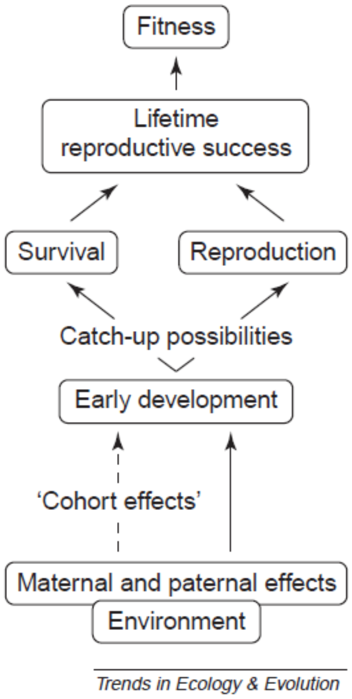

Figure 1. 1 Schematic representation of the fitness consequences of conditions experienced during early development. Source: Lindström, 1999.

reproduction for females specifically. Examining maternal allocation allows not only to investigate the ability of breeding individuals to respond to environmental variation, but is also the first step to understand lasting effects of environmental variation transmitted across generations (Fig. 1.1; Bernardo, 1996a; Lindström, 1999; Marshall & Uller, 2007).

Environmental effects on prenatal maternal allocation

While in mammals mothers continuously interchange resources with offspring through the placenta (Maestripieri & Mateo, 2009), in egg-laying species all the essential resources for embryonic development until hatching are accumulated in the eggs (Carey, 1996). Eggs are thus 'sealed capsules' of maternal origin that may represent maternal reproductive investment at laying (Bernardo, 1996b). Studies on oviparous species, and birds in particular, have provided important insights on how different environmental factors shape prenatal resource allocation from mothers to their offspring and how this in turn affects offspring phenotype and survival (Bernardo, 1996b; Christians, 2002).

Egg size has been extensively studied and shown to positively associate with offspring hatching success, body size, and survival (Krist, 2011). However, females' ability to lay eggs of variable size may be limited, especially in bird species, as numerous studies find high egg size consistency within females across environments (Christians, 2002; Lejeune et al., 2016; but see Pick et al., 2016).

Egg components, as nutrients and hormones, are crucial for embryo development and their respective quantity can also affect offspring phenotype and survival (Groothuis et al., 2005; McGraw et al., 2005; Mentesana et al., 2021; Saino et al., 2003). For instance, eggs richer in yolk carotenoids and yolk fatty acids were found to be associated with higher hatching and fledging success (McGraw et al., 2005; Mentesana et al., 2021). In addition, yolk hormonal levels, as testosterone and androstenedione (A4) concentration, are thought to be 'cheaper' ways of benefiting offspring (Groothuis & Schwabl, 2008) by inducing faster development (Eising et al., 2001; Schwabl, 1993) and stronger begging behaviour (Eising & Groothuis, 2003), altogether improving offspring competitive abilities. The allocation of egg components appears variable within clutches of the same female, changing with egg laying order (Royle et al., 1999; Slagsvold et al., 1984), and across clutches depending on females' environmental conditions (Ardia et al., 2006; Safran et al., 2010; Saino et al., 2005), thus representing an important alternative pathway for flexible maternal allocation.

Climatic conditions

Favourable climatic conditions, besides influencing the onset of breeding activity (Mares et al., 2017; Saino et al., 2004), have been shown to associate with increased maternal allocation to reproduction (Aranzamendi et al., 2019; Lloyd, 1999). In birds, rainfall was positively associated with the production of more eggs per clutch, especially in arid zones and tropical areas, likely mediated by its effects on resource availability through vegetation growth and insect abundance (Aranzamendi et al., 2019; Dean & Milton, 2001; Lloyd, 1999; Oppel et al., 2013). There are also some reports of positive associations of ambient temperature with egg size, especially in temperate regions where temperature can influence conditions to breed and resource availability (Hargitai et al., 2016; Kvalnes et al., 2013; Saino et al., 2004; but see Christians, 2002; Griffith et al., 2020), and yolk mass (Remeš, 2011). Egg mass and yolk mass have also been found to vary positively with insect availability related to temperature (Ardia et al., 2006), and food-supplemented females were also seen to lay eggs with heavier yolks (Morosinotto et al., 2019). Eggs' nutritional content is thus expected to be strongly associated with food availability, and some components such as vitamin E and carotenoids cannot be synthesized *de novo*, but only be obtained from the females' diet (Catoni et al., 2008; Goodwin, 1980). In contrast, effects of climate on egg hormonal components are not usually found (Bleu et al., 2019; Lessells et al., 2016; Remeš, 2011). Overall, these studies suggest that females allocate more resources to reproduction in favourable climatic conditions, mostly via clutch size and egg/yolk size and nutrient composition.

Predation risk

Predation is amongst the most influential environmental variables on individuals' survival and reproductive success (Allen et al., 2022; Zanette et al., 2011). Besides directly affecting individuals through mortality, antipredator responses to perceived predation risk, or 'fear', may entail fitness costs that are as important as lethal effects (Creel & Christianson, 2008). As mentioned above, female birds were found to lay less eggs per clutch when offspring incurred higher predation risk (Doligez & Clobert, 2003) but also when females themselves perceived to be under higher risk of predation (e.g. in Eastern bluebirds *Sialia sialis* Hua et al., 2014). Furthermore, females exposed to reduced offspring predation risk were found to lay larger eggs in several species of passerines (Fontaine & Martin, 2006). This concurs with the idea that females allocate more resources to reproduction when breeding in more favourable environments, in this case due to lower predation risk. Females in high-risk environments were also found to lay eggs with higher corticosterone levels and less concentrated in testosterone (Coslovsky et al., 2012; Saino et al., 2005; but see Morosinotto et al., 2016). Yet, even though these differences in hormonal levels can be detrimental for offspring growth (Henriksen et al., 2011; Pitk et al., 2012; Saino et al., 2005), they have been suggested to also have positive effects, specifically by enhancing offspring flight performance and success at escaping predators, and females may thus be preparing offspring to better survive in riskier environments (Chin et al., 2009; Coslovsky & Richner, 2011; Sheriff & Love, 2013; Storm & Lima, 2010; see also in fish Sharda et al., 2021).

Social environment

Environments are not only characterised by climatic and ecological variables, but also by the social context that individuals experience. Social behaviours, such as foraging in a group, may reduce individual predation risk and increase foraging efficiency (Bednarz, 1988; Bertram, 1978). Communal roosting can also decrease individuals' thermoregulation costs under low temperatures (Beauchamp, 1999; McKechnie & Lovegrove, 2015), potentially improving body condition. In white-backed mousebirds *Colius colius* for example, an individual clustering in a group of six was predicted to spend 50% less energy in thermoregulation than a solitary individual (McKechnie & Lovegrove, 2015). Social interactions may also affect individuals' aggression or stress levels (see review Creel et al., 2013) and thus circulating hormonal levels (Creel, 2001; Scheiber et al., 2009).

It is thus expected that similarly to climate and to predation risk, the presence of social mates influences maternal allocation patterns. Accordingly, in house sparrows *Passer domesticus*, eggs' testosterone content was found to increase with coloniality, which was interpreted as potential maternal hormonal effects that can prepare offspring to better compete in future high-density social conditions (Schwabl, 1997; see also Gil, 2008; Gil et al., 2007; Pilz & Smith, 2004; but see Safran et al., 2010). Social group effects on reproductive allocation may be especially evident when other individuals directly intervene and contribute to breeders' reproduction, as in species that breed cooperatively (Russell et al., 2007; Russell & Lummaa, 2009).

Cooperatively breeding systems are a type of social systems broadly defined as three or more individuals collectively raising young in a single brood or litter (Koenig &

Dickinson, 2016). This definition includes species breeding in cooperative polygamy and species where some individuals forgo reproduction and help raising offspring that are not their own (Cockburn, 2006). The latter, commonly identified as 'helpers', can provide care in the form of food provisioning, defence from predators, and contribute to other tasks such as nest building and maintenance in birds (Francis et al., 1989; Skutch, 1935).

In most cooperative breeders, helpers are related to the offspring they assist (Hatchwell, 2009), and may therefore offset the costs of helping (e.g.: energy expenditure, exposure to predators; Cockburn, 1998; Heinsohn & Legge, 1999) by propagating their own genes through the offspring of their relatives (i.e.: indirect fitness benefits or inclusive fitness; Hamilton, 1964; West et al., 2007). However, help can also be provided by non-relatives (Riehl, 2013; Wright et al., 2010), and other explanations have been proposed that involve direct fitness benefits, such as gaining a survival or reproductive advantage through group augmentation, territory inheritance, access to mating opportunities, among others (see Cockburn, 1998). Regardless of the mechanism, the expected outcome of many of these direct and indirect helping benefits is that helpers improve the reproductive success of breeders. In accordance, a general positive effect of helpers on annual reproductive success has been recently detected in a meta-analysis across cooperatively breeding birds (Downing et al., 2020), but positive associations between the presence of helpers and breeding success are not consistently found in cooperative breeders (Cockburn, 1998; Kingma et al., 2010; Van de Loock et al., 2017).

One of the explanations for not finding evidence of helper effects on reproductive success in every study on cooperatively breeding species may be related to the environment in which many of these species occur. Cooperative breeding is often linked to temporally variable and low-rainfall environments (Jetz & Rubenstein, 2011; Fig. 1.2) and, in some cases, positive helper effects on reproductive success are more evident under adverse climatic conditions (Capilla-Lasheras et al., 2021; Covas et al., 2008; Groenewoud & Clutton-Brock, 2021; but see Bourne et al., 2020; D'Amelio et al., 2021). Hence, it has been suggested that helpers may be especially important to mitigate the negative effects of unfavourable climatic conditions on breeding success (Jetz & Rubenstein, 2011; Rubenstein & Lovette, 2007).

Yet, most of the studies done so far focused on annual reproductive success (Downing et al., 2020), and helper effects on longer-term offspring survival, or how these interact with climatic conditions, are further from being understood (Van de Loock et al., 2017). The number of helpers in a breeding group can be expected to have lasting effects on offspring survival, as offspring may receive more care (Langen, 2000; Ridley, 2007; Van de Loock et al., 2017), thus reaching independence in better condition (Russell, 2003), and may also associate with the helpers after nutritional independence (Mcgowan et al., 2006). Offspring interannual survival has been found to positively associate with number of helpers in some species (e.g.: long-tailed tits *Aegithalos caudatus* Hatchwell et al., 2004; McGowan et al., 2003; see literature review in Van de Loock et al., 2017), while in other cooperative breeders, as southern pied babblers *Turdoides bicolor*, no evidence of helper effects was found (Bourne et al., 2020). The latter study system is also, to our knowledge, the only where interactive effects of group size and climatic conditions on offspring interannual survival have been investigated, showing that helpers do not appear to successfully counteract lasting negative effects of hot and dry weather during the breeding period (Bourne et al., 2020). Generally, this underlines the need and the relevance of studying how different environmental cues, particularly social and climatic factors, interact to affect short- and long-term reproduction outcomes.

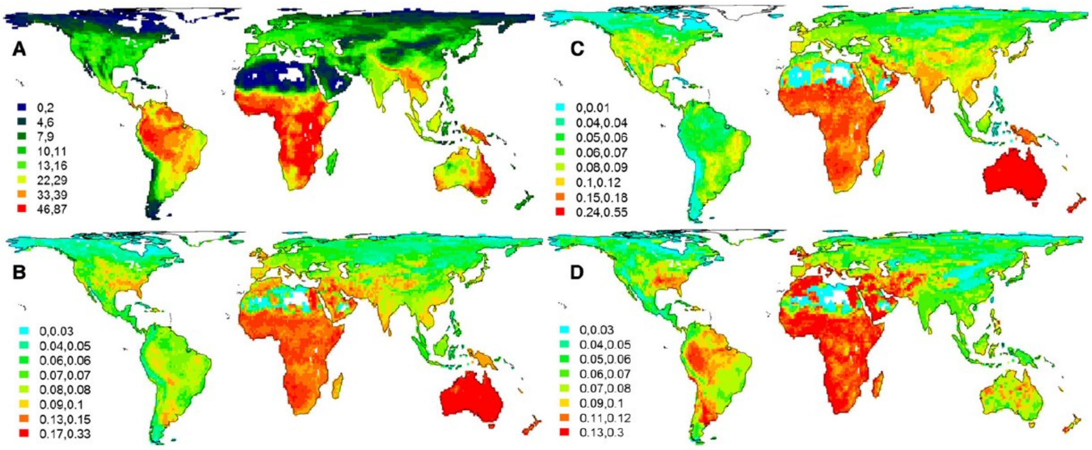

Figure 1. 2 Biogeographic Distribution of Cooperative Breeding Behaviour in Birds. (A) Total richness of cooperative breeders, (B) proportional richness of all, (C) proportional richness of passerine, and (D) proportional richness of non-passerine cooperative breeders. Colour codes show the proportion of species, with higher proportions in red and lower in blue. E.g.: In (B) we can see that cooperative breeders represent over 20% of all bird species in some African regions, and over 30% of all bird species in Australian regions. Source: Jetz & Rubenstein 2011.

An alternative explanation for not detecting helper effects in reproductive success is that breeders may be reducing their own workload in the presence of helpers, or load-lightening (Crick, 1992; Hatchwell, 1999). This could lead to negligible differences in terms of current breeding success between pairs with and without helpers, but to potentially significant advantages for helped breeders in terms of survival and future reproduction (Downing et al., 2021).

Load-lightening in the presence of helpers has first been proposed as reductions in offspring feeding effort (Crick, 1992), but was latter suggested as a mechanism that could also act on females' prenatal reproductive strategies (Russell et al., 2007; Taborsky et al., 2007). This would be possible if the number of helpers a breeding pair has at each breeding attempt is predictable, which is likely since in most species helpers are previous offspring of the pair that stay in their natal territory (Hatchwell, 2009). Under the prenatal load-lightening hypothesis (or 'negative differential allocation', see Haaland et al., 2017), females would benefit from the presence of helpers by investing less resources in eggs, which could later be compensated by the additional food provided by helpers, allowing helped females to save energy for future reproduction or survival (Paquet et al., 2015; Russell et al., 2007; Taborsky et al., 2007). In birds, prenatal load-lightening was first reported in superb fairy-wrens *Malurus cyaneus* (Russell et al., 2007) and several subsequent studies in other cooperatively breeding species found a similar maternal allocation pattern since then (Canestrari et al., 2011; Paquet et al., 2013; Santos & Macedo, 2011).

Nevertheless, females have also been suggested to adjust prenatal reproductive investment according to the presence or number of helpers using the opposite strategy (Russell & Lummaa, 2009; Savage et al., 2015). Helpers appear to improve breeding conditions and success, which under life-history theory would lead to the expectation that females should allocate more resources, and not less, to reproduction when breeding with helpers (differential allocation, or 'positive differential allocation'; Haaland et al., 2017; Sheldon, 2000; Stearns, 1992). Accordingly, positive associations between helpers' presence and clutch size have been observed in some cooperatively breeding species as apostlebirds *Struthidea cinerea* (Woxvold & Magrath, 2005) and red-winged fairy-wrens *Malurus elegans* (Lejeune et al., 2016; see also Liebl et al., 2016; Lloyd et al., 2009). In terms of egg size, evidence for differential allocation, i.e.; larger eggs when expecting more help, has only been found in Iberian magpies *Cyanopica cooki* (Valencia et al., 2017; see also reports on chestnut-crowned babblers *Pomatostomus ruficeps* in Russell & Lummaa, 2009).

A recent meta-analyses combined the existing results on egg size variation with helper presence, revealing a general tendency for prenatal load-lightening as the most common strategy across cooperatively breeding species (Dixit et al., 2017). However, across studies, an overlooked pathway for adjustments in maternal allocation is via egg composition (Paquet et al., 2013; Russell et al., 2007). This is surprising since the first study proposing prenatal load-lightening via egg size in birds also reported load-lightening via yolk mass, lipid and protein content, thus showing that the decrease in egg volume corresponded to a decrease in eggs' nutritional content (Russell et al., 2007). Only one other study explored differences both in egg size and components in the presence of helpers (Paquet et al., 2013). Paquet and co-authors (2013) found that, similar to superb fairy wrens, sociable weaver *Philetairus socius* females with helpers laid lighter eggs than females without helpers. In addition, and although no differences in eggs' carotenoid content were detected, females without helpers produced eggs with higher hormonal content (testosterone, androstenedione and corticosterone) which was speculated to increase offspring competitive abilities when pairs were breeding without help (Paquet et al., 2013). Experimental work in black-headed gulls *Larus ridibundus* showed that testosterone and androstenedione levels in the eggs were associated with faster offspring growth, increased body mass and size (Eising et al., 2001), and offspring from eggs injected with androgens begged more frequently and received a larger share of food (Eising & Groothuis, 2003). These competitive abilities may be less important when females breed with helpers and more food is available to the brood, but further investigations are necessary to understand how hormones' accumulation in the eggs varies within and across cooperatively breeding birds (Bebbington & Groothuis, 2021; Russell & Lummaa, 2009).

Interactive effects of climate, predation, and helper number

Since having helpers is in general positively associated with higher reproductive success and survival (Downing et al., 2020, 2021), and helpers' presence may mitigate negative effects of climatic conditions on reproductive success (Groenewoud & Clutton-Brock, 2021), maternal allocation strategies in relation to number of helpers may also vary according to the environmental conditions experienced. Concurring with this idea, results from a ten-seasons study in superb fairy-wrens showed that females with helpers laid smaller eggs in cooler conditions and larger eggs in hotter conditions, hence suggesting that females with helpers may facilitate offspring survival in harsh hot conditions and instead show prenatal load-lightening in cool conditions (Langmore et al., 2016).

Long-term data collections as the latter provide a unique opportunity to estimate the effects of multiple environmental effects, across time, on life-history strategies (Clutton-Brock & Sheldon, 2010; Cockburn, 2014). In these long-term investigations, extensive knowledge is gathered on the environmental variables likely to be of greatest significance for the species' life history (Bourne et al., 2020; Clutton-Brock & Sheldon, 2010; Cockburn, 2014; Groenewoud & Clutton-Brock, 2021). When this knowledge is coupled with long-term individual-based data on reproductive investment, one can address plasticity in reproductive allocation by performing longitudinal analyses to test whether breeding females flexibly adjust investment in reproduction in relation to variation in critical environmental factors (Langmore et al., 2016; Lejeune et al., 2016; Nussey et al., 2005). Moreover, one can take advantage of natural variation in environmental variables across time, such as climatic conditions (Langmore et al., 2016), to better understand how dynamic environmental cues interact and affect individuals' reproductive strategies and fitness.

The findings by Langmore and co-authors (2016) open new research avenues on whether similar flexible strategies might have evolved in other cooperative systems, and on how helpers may interact with other environmental variables that have substantial effects on reproductive success, such as predation risk. Females exposed to increased adult or offspring predation risk may not reduce resource allocation to reproduction as severely (Fontaine & Martin, 2006; Hua et al., 2014; Saino et al., 2005; Zanette et al., 2011) if their breeding conditions are improved due to the presence of helpers (Sheriff et al., 2017). However, the interactive effect of helper number and predation risk on maternal allocation has never been investigated in cooperative breeders.

Maternal effects on offspring phenotype

Despite the undeniable associations between environmental variables and maternal resource allocation to offspring, these may not always represent active strategies, and the fitness consequences of maternal effects are still under debate.

Maternal effects can be passive consequences, i.e. by-products of females' adaptations to their environment, with potential benefits for the offspring emerging as a consequence, or can be active strategies if the maternal effect arose specifically because it conveys adaptive advantages (Badyaev, 2005). Moreover, adaptive maternal effects can be 'anticipatory' when females adjust the phenotype of their offspring to match their environment, thus increasing offspring fitness when maternal and offspring environments match (Burgess & Marshall, 2014; Marshall & Uller, 2007). An example of an anticipatory maternal effect would be the advantage of seed beetles' larvae from larger eggs in poor-quality host plants mentioned before (Fox et al., 1997; Fox & Mousseau, 1996), or offspring from predator-exposed females being better at escaping predation themselves (Coslovsky & Richner, 2011, 2012). Yet, evidence for anticipatory maternal effects across organisms appears arguable and may be subtle (Sánchez-Tójar et al., 2020; Uller et al., 2013; Yin et al., 2019). When maternal effects instead increase maternal fitness at the expense of offspring fitness, these can be called ‘selfish’ maternal effects, as in the bighorn sheep example where females saved energy by favouring their own mass over their lambs when breeding in adverse environments (see above Festa-Bianchet et al., 2000; Festa-Bianchet & Jorgenson, 1998). Overall, maternal effects are considered an important source of phenotypic variation in natural populations, showing particularly strong effects on morphological and phenological traits, and at the juvenile stage, and thus have the potential to influence ecological and evolutionary processes (Moore et al., 2019).

An overlooked consequence of maternal effects is that these may not only influence mothers and their offspring, but also the behaviour of other care provisioners (Bebbington & Groothuis, 2021; Moreno-Rueda, 2007; Müller et al., 2007). For instance, when females’ prenatal resource allocation influences development and/or begging behaviour (Groothuis et al., 2005), it may in turn affect the amount of postnatal care provided by their breeding partner, in biparental care systems, or breeding group in cooperatively breeding systems (Moreno-Rueda, 2007; Müller et al., 2007; Paquet & Smiseth, 2016, 2017). Variations in feeding effort are relatively well studied in biparental care systems (reviewed in Müller et al., 2007), but whether and how helpers adjust feeding investment to offspring phenotype is less understood, especially when helpers of different sex and relatedness levels to the offspring co-exist within cooperatively breeding species (MacLeod & Brouwer, 2018; McDonald et al., 2009; Wright, 1998; Wright et al., 2010).

Objectives

The general objective of this thesis is to investigate the effects of multiple and fluctuating environmental variables – social group sizes, climatic conditions, predation risk – on maternal allocation strategies and offspring phenotype and survival in cooperatively breeding species. To achieve this, three specific aims were defined:

- Investigate how prenatal reproductive allocation varies with social group sizes, climatic conditions and predation risk using both long-term data and/or field experiments (**Chapters 2, 3 and 4**).
- Test how offspring phenotype, and specifically a feature that may be influenced by prenatal maternal effects – begging behaviour – influences breeders and helpers' postnatal investment (**Chapter 5**).
- Explore how number of helpers and climatic conditions interactively associate with offspring first-year survival (**Chapter 6**).

The study system

These questions were investigated in sociable weavers *Philetairus socius*, a colonial and cooperatively breeding passerine endemic to southern Africa (Fig. 1.3). Sociable weavers' biology and environment make them a particularly relevant species to address how social, ecological, and climatic factors interact (see below). These birds are endemic to the semi-arid savannas of Namibia and South Africa's Northern Cape Province (Maclean, 1973a) and this study was conducted at Benfontein Nature Reserve, Northern Cape Province, South Africa (28°520 S, 24°500 E).

Sociable weavers build massive communal nests, or 'colonies', with several chambers where they breed and roost throughout the year (Maclean, 1973b; Fig. 1.3). Colony sizes can vary among colonies and within colonies across time, ranging from a few to several hundred individuals (Maclean, 1973b). Moreover, they are facultative cooperative breeders, so breeding pairs can reproduce by themselves or be assisted by one or several helpers with nestling feeding (Covas et al., 2008; Maclean, 1973d), nest building and sanitation (A. Ferreira, 2015). Helpers are typically the offspring of one or both breeders, but other second-order relatives and distantly related/unrelated birds also provide help (Covas et al., 2006). Moreover, helpers are of both sexes, but females disperse to breed, whereas males typically remain in their natal colonies (Covas et al., 2006; Doutrelant et al., 2004; van Dijk et al., 2015).

Sociable weavers' breeding seasons can last for several months and they usually lay several breeding attempts per season (Covas et al., 2008; Mares et al., 2017). Clutch size typically ranges between two and four eggs and females usually lay one egg per day (Covas & Du Plessis, 2005). The duration of the incubation period is around 15 days and both sexes incubate (Covas & Du Plessis, 2005; Maclean, 1973c). Nestlings normally hatch asynchronously and the subsequent nestling period lasts for 21–25 days (Covas & Du Plessis, 2005; Maclean, 1973c).

Figure 1. 3 The sociable weavers' study system. Top left photo shows one of the monitored colonies with numerous chambers where individuals roost and breed (photo by Franck Theron). Top right photo shows a group of sociable weavers perched on a branch of their colony's tree (photo by Alexandre Vaz). Bottom photo shows the study area environment in the particularly dry breeding season of 2015/2016 (photo by Rita Fortuna).

In this system, helper number seems to be predictable by females at laying, since most helpers are previous offspring of the breeders (Covas et al., 2006), roosting group sizes before breeding were found to correlate with breeding group sizes (Paquet et al., 2016), and social bonds are stronger within breeding groups (A. C. Ferreira et al., 2020).

Sociable weavers are typically associated to Kalahari sandvelt (Maclean, 1973a), which consists of open *Acacia* savanna with grassland (Fig. 1.3). In the study area, temperatures are extreme (from 1990-2019, average minimum temperature 10 °C [range = -8 to 25 °C] and average maximum temperature 26 °C [range = 1 to 43 °C]) and rainfall is low and seasonally irregular (between less than 250 mm per year to over 700 mm), strongly influencing breeding seasons' duration and fledging success (Covas et al., 2008; Mares et al., 2017). Reproductive success is also drastically affected by nest predation by snakes, which can take 70% of all breeding attempts (Covas et al., 2008).

Individuals at the monitored colonies have been captured using mist nests once or twice per year on most years since 1993 (Covas et al., 2002). Birds are ringed with a uniquely coded aluminium ring and a unique colour ring combination, allowing individual visual identification. Blood samples are collected for genetic sexing and determination of parentage relationships. Breeding activity has been monitored from start to end every season since 2008/2009.

Chapters' overview

This thesis is divided in seven chapters. After the General Introduction (**Chapter 1**), I present the first study, in which a long-term dataset collected over 9 breeding seasons was used to test if climate, nest predation and number of helpers had interactive effects on egg mass and clutch size in sociable weavers – **Chapter 2** (Fortuna et al., 2021). For this, natural variation in climatic conditions was combined with a long-term nest predator exclusion experiment and with within-female sampling of reproductive allocation measures as their number of helpers varied. This study showed that egg mass did not detectably vary with number of helpers, nest predation risk or climatic conditions. Clutch size was larger after more rainfall and under reduced predation risk and did not evidently vary with helper number.

The second study focused on maternal allocation to egg components in relation to number of helpers and egg laying order – **Chapter 3** (in prep.). The aim of this work was to test whether helpers could mitigate negative laying order effects on maternal allocation and offspring survival, and for this, ten measures of egg nutrients and hormones' allocation were collected – egg mass, yolk mass, proteins, lipids, carotenoids, vitamin A and vitamin E, testosterone, androstenedione, and corticosterone. In brief, results showed that group size and laying order interactively associated with yolk mass, as later-laid eggs from females with more helpers had heavier yolks, but not with the remaining allocation measures, and that group size was generally positively related to yolk lipids concentration and to nestlings' fledging probability.

To further understand the role of predation in maternal allocation strategies, I performed a field experiment to test how increased adult predation risk affected clutch size, egg mass, yolk mass and yolk corticosterone, and whether helpers modulated predator-induced changes in maternal allocation – **Chapter 4** (in prep.). This work showed that predator-exposed females laid eggs with lighter yolks independently of their group size, and no effects of predation treatment were found for the remaining variables.

The fourth study included in this thesis investigated how breeders and helpers, distinguished by sex and relatedness to the offspring, experienced and responded to brood begging – **Chapter 5** (Fortuna et al., 2022). The aims of this work were to better understand direct and indirect fitness benefits of responding to offspring demand, and to test how this feature of offspring phenotype, which may be influenced by maternal effects, influences feeding rules in this system. Results showed that only breeding males reduced nest inter-visit feeding intervals at higher offspring begging rates, indicating that the benefits and costs of adjusting feeding effort to begging differ with sex and life history stage in sociable weavers.

Finally, capture-recapture analyses were used to investigate interactive effects of breeding group size and climate on offspring first-year survival – **Chapter 6** (in prep.). The goal of this study was to test if being raised with more helpers would modulate the effects of climatic conditions during rearing and first winter on offspring survival. The findings provided some but limited support of the prediction that adverse climatic effects on offspring survival are buffered by group size, as only low rainfall effects on female offspring survival appeared mitigated by helper number. Results also indicated that under benign climatic conditions, larger breeding groups may be potentially disadvantageous for offspring survival.

At the end, the General Discussion summarizes the specific and overall findings of this thesis and proposes future avenues of research in the fields of maternal allocation strategies, cooperative breeding, and their intersection – **Chapter 7**.

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Chapter 2

Maternal allocation in relation to weather, predation and social factors in a colonial cooperative bird

Maternal allocation in relation to weather, predation and social factors in a colonial cooperative bird

Rita Fortuna[1], Matthieu Paquet[2], André C. Ferreira[1,3], Liliana R. Silva[1], Franck Theron[3], Claire Doutrelant[3] and Rita Covas[1,4]

[1]CIBIO-InBIO - Research Centre in Biodiversity and Genetic Resources, Campus Agrário de Vairão, 4485–661 Vairão, Portugal
[2]Swedish University of Agricultural Sciences, Uppsala, Sweden
[3]CEFE-UMR5175 CNRS - Université de Montpellier, 1919 route de Mende, 34293 Montpellier Cedex 5, France
[4]Percy FitzPatrick Institute, DST-NRF Centre of Excellence, University of Cape Town, Cape Town, South Africa

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Abstract

1. Females may adjust prenatal allocation in relation to ecological conditions that affect reproductive success, such as weather conditions or predation risk. In cooperative breeders, helpers might also influence reproductive success and previous studies suggest that females can lay smaller eggs or larger clutches when breeding with more helpers. Although recent work suggests that helper effects can vary according to climatic variables, how social and ecological factors interact to shape prenatal allocation is poorly understood.

2. Here, we examine how ecological and social components of the breeding environment co-vary with egg mass and clutch size, using as a model the sociable weaver (*Philetairus socius*), a colonial, cooperatively breeding passerine. The study spanned 9 years and included over 1900 eggs from over 550 clutches. Our analyses combined natural variation in weather conditions (rainfall before each reproductive event) with a nest predator-exclusion experiment and continuous monitoring of the mother’s social environment, allowing us to estimate how individual females adjust allocation to reproduction as their number of helpers varies.

3. We found that egg mass varied consistently within females and did not clearly differ in relation to rainfall or predation risk. Contrary to previous studies, there was no evidence for plastic adjustments as females gained and lost helpers and egg mass was instead better predicted by mother size and identity.

4. Females laid larger clutches when breeding in environments where predation risk was experimentally reduced and after higher rainfall levels. Yet, there was no evidence for increasing clutch size as the number of helpers increased, nor for an interaction between helper effects and ecological factors.

5. We conclude that while sociable weaver females can vary their clutch size, they show high individual consistency in egg mass. In addition, we found no evidence that females may maximise fitness through plastic prenatal allocation in relation to the number of helpers, or that the presence/absence of helper effects is modulated by rainfall levels or predation risk. These results challenge our current knowledge on some of the possible benefits of breeding with helpers and call for more long-term analyses on reproductive allocation adjustments in other cooperative systems.

Keywords: Clutch size; Cooperative breeding; Differential allocation; Egg mass; Load-lightening; Maternal allocation; Nest predation; Sociable weaver

1. Introduction

Life-history theory predicts that individuals should balance current reproductive investment against their future survival and breeding prospects (Stearns, 1992). These trade-offs are often modulated by a complex set of ecological conditions that define breeding environments (Erikstad, Fauchald, Tveraa, & Steen, 1998; Stearns, 1992). Breeding females' investment strategies may involve adjusting prenatal allocation in response to ecological factors that have a predictable effect on reproductive success, thereby maximising their reproductive output (Lindström, 1999; Mousseau & Fox, 1998).

Variation in climatic factors is among the set of ecological conditions that can influence reproductive allocation (Christians, 2002; Przybylo, Sheldon, & Merilä, 2000; Saino, Romano, Ambrosini, Ferrari, & Møller, 2004). In birds, favourable temperature and rainfall levels were found to associate with the production of larger eggs and clutches (Lepage & Lloyd, 2009; Schaper & Visser, 2013; but see Thomson & Hadfield, 2017). Another key ecological factor with a major influence on reproductive outcome is offspring predation risk (Martin, 1995; Zanette, White, Allen, & Clinchy, 2011). Experimental manipulations of predation risk have revealed that mothers produced heavier eggs when nest predators were excluded (Fontaine & Martin, 2006) and laid smaller clutches when predator pressure seemed higher (Doligez & Clobert, 2003; Zanette et al., 2011). Saving energy when breeding in riskier environments, where progeny survival prospects are lower, can be advantageous over a lifetime if the immediate costs of reduced investment are counterbalanced by increased probability of breeding in the future (Mousseau & Fox, 1998; Stearns, 1992; Williams, 1966).

A species' social organisation can also influence reproductive trade-offs, through variation in the number of conspecifics that are part of a colony or breeding group. Colonial living can benefit individuals by increasing foraging efficiency or reducing predation (Brown & Brown, 2001), but the resulting competition for resources can also be detrimental, affecting both maternal allocation and reproductive success (Bentz, Navara, & Siefferman, 2013; Fuentes, Rubalcaba, Veiga, & Polo, 2019; Spottiswoode, 2007). In cooperatively breeding species, helpers assist breeding pairs by offering additional food to offspring, and larger groups are usually found to improve breeding environments (Cockburn et al., 2008; Downing, Griffin, & Cornwallis, 2020). Hence, when breeding group sizes are predictable (Paquet et al., 2016), helpers presence may trigger differential prenatal maternal allocation (Russell & Lummaa, 2009; Savage, Russell, & Johnstone, 2015). Larger groups may allow females to raise additional offspring, which may explain the positive correlation between helpers and clutch size previously reported in, for example, apostlebirds *Struthidea cinerea* (Woxvold & Magrath, 2005) or red-winged fairy-wrens *Malurus elegans* (Lejeune, van de Pol, Cockburn, Louter, & Brouwer, 2016; see also Liebl, Browning, & Russell, 2016; Lloyd, Andrew Taylor, Du Plessis, & Martin, 2009). However, this correlation is not found in all cooperatively breeding systems (Canestrari, Marcos, & Baglione, 2011; Koenig, Walters, & Haydock, 2009; Russell, Langmore, Cockburn, Astheimer, & Kilner, 2007; Santos & Macedo, 2011; Valencia, Mateos, de la Cruz, & Carranza, 2016), suggesting that the benefits of breeding with helpers may vary across species and/or environments.

Helper presence could also allow mothers to allocate differently to individual offspring, an idea that has been supported by findings of concealed helper effects on egg size (Dixit et al., 2017; Russell et al., 2007). Specifically, the load-lightening hypothesis suggests that producing smaller eggs when breeding with helpers could improve mothers' survival without reducing offspring fitness, if this decrease in prenatal allocation is compensated by additional help to raise the young (Crick, 1992; Russell et al., 2007; Savage et al., 2015; Taborsky, Skubic, & Bruintjes, 2007). This strategy was found in different taxa (Russell et al., 2007; Taborsky et al., 2007) and seems to be a general trend across cooperatively breeding birds (Dixit, English, & Lukas, 2017). It should be favoured in species with higher future breeding probability, as individuals could maximize lifetime reproductive success through maximizing survival (Clutton-Brock, 1988). Alternatively, the differential allocation hypothesis (Sheldon, 2000) proposes that larger eggs are expected when breeding with more helpers, especially in cases where pre-birth care cannot be compensated by postnatal care or for species with a shorter reproductive lifespan (Russell & Lummaa, 2009; Savage et al., 2015).

However, most studies on the correlation between maternal allocation and helpers have compared differences among females (but see Lejeune et al., 2016), and therefore it remains unclear whether females plastically adjust their allocation to variation in their group size (Dixit et al., 2017). Alternatively, this correlation could be linked to habitat quality or to female traits, such as size, age or reproductive qualities, which are known to correlate with maternal allocation (Christians, 2002) and possibly also group size, if better quality females attract/produce more helpers (Cockburn, 1998; Dickinson & Hatchwell, 2004). Since manipulating helpers' number in wild systems is difficult, long-term studies provide a unique opportunity to study maternal allocation strategies. As the same female will likely gain and lose helpers over the years, it is possible to examine within-female plasticity in response to the number of helpers (Langmore, Bailey, Heinsohn, Russell, & Kilner, 2016; Lejeune et al., 2016). Moreover, the fitness benefits of adjusting allocation to helpers may depend on ecological factors that influence the success of current reproduction (Hatchwell, 1999). For example, a long-term study in superb fairy-wrens (*Malurus cyaneus*) found that females with helpers produced smaller eggs only under more favourable, cooler temperatures (Langmore et al., 2016). Conversely, in poor environments, the additive care of helpers and parents might be determinant for offspring survival (Hatchwell, 1999). It is therefore important to integrate multiple environmental variables and how they interact when studying reproductive strategies, which few studies have done (but see Koenig et al., 2009; Langmore et al., 2016; Lejeune et al., 2016).

Here, we examine how prenatal maternal allocation in a wild passerine relates to three key factors known to affect reproductive outcome – weather, predation risk and social environment. Our study spanned 9 years and combined a predator-exclusion experiment with natural variation in social and climatic factors. Repeated sampling allowed to disentangle fixed differences between females from allocation plasticity in relation to variation in number of helpers. We used as a study species the sociable weaver (*Philetairus socius*), a colonial cooperative breeder inhabiting the arid Kalahari savannahs, where variation in rainfall and temperature is extreme (Mares, Doutrelant, Paquet, Spottiswoode, & Covas, 2017). These are relatively long-lived weavers (Paquet, Doutrelant, Hatchwell, Spottiswoode, & Covas, 2015) that breed opportunistically, leading to long breeding seasons (Mares et al., 2017). However, reproductive success is low due to nest predation by snakes which can take 70% of all breeding attempts (Covas, du Plessis, & Doutrelant, 2008). For the surviving broods, a higher number of helpers correlates with higher feeding rates (A.C. Ferreira et al., unpublished data; Covas et al., 2008), but breeding with helpers was only associated with improved fledgling condition during periods of low rainfall (Covas et al., 2008). Young female breeders, but not males, have shown increased survival associated with helpers' presence (Paquet et al., 2015). Importantly, in sociable weavers there is evidence that females assisted by helpers lay lighter eggs (Paquet, Covas, Chastel, Parenteau, & Doutrelant, 2013), but whether this result is replicable across environmental conditions and represents plasticity has never been tested.

Given this species' life history, social behaviour and breeding environment, we made the following predictions for how maternal allocation strategies may vary with breeding conditions (Fig. 2.1). In relation to ecological factors (weather and predation), we predicted that heavier or more eggs would be produced by mothers in favourable conditions, i.e. higher rainfall/less extreme temperatures (Covas et al., 2008; Maclean, 1973b) and lower nest predation. However, in these favourable environments, mothers with more helpers are predicted to lay lighter eggs, in accordance with the load-lightening hypothesis (Fig. 2.1A), and to lay even more eggs than females without helpers (Fig. 2.1B). Since we re-sampled females, we could test our hypotheses at the relevant biological level (within-female adjustments, see Dingemanse & Dochtermann, 2013), with the prediction that egg mass negatively correlated with the number of helpers within females, similarly to between females (equal slopes; Fig. 2.1C). Likewise, we expected a similar positive correlation between clutch size and number of helpers within and between females (equal slopes; Fig. 2.1D).

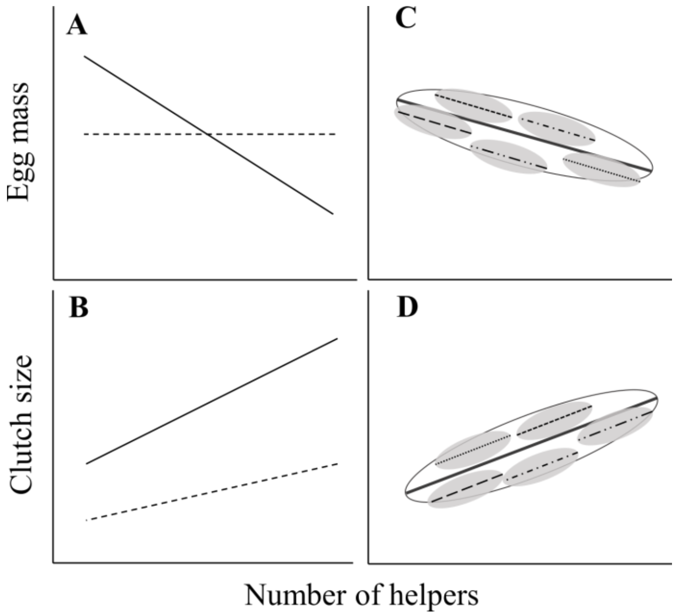

Figure 2. 1 On the left, predicted interaction between number of helpers and breeding conditions on (A) egg mass and (B) clutch size. Solid lines represent good conditions (favourable weather/low predation) and dashed lines represent harsh conditions (adverse weather/high predation). For egg mass (A), we predicted lighter eggs as the number of helpers increases (load-lightening), only under favourable ecological conditions. For clutch size (B), we expected larger clutches with more helpers, with a weaker effect in harsh environments. On the right, predicted direction of the correlation between number of helpers and egg mass (C) or clutch size (D) between females (solid line) and within females (dashed lines).

2. Materials and methods

2.1 Study system

Sociable weavers are colonial cooperatively breeding birds endemic to southern Africa that build massive communal nests (Maclean, 1973a; colony size ranged from 3 to 134 individuals in this study). In our study population, most helpers (73%) are previous years' offspring of one or both breeders (A.C. Ferreira et al., unpublished data; Covas, Dalecky, Caizergues, & Doutrelant, 2006), and helpers can assist one or several pairs with nestling feeding (Maclean, 1973c), nest building and sanitation (Ferreira, 2015; see Groups' identification for details on breeding groups).

This work was conducted at Benfontein Nature Reserve in Northern Cape Province, South Africa (28°520 S, 24°500 E), under permission from landowners, provincial authorities and the UCT Ethics committee.

2.2 Egg mass and clutch size

From 2008 to 2017, breeding monitoring was conducted in 20 different colonies (see protocol in Supplementary material section A). We weighed a total of 9120 eggs and monitored 3418 clutches. From these, we were able to sample 1928 eggs and 569 clutches for all the variables included in our analyses. Data estimates are reported for the latter dataset, which is also accessible in the Dryad Digital Repository archive. Sample sizes may vary between analyses of egg mass and clutch size due to missing parameters at specific breeding attempts (i.e. clutch size was known, but not all eggs were weighed).

2.3 Nest predation experiment

From 2010 to 2017, we conducted a nest predator-exclusion experiment. By wrapping tree trunks with heavy duty cling plastic film, we prevented snakes from climbing up the trees and reaching the colonies. In natural conditions, snakes forage conspicuously at the colonies, moving between nests (where they can spend several days), and sociable weavers might mob them, although rarely successfully (pers. observations from all authors). We protected 8 colonies from snake predation for 1-6 years (Table S2.1). Four control colonies became protected and 5 protected colonies were posteriorly used as control. Among the re-sampled females (a total of 159; Table 2.1), 46 have experienced both treatments in different breeding seasons, 60 have only experienced natural conditions and 53 only bred in protected colonies (51 in natural and 49 in protected for the clutch size dataset).

Our experiment decreased nest failure from 64% in control colonies to 44% in protected colonies (F=-12.5, P<0.001; see Supplementary material section B and table S2). Nest failure recorded after casual snake sightings was reduced from 35% in natural conditions to 13% in protected colonies. Fledgling success of each egg laid increased from 11% in control colonies to 25% in protected colonies (Fortuna R., unpublished data).

2.4 Groups' identification

We identified 107 breeding groups using direct observations and 507 from video recordings. When we had several video recordings per nest, mean number of helpers was estimated. Over the study period (2008-2017), 79% of the broods had at least one helper. Mean number of helpers per breeding attempt was 1.7 (s.d.=1.3, range 0-6.7) and number of helpers was repeatable within the nestling period (R=0.47; s.e.=0.037;95% CI=[0.36,0.51]; P=0.001; N=1523). To identify breeding pairs, we used a combination of genetic analyses (Paquet et al., 2015) and monitoring data. Our final dataset included 253 female breeders. The number of helpers' repeatability within re-sampled females was 0.21 (s.e.=0.047; 95% CI=[0.126,0.307]; P=0.001; N=520). Details on groups and breeders' identification are available in Supplementary material sections C-D.

Table 2. 1 Number of female breeders partitioned by number of clutches sampled per female. The number of eggs sampled per female ranged between 2 and 22.

No. clutches per female	**No. females**	
	Egg mass dataset (N=1928)	Clutch size dataset (N=569)
1	94	100
2	60	54
3	42	41
4	27	30
5	15	9
6	14	11
7	1	1
No. re-sampled females	159	146
Total no. females	253	246

2.5 Weather data

Weather data was provided by the South African Weather Service for the Kimberley Airport weather station (12 km from the study site).

Hot temperatures are known to affect birds' breeding success in this region (Cunningham, Martin, Hojem, & Hockey, 2013) and sociable weaver's breeding seasons include the hottest months (December to February). In this study, most clutches (98%) were laid between September-April.

Rain is the major determinant of food abundance for this species (Maclean, 1973c), influencing their breeding onset and outcome (Altwegg, Doutrelant, Anderson, Spottiswoode, & Covas, 2014; Covas et al., 2008; Mares et al., 2017). In this study, total annual rainfall ranged from 238 mm (2013) to 766 mm (2011).

We calculated three weather variables – total rainfall, mean maximum temperature and mean minimum temperature – over two short time windows of 30 days and 15 days before laying-dates, which were *a priori* chosen to represent short-term effects of weather variation experienced by females before laying each clutch. Periods shorter than 15 days were not included but were highly correlated to the used windows (Fig. S2.1).

2.6 Statistical analyses

2.6.1 Climatic predictors

Due to limited knowledge of the climatic conditions that influence maternal allocation in this system, we tested which weather variable better improved the models by comparing Akaike information criterion (AIC) scores. We separately added each of the six weather variables to a model including all variables of interest and accounting for the multiple other covariates likely to affect egg mass or clutch size (see below). We then selected the models with lowest AIC value for further inference. Models were fitted using maximum likelihood (ML) for comparison.

None of the weather variables clearly improved the egg mass model, although including total rainfall (mm) over 30 days before laying showed the lowest AIC model score (Table S2.3). Similarly, the best clutch size model included total rainfall (mm) over a 30 days-period, but both rainfall and minimum temperature variables improved the clutch size baseline model (Table S2.3).

2.6.2 Effects on maternal allocation

To test whether helpers' effects on egg mass and clutch size were conditional on the predation experiment and/or weather conditions, we included 2 two-way interactions between these ecological variables and number of helpers. The weather variable used was total rainfall over the 30 days before laying (see above) and predation experiment was included as a binary factor (0-1 for natural conditions and protected colonies, respectively). Remaining covariables aimed at controlling for allocation trade-offs and female attributes were: clutch size or mean egg mass of the clutch (for egg mass and clutch size models, respectively) and number of clutches previously laid by that female in that season (called 'breeding attempt'; sociable weavers are multi-brooded), mothers' minimum age (in days) and tarsus length (Christians, 2002; Spottiswoode, 2007). Colony size was included as a proxy of breeding density, since egg mass was negatively correlated to this factor in previous studies (Spottiswoode, 2007). To account for repeated sampling of females and inter-seasonal and inter-colony variation, we included season, colony and female identity as random effects (in egg mass models, clutch identity was nested in female identity). All analyses were conducted using the R software v.3.6.0 (R Development Core Team, 2019).

Egg mass linear mixed models (LMM) assumed a Normal distribution and were fitted by restricted maximum likelihood in lme4 (Bates, Mächler, Bolker, & Walker, 2014; see Supplementary material section E). Clutch size models were under-dispersed using a Poisson error and we thus fitted both a LMM assuming a Normal distribution (see Results) and a cumulative link mixed model with clutch size as an ordinal categorical variable for comparison, both yielding similar results (see Supplementary material section E and Tables S2.6-S2.7).

For both response variables, numerical inputs were rescaled by subtracting the mean and diving by two standard deviations, s.d. (Gelman, 2008). Collinearity among predictors was assessed by calculating Spearman rank correlation coefficients (<0.52). Residuals' distribution and Normal distribution of random effects were assessed through diagnostic plots. Effects were considered significant when 95% confidence intervals did not overlap 0 and P values were lower than 0.05. Non-significant interactions were excluded to obtain final estimates, but no further model simplification was performed. Egg mass and clutch size repeatability within-females was estimated by fitting the final models using the rptR package (Stoffel, Nakagawa, & Schielzeth, 2017), which quantifies uncertainty in estimators by parametric bootstrapping (we used 1001 bootstraps and 1000 permutations; clutch size was log transformed for convergence). For each model, we present rescaled coefficients of numerical variables (see Table S2.4 for mean and s.d.). We also report marginal and conditional R^2 (variance explained only by fixed effects and by both fixed and random effects, respectively), calculated using the MuMIn package (Barton, 2009). Plots with raw data or predicted probabilities show untransformed numerical predictors.

2.6.3 Covariance partitioning

Univariate models allowed us to test if the general helper effect interacts with ecological conditions, but not to distinguish variation within-females in relation to number of helpers from fixed differences among females. To do this, we built mixed-effect models using egg mass and number of helpers, or clutch size and number of helpers, as bivariate responses. We used bivariate models instead of a subject-centering approach (Lejeune et al., 2016), to estimate female means as latent variables, and account for their uncertainty (credible intervals). This results in unbiased estimates of the within/between-individual effects, which could otherwise be substantially affected by measurement error (Lüdtke et al., 2008; see also Westneat et al., 2020).

We performed a Bayesian analysis using the MCMCglmm package (Hadfield, 2010) with the same fixed effect structure and transformations as for the univariate models. The fixed effects were estimated on egg mass/clutch size and an intercept was estimated for each response. A Normal distribution was used for egg mass, clutch size and number of helpers, the latter log transformed (0.5 was added before transformation to deal with zeros; Yamamura, 1999). Within and among females, we estimated a 2x2 matrix with a variance component for egg mass/clutch size, number of helpers, and the covariance between each allocation variable and number of helpers, by fitting a random interaction between the bivariate response and each female observation or female identity, respectively. We further added colony, season and clutch identities (for the model with egg mass) to the random structure. Estimates were obtained using vague priors (see Supplementary material section E for priors, model specification and convergence details). MCMCglmm was used to calculate posterior means with 95% credible intervals (highest posterior densities intervals or HPDs) for variances (V) and covariances (cov) estimated across thinned samples. We estimated a regression slope for the between-females (B) and within-females (w) random effects by dividing the estimated covariance by the number of helpers' variance for all posterior samples (Phillimore, Hadfield, Jones, & Smithers, 2010). The difference between the two slopes was as well calculated (Δ slopes) from the posterior distributions. The 95% HPD of each slope and of their difference were used to determine whether slopes differed from zero and from each other, respectively, considering significant any credible intervals that did not include zero. Correlations between traits (r) were calculated by dividing traits covariance by the square root of both traits' variance multiplied (Houslay & Wilson, 2017).

3. Results

3.1 Egg mass

Egg mass ranged between 1.697 g and 3.300 g (mean=2.518 g, s.d.=0.195; N=1928; Table S2.4) with an adjusted repeatability within females of 0.502 (standard error s.e.=0.034; 95% CI=[0.437,0.568]; P=0.001). Altogether, random effects explained most variation in egg mass, as a conditional R^2 of 63% was obtained for the best model, but fixed effects alone explained only 4% of the variance (marginal R^2) and showed quite small effect sizes on egg mass (Fig. 2.2). Mother identity was the random factor explaining the largest variance (Mother ID variance=0.019, Table S2.5).

No clear effects of rainfall before laying were detected on egg mass (F=1.72, df=336.8, P=0.09, estimate=0.020±0.012, 95% CI=[-0.003,0.042]; Figs 2.2 and S2.3A; Table S2.5). The predator exclusion experiment did not have a detectable influence on egg mass (F=0.90, df=142.3, P=0.37, estimate=0.013±0.014, 95% CI=[-0.015,0.042]; Figs 2.2 and S2.3C; Table S2.5), representing a minor mass increase of 0.5% in protected colonies compared to an egg laid in natural conditions.

We found no evidence for a correlation between egg mass and number of helpers (F=-1.30, df=483.4 ,P=0.19, estimate= -0.014 ± 0.011; Figs 2.2 and S2.3B; Table S2.5) and this was independent of the predation treatment or rainfall levels (Table S2.5; Figs S2.2A-S2.2B). There was also no evidence for a relationship between colony size and egg mass (F=-1.40, df=30.8, P=0.17, estimate=-0.027±0.019; Fig. 2.2; Table S2.5).

Egg mass variation seemed to depend on female body size as indicated by the tarsus length effect (F=2.99, df=235.7, P=0.003, estimate=0.059±0.020; Fig. 2.2; Table S2.5). There was no indication of an effect of clutch size on egg mass (F=-0.22, df=463.5, P=0.83, estimate=-0.002±0.010; Fig. 2.2; Table S2.5).

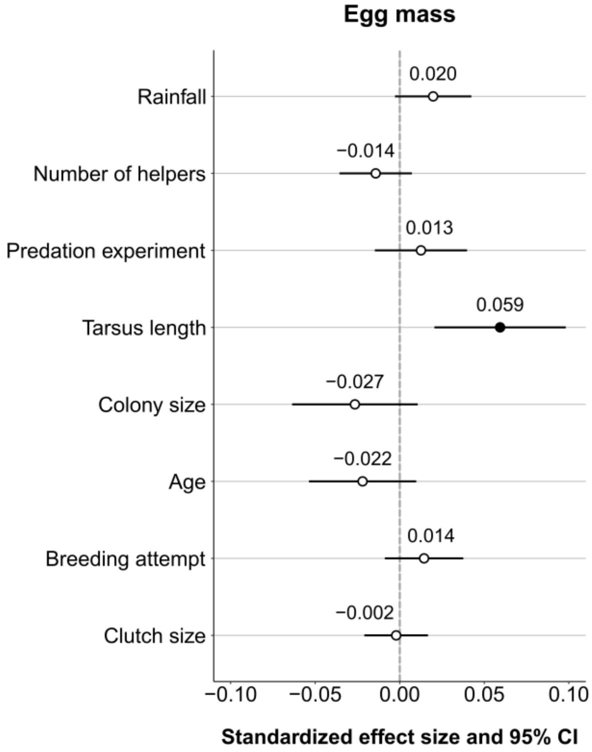

Figure 2. 2 Standardized estimates and 95% CI of variables included in the egg mass LMM. Variables of interest are placed first and remaining variables are ordered by effect size. Values indicate the effect on egg mass of a 2 s.d. change in numerical variables or from 0 to 1 in the predation experiment variable. Statistically significant effects are represented by filled circles.

3.2 Clutch size

Over 90% of the clutches laid had 2-4 eggs (mean =3.2, s.d.=0.6; N=569; Table S2.4). Contrasting with egg mass results, mother identity did not clearly predict clutch size (variance mother ID=0.019, df=1, P=0.12; Table S2.6) and there was no evidence for repeatability within females (R=0.05; s.e.=0.039; 95% CI=[0,0.137]; P=0.167). Clutch size was instead related to the random term ‘season’ (variance season=0.044, df=1, P=0.002; Table S2.6) and there was a considerable proportion of variance unexplained by the model (residual variance=0.287, R^2 marginal=0.074; R^2 conditional=0.246).

Higher rainfall levels were associated with larger clutches (F=2.61, P=0.01, estimate=0.157±0.06; Figs 2.3 and S2.5A; Table S2.6). Clutch size also differed with predation treatment, with a higher mean clutch size predicted in protected colonies (F=2.31, P=0.02, estimate=0.137±0.059; Figs 2.3 and S2.5B; Table S2.6).

Clutch size did not clearly change as the number of helpers increased (F=-0.32, P=0.75, estimate=-0.017±0.053, Figs 2.3 and S2.5C; Table S2.6), and this was independent of rainfall levels (F=1.20, P=0.25; Table S2.6; Fig. S2.4A) or the predation experiment (F=1.39, P=0.17; Table S2.6; Fig.S4B). Colony size had no detectable effect on clutch size (F=-0.11, P=0.91, estimate=0-0.007±0.062; Fig. 2.3; Table S2.6).

Additionally, females laid larger clutches in latter reproductive attempts of the same season (F=3.61, P=<0.001, estimate=0.211±0.059; Fig. 2.3; Table S2.6). There was no evidence that clutch size was correlated with mother size (F=1.46, P=0.15, estimate=0.074±0.051; Fig. 2.3; Table S2.6) or mean egg mass (F=-1.58, P=0.12, estimate=-0.079±0.05; Fig. 2.3; Table S2.6) .

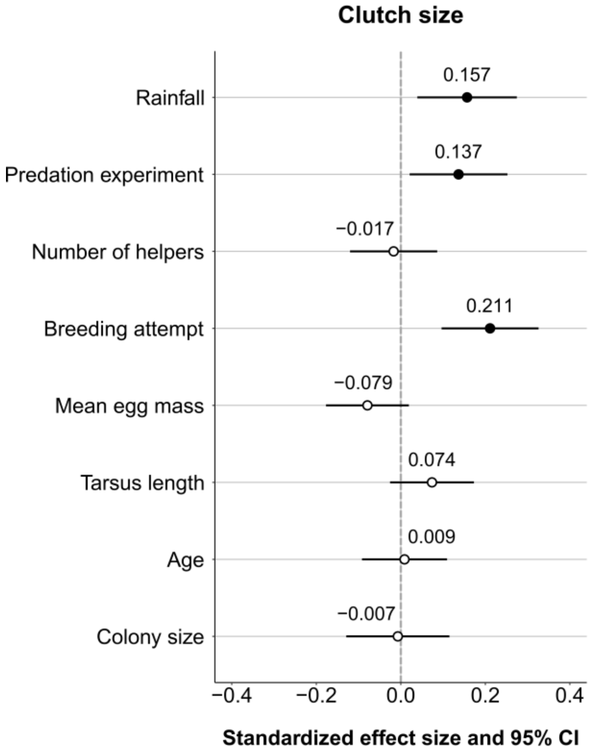

Figure 2. 3 Standardized estimates and 95% CI of variables included in the clutch size LMM. Variables of interest are placed first and remaining variables are ordered by effect size. Values indicate the effect on clutch size of a 2 s.d. change in numerical variables or from 0 to 1 in the predation experiment variable. Statistically significant effects are represented by filled circles.

3.3 Helper effects between and within-females

The covariance analyses between allocation measures (egg mass and clutch size) and number of helpers, across and within females, revealed no credible evidence for helper effects (Table 2.2; Fig. 2.4). In the bivariate model with egg mass (Table S2.8), we found a weak trend for a negative correlation between females (r =-0.078; CI=[-0.222;0.077]) and an even weaker correlation within females (r =-0.039; CI=[-0.100;0.029]), both with credible intervals overlapping zero (Table 2.2; Fig. 2.4). There was no evidence that the between-female and within-female's slopes were credibly different from each other (Δ slopes = -0.013; CI=[-0.058;0.036]; Table 2.2). Thus, we did not detect egg mass adjustments according to number of helpers, or fixed differences between females.

For the relationship between clutch size and number of helpers (Table S2.9), our estimates showed opposite but unclear correlations when comparing between and within-female trends (Table 2.2). The posterior mean correlation of clutch size and number of helpers between females was slightly above zero (r = 0.039; CI=[-0.243;0.281]) and within females was below zero (r = -0.02; CI=[-0.113;0.092]), both with credible intervals overlapping zero (Fig. 2.4). Similarly, there was no indication that slopes between and within females were credibly different from each other (Δ slopes = 0.043; CI=[-0.184;0.240]; Table 2.2).

Table 2. 2 Results from the variance-covariance matrices between and within females after modelling egg mass and number of helpers (top), and clutch size and number of helpers (bottom), as bivariate responses. Mean estimated variances (V) are presented on the diagonals, correlations (r) above and covariances (cov) below. The posterior mean of regression slopes between and within females, and their difference, are also presented. Below each value, 95% credible intervals are shown.

		Egg mass	No. helpers	Slope (cov /V_h)	Δ slopes (B-w)
Between females (Mother ID)	Egg mass	V_e = 0.03 (0.024,0.036)	r = -0.078 (-0.222,0.077)	-0.023 (-0.07,0.02)	-0.013 (-0.058,0.036)
	No. helpers	cov = -0.008 (-0.022,0.009)	V_h = 0.339 (0.274,0.411)		
Within females (Residuals)	Egg mass	V_e = 0.016 (0.015,0.017)	r = -0.04 (-0.1,0.029)	-0.01 (-0.025,0.007)	
	No. helpers	cov = -0.0026 (-0.006,0.002)	V_h = 0.263 (0.245,0.28)		

		Clutch size	No. helpers	Slope (cov /V_h)	Δ slopes (B-w)
Between females (Mother ID)	Clutch size	V_{cs} = 0.077 (0.05,0.104)	r = 0.040 (-0.244,0.281)	0.027 (-0.167,0.197)	0.043 (-0.184,0.24)
	No. helpers	cov = 0.005 (-0.027,0.035)	V_h = 0.171 (0.108,0.233)		
Within females (Residuals)	Clutch size	V_{cs} = 0.271 (0.238,0.309)	r = -0.119 (-0.113,0.092)	-0.016 (-0.098,0.074)	
	No. helpers	cov = -0.006 (-0.038,0.029)	V_h = 0.393 (0.336,0.449)		

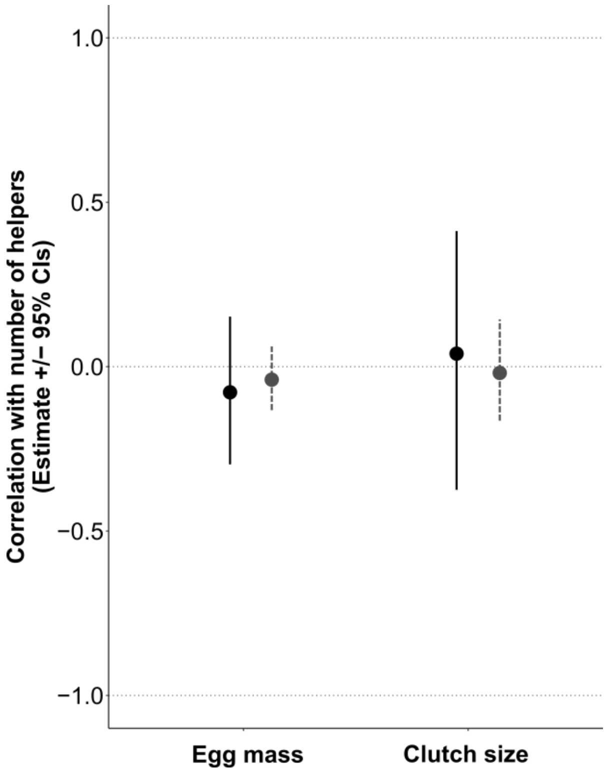

Figure 2. 4 Correlation between number of helpers and egg mass (left side) and clutch size (right side), between females (black full line bars) and within females (grey dashed line bars), calculated from respective bivariate models (Table 2.2). Circles show posterior mean correlations and vertical bars represent 95% credible intervals. Within and between-female slopes were not credibly different (see Table 2.2).

4. Discussion

In this study we investigated how maternal allocation relates to females' breeding environment in a cooperatively breeding species. Our results show that egg mass did not clearly correlate with weather conditions, experimentally reduced nest predation or the size of social groups. Clutch size was flexible within females and positively associated with higher rainfall levels and experimentally reduced nest predation. Females did not show egg or clutch size adjustments when breeding with more helpers and ecological conditions at laying were not found to modulate helper effects on maternal allocation. We thus found no evidence for fixed or plastic prenatal reproductive strategies in relation to number of helpers in sociable weavers.

4.1 Number of helpers and within-female allocation

Contrary to expected, we found no indication that sociable weaver mothers adjust prenatal allocation to the number of helpers in their group. Similarly, a previous long-term study that investigated plastic responses to number of helpers did not find egg size adjustments, but females increased clutch sizes when breeding in larger groups (Lejeune et al., 2016). In our study, covariance partitioning analyses showed that mothers do not seem to benefit from the presence of helpers by plastically load-lightening or producing more offspring when breeding in larger groups. These egg mass results differ from previous work in this population (Paquet et al., 2013) and challenge the overall evidence for prenatal load-lightening in cooperatively breeding systems reviewed in Dixit et al., (2017). In fact, this effect was mainly driven by three species (Canestrari et al., 2011; Paquet et al., 2013; Taborsky et al., 2007 one fish species) and after updating Dixit et al (2017) analysis with the effect obtained here, we found no general tendency of load-lightening at the egg stage in cooperative breeders (estimate=-0.1320, CI =[-0.2921;0.0281]; P=0.1061; Fig. S2.7; details in Supplementary material section F). Moreover, three additional studies have recently reported no evidence of prenatal load-lightening in other cooperative breeders (Cusick, Villa, Duval, & Cox, 2018; Van de Loock, 2019; Zhao et al., 2019). The meta-analysis on prenatal load-lightening in cooperative breeders should therefore be revisited in a future investigation. That the results obtained here contrast with a previous 1-year study in this species (Paquet et al., 2013) demonstrates the importance of replicating short-term investigations, as these might provide limited insights of evolutionary processes acting on natural populations in fluctuating environments (Cockburn, 2014; Fargevieille, Grégoire, Charmantier, del Rey Granado, & Doutrelant, 2017; Langmore et al., 2016). Furthermore, our work shows that clutch size does not clearly correlate with helpers' number in sociable weavers, concurring with investigations on several other species (Canestrari et al., 2011; Koenig et al., 2009; Russell et al., 2007; Santos & Macedo, 2011; Valencia et al., 2016). The failure of social factors to predict maternal allocation extended to colony size, our proxy of breeding density, which did not clearly correlate with egg mass or clutch size (but see Spottiswoode, 2007).

Our analyses relied on natural variation in group sizes and, if variation sampled within females is small, helper effects could be harder to detect. However, we found low repeatability in number of helpers for individual females (R=0.2), suggesting that little within-female variation is an improbable cause for failing to detect helper effects. Lack of plasticity in maternal allocation could also arise if females cannot predict the amount of help they expect to receive (Russell et al., 2007), but previous work in our population suggests that mothers have reliable cues regarding their number of helpers, since most helpers are previous offspring of the breeders (73%; A.C. Ferreira et al. unpublished data; Covas, Dalecky, Caizergues, & Doutrelant, 2006), social bonds are stronger within breeding groups (Ferreira et al., 2019) and roosting groups before breeding were correlated to breeding group sizes (Paquet et al., 2016). However, in sociable weavers, there appears to be substantial within-individual variation in the amount of help provided (A.C. Ferreira et al., unpublished) and further assessments of helping behaviour repeatability within and across broods would help to understand which cues are available for mothers prior to laying.

Long-term investigations have suggested that helper effects on female allocation may be detectable only under favourable climatic conditions (Langmore et al., 2016) and we therefore examined the effects of weather, namely rainfall, in interaction with number of helpers. This was especially relevant given that evidence for prenatal load-lightening in sociable weavers had been found during the season with the highest total annual rainfall in our dataset (Paquet et al., 2013). Yet, our findings suggest that the likelihood of observing helper effects on maternal allocation does not seem to be determined by climatic conditions, unlike what was shown in superb fairy-wrens *M. cyaneus* (Langmore et al., 2016).

4.2 Response to nest predator exclusion

By decreasing actual nest predation rates by snakes, we increased brood survival in manipulated colonies, which together with the decrease in snake foraging activity (indirect predation effects) was expected to increase mothers' allocation to reproduction. Our results indicate that females responded to these cues as they laid larger clutches in protected colonies than in natural conditions. This concurs with previous studies that reported adjustments in clutch size in response to offspring predation risk (Doligez & Clobert, 2003; Julliard, McCleery, Clobert, & Perrins, 1997; Zanette et al., 2011). In contrast, and unlike a previous study (Fontaine & Martin, 2006), egg mass was not clearly affected by our predator-exclusion experiment. For both egg mass and clutch size, helper effects did not detectably differ across predation treatments.

Larger clutches in protected colonies could have been caused not by reduced predation risk per se, but by females being in better condition. Mothers in protected colonies could save energy by laying less clutches when compared to females in natural conditions (which suffer higher predation and hence lay more replacement clutches).

However, our variable ‘breeding attempt’, which accounts for the number of clutches previously laid that season, showed no evidence of a negative effect on females’ fecundity. Females’ response to reduced predation could also arise from assessing self or conspecifics breeding success instead of predation risk (reviewed in Ibáñez-álamo et al., 2015). Here, we cannot determine whether the mechanism underlying females’ response is a decrease in perceived or actual predation risk. Nevertheless, our results suggest that responding to safety cues can be as much an adaptive mechanism as responding to danger cues (i.e.: increased predation; Luttbeg, Ferrari, Blumstein, & Chivers, 2020). Sociable weaver females therefore seem to assess the quality of their breeding environment and increase the number of offspring produced when the expected value of the current breeding attempt is higher (Mousseau & Fox, 1998; Stearns, 1992).

4.3. Weather effects

Females laid larger clutches after higher rainfall levels, which represents favourable conditions in these arid habitats (e.g. Covas et al., 2008; Maclean, 1973b; Mares et al., 2017; see also Aranzamendi, Hall, Kingma, van de Pol, & Peters, 2019; Lloyd, 1999). Moreover, there was no evidence for within-female clutch size repeatability and mothers showed a clear tendency for producing larger clutches in latter breeding attempts of the breeding season. These climatic and seasonal correlations are likely due to an increase in resources following summer rainfall peaks (Dean & Milton, 2001), which is expected to improve females’ condition and allow them to raise more young.

Unlike clutch size, egg mass did not clearly correlate with rainfall levels before laying. This may indicate that egg mass is not highly dependent on resource availability in this system, a result that has also been reported in other birds (Christians, 2002; Thomson & Hadfield, 2017).

4.4. Egg mass consistency

The wide range of egg mass values was mostly predicted by mother identity and body size, which concurs with previous results on low levels of egg size variation across ecological conditions and high consistency within-females (Christians, 2002; Griffith et al., 2020). The effect of ‘mother identity’ may be explained by genetic features that define the amount of resources that each female allocates to her eggs (Christians & Williams, 2001). Future estimates of heritability and fitness differences between females could help explaining the adaptive causes of egg mass consistency in our system (Christians, 2002).

Mother identity effects could also be influenced by the identity of their breeding partner. Sociable weavers exhibit long-term monogamy (P.B. D'Amelio et al., unpublished data) and females' prenatal allocation can vary with male quality proxies (Horváthová et al., 2012). Additionally, we found substantial egg mass residual variance, which might be attributed to intra-clutch differences according to the laying sequence (Kozlowski & Ricklefs, 2010).

5. Conclusions

We found that sociable weavers' clutch size varies with rainfall and predation, two ecological factors known to impact different aspects of this species' breeding biology, and suggesting an opportunistic strategy to maximise reproductive output in their highly variable ecosystem. In contrast, egg mass was consistent within females and across ecological conditions. Unexpectedly, we found no evidence for clutch size or egg mass plasticity in relation to number of helpers. These results challenge our current understanding of helper effects in our system and other cooperatively breeding species. The present results, together with the large variation in egg mass generally found among-females (Christians, 2002; this study), highlight the value of testing within-individual differences, as well as the importance of repeated sampling across variable environments when studying reproductive strategies.

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Authors' contributions

R.C. and C.D. conceived the study; All authors collected field data; R.F., A.C.F., L.R.S. and F.T. extracted and compiled data; R.F. analysed the data with input from M.P., R.C., C.D. and A.C.F.; R.F. led the writing of the manuscript with input from M.P., C.D. and R.C.; All authors gave feedback on the manuscript and their final approval for publication.

Data availability statement

Data available from the Dryad Digital Repository:
https://doi.org/10.5061/dryad.jm63xsj97 (Fortuna et al., 2021).

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Supplementary material

A. Egg mass and clutch size

From mid-September, nests contents were inspected every 3 days and when first eggs were found, nests were inspected every day to mark every new egg laid. Two days after clutch initiation, we weighed all eggs to the nearest 0.001 g with a digital Pesola scale. Nests were checked the following day to weigh a possible fourth egg. As five eggs' clutches are rare, we did not intentionally look for 5th eggs - but all nests were routinely inspected every 3 days – so whenever found, 5th eggs were also weighed (4% of the clutches).

B. Nest predation experiment

Our experiment decreased total nest failure from 64% in control colonies to 44% in treatment colonies (Table S2.2). These percentages include nests that failed due to snake predation but also unknown causes (e.g.: other predators, starvation, disease, infanticide, etc.) but exclude nests that only partially failed as snakes usually predate whole broods. Moreover, we registered every encounter with snakes when we visited the colonies (see main text).

Table S2. 1 Treatment status and data collected at each study colony throughout the nine breeding seasons. Natural conditions are represented with a zero and protected colonies are represented with a 1. Blank cells that have a 0/1 represent colonies that were under the mentioned treatment and were monitored but were not included in our analysis due to lack of data for some parameters. Grey cells represent control colonies included in the final datasets and blue cells represent protected colonies included in the final datasets. Red number cells represent colonies that were included in the egg mass analyses but not the clutch size analyses. Gaps represent colonies in which egg mass and clutch size were not monitored that season or not considered for this study (e.g.: 2 colonies were excluded because removal of predators repeatedly failed).

Colony ID	2008/2009	2009/2010	2010/2011	2011/2012	2012/2013	2013/2014	2014/2015	2015/2016	2016/2017
13	0								
2			0	0	0	0	0	0	0
21						0	0	0	0
25	0		0	0	0	0			
28	0		0						
32	0	0	0	0	0	0	0	0	0
36	0		0	0	0				
38			0	0	0	0	0	0	0
39	0	0	0		0				
6	0		0	0	0	0			
7						0	0	0	0
81						0	0		
43								0	1
27	0		0	0	1	1	1		1
20	0	0	1	1	1	1	1	0	
31			1	1	1	1	1	0	0
37			1	1	1	1	1	0	0
71					1	1	1	1	1
11		0	1	1	1	1	1	1	0
8	0	0	1	1	1	1	1	1	0

Table S2. 2 Estimates from a general linear model (GLM) on the effect of the predation experiment on brood failure probability (N= 3952). We ran a GLM with a binomial error function and logit link function. The response variable represents whether the clutch failed due to predation and other unknown causes or not (1 for total brood failure and 0 for other fates or only partial brood failure). The independent variable had two levels: 0 for natural conditions and 1 for protected colonies. Reference level (intercept) for "Predation experiment" is 0 (natural).

Fixed effect	**Estimate**	**Std. error**	**2.5%**	**97.5%**	**z**	***P***
(Intercept)	0.569	0.044	0.484	0.655	13	<0.001
Predation experiment	-0.820	0.066	**-0.949**	**-0.692**	-12.5	**<0.001**

C. Groups' identification

Before each breeding season, individuals were captured at their colonies using mist nests and given a uniquely numbered aluminium ring and colour-ring combination for visual identification. Blood samples were collected for genetic sexing and parentage inference. The number of individuals caught at each colony was used as colony size measure.

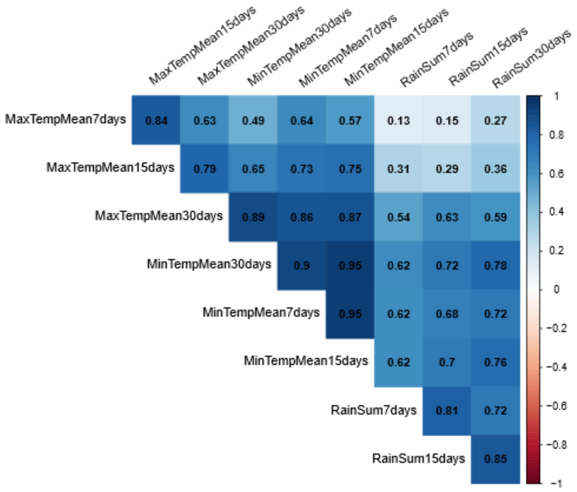
From 2008/09 to 2013/14, individuals were identified by 1 to 2 hours of daily observations for at least 3 days. Observers were situated in a hide placed at 3–5 m from the colony. These observations started when nestlings were around 6 days old. Group size was established when no new birds were seen feeding after several consecutive observations. From 2014/15 to 2016/17, group size was quantified by videotaping nests for a minimum of 2h. Video cameras were placed under the colonies focusing on nest entrances to record which and how many birds were seen feeding. Birds only visiting for purposes other than feeding (e.g. prospecting) were excluded from the number of helpers estimate. Groups that included un-ringed individuals (or with incomplete colour combinations) were also excluded.

Number of helpers' repeatability within breeding attempt i.e., across the nestling period, was estimated by fitting number of helpers counted in each observation as a Poisson distribution in an intercept only model with clutch identity as random effect and the original-scale approximation is reported. Number of helpers' repeatability within females was estimated by fitting mean number of helpers (in logarithmic scale, adding 0.5 to values before transformation) as a Normal distribution in an intercept only model with mother identity as random effect (dataset included only re-sampled females). We used the rptR package (Stoffel, Nakagawa, & Schielzeth, 2017) to quantify uncertainty in estimators by parametric bootstrapping using 1001 bootstraps and 1000 permutations.

D. Breeders' attribution

To estimate allele frequencies of the population we used Cervus v3.0.7 (Kalinowski, Taper, & Marshall, 2007) and included all individuals ever genotyped. We then performed full-likelihood parentage inference in Colony v. 2.0.5.9 (Jones & Wang, 2010). Parentage analyses were conducted by season and available genotypes of all born offspring were included, together with a list of genotypes of potential mothers and fathers. Birds were considered as candidate mothers or fathers only if the individual had been captured in that season, or the season just before, or in any of the seasons after (thus known or likely to be alive in the focal season). For each laying date, we excluded individuals that were considered too young to be breeding (minimum breeder age recorded is 8 months old, R. Covas et al., unpublished data). Marker typing error was set to 1% and the probability of the genetic parents being present among the genotyped candidate parents was set to 90% to allow for the possibility of an unknown bird being the parent (all other settings were set to default). Only pairs with a minimum assigned probability of 99% were included in further analysis. When the genotype data for the complete brood was not available, we assumed assigned pairs of one nestling to be the parents of all offspring, as there is no evidence of extra-pair or extra-group paternity in this species (Covas, Dalecky, Caizergues, & Doutrelant, 2006; Paquet, Doutrelant, Hatchwell, Spottiswoode, & Covas, 2015).

When there was no genetic data available for nestlings or parents, we would still attribute breeder status if in the group there were only two individuals that were old enough to breed, if they were related by less than 0.25 to each other or if that pair was previously seen breeding together (since divorce is extremely rare in this population; Paquet et al., 2015; P.B. D'Amelio et al., unpublished data). When there was only one male or one female feeding the nestlings, we also assumed this individual was one of the breeders. Moreover, when broods failed before we collected blood samples, we assumed nest parents to be the couple that bred in the same nest during that season (since only 8.6 % of nest chambers are occupied by different couples within a season, R. Covas et al., unpublished data), as long as no more than one couple had been seen in that chamber.



	MaxTempMean15days	MaxTempMean30days	MinTempMean30days	MinTempMean7days	MinTempMean15days	RainSum7days	RainSum15days	RainSum30days
MaxTempMean7days	0.84	0.63	0.49	0.64	0.57	0.13	0.15	0.27
MaxTempMean15days		0.79	0.65	0.73	0.75	0.31	0.29	0.36
MaxTempMean30days			0.89	0.86	0.87	0.54	0.63	0.59
MinTempMean30days				0.9	0.95	0.62	0.72	0.78
MinTempMean7days					0.95	0.62	0.68	0.72
MinTempMean15days						0.62	0.7	0.76
RainSum7days							0.81	0.72
RainSum15days								0.85

Figure S2. 1 Correlation between climatic variables and time windows based on 569 clutches from the clutch size dataset (one data point per clutch). Egg mass dataset shows similar correlation coefficients. Positive correlations are displayed in blue against negative correlations in red. Colour intensity is proportional to the correlation coefficients.

Table S2. 3 Climate variable selection tables: AIC comparison of full egg mass and clutch size models. Baseline models include all random and fixed terms of the full model but do not include a climate variable.

Egg mass (N=1928)	∆ AIC	D.f.	Clutch size (N=569)	∆ AIC	D.f.
Total rainfall last 30 days	0	16	**Total rainfall last 30 days**	0	15
Baseline model	0.3	14	Total rainfall last 15 days	0.2	15
Total rainfall last 15 days	1.1	16	Mean minimum temperature last 15 days	4.4	15
Mean minimum temperature last 15 days	2.6	16	Mean minimum temperature last 30 days	4.8	15
Mean minimum temperature last 30 days	2.8	16	Baseline model	5.8	13
Mean maximum temperature last 15 days	3.8	16	Mean maximum temperature last 15 days	8.6	15
Mean maximum temperature last 30 days	4.1	16	Mean maximum temperature last 30 days	9.2	15

E. Statistical methods

Helper effects on maternal allocation

Egg mass and clutch size models were fitted using the lme4 package (Bates, Mächler, Bolker, & Walker, 2014). The “bobyqa” optimiser was used due to convergence warnings when using lme4 default optimiser. Trying different optimisers resulted in equivalent parameter estimates for both response variables, confirming that convergence warnings were likely false positives (Bates et al., 2015). Fixed effects degrees of freedom and P values were estimated using Satterthwaite approximation and random effects' significance was assessed by likelihood-ratio tests (LRT), both using the lmerTest package (Kuznetsova, Brockhoff, & Christensen, 2017).

Besides LMM, we used cumulative link mixed models (CLMM) to fit clutch size as an ordinal variable with 5 categories (1 to 5 eggs) in the ordinal package (Christensen, 2019). Coefficients, standard errors (s.e.) and confidence intervals were back transformed from the logarithmic scale and are presented as odds ratios (OR). Cumulative link mixed models (CLMM) were fitted using the ordinal package (Christensen, 2019b) which estimates via maximum likelihood and fits mixed models with Laplace approximation. Distance between consecutive clutch size thresholds was set as equidistant. Models were fit with the logit link function. CLMs assume proportional odds (i.e.: the relationship between each pair of outcome groups is the same) and we verified that final estimates would not change when excluding terms that violated this assumption (only ‘colony size’). The condition number of the Hessian, which measures empirical identifiability of CLMMs, is reported with coefficients tables (values over 10^4 indicate ill-defined models; Christensen, 2019a). P values and 95% confidence intervals were estimated via Wald tests. Effects were considered statistically significant when confidence intervals did not overlap 1 (in the odds ratio scale) and P values were lower than 0.05. Random effects' significance was assessed through likelihood-ratio tests (LRT) comparing the final model with a model without the target random factor (Christensen, 2019a).

Covariance partitioning

MCMCglmm iterations were run with default fixed effect priors, a degree-of-belief parameter (nu) equal to the dimensions of the variance-covariance matrixes and a variance (V) of 1 for each variance component and for the residuals. A nu of 0.002 and V of 1 were used for clutch ID, season and colony random terms. Using different priors did not qualitatively change any result. For each model, three separate chains were run and convergence between models was assessed by calculating Gelman–Rubin statistic (Gelman & Rubin, 1992). For each chain, 2,000,000 iterations were run, with samples taken every 750 iterations and the first 500,000 removed as burn-in, resulting in 2000 samples and ensuring low autocorrelation among thinned samples (<0.1). Effective sample size was >1000 for all parameters.

Table S2. 4 Mean, standard deviation and range of untransformed numerical model inputs (values on the left were estimated from the egg mass dataset and values on the right were estimated from the clutch size dataset; when both datasets provided equal estimates, only one value is shown).

	Mean		Std. dev.		Minimum		Maximum	
Numerical inputs	Eggs data	Clutches data	Eggs data	Clutches data	Eggs data	Clutches data	Eggs data	Clutches data
Egg mass (g) | Mean egg mass (g)	2.52	2.51	0.20	0.17	1.70	2.06	3.30	3.17
Clutch size	3.35	3.22	0.59		1		5	
Age (days)	1154.97	1137.93	705	699.31	258		4440	
Breeding attempt	2.27	2.18	1.68	1.60	1		11	
Colony size	61.86	62.52	33.17	32.94	5		134	
Tarsus length (cm)	23.62		0.58		21.64		25.28	
Rainfall (mm)	34.39	32.94	35.16	35.07	0		175.4	
Number of helpers (obs. mean)	1.67	1.69	1.34	1.35	0		6.67	

Table S2. 5 Effect of climate, predation, number of helpers and other variables of the breeding environment on egg mass (N=1928). Results from a LMM fitted with restricted maximum likelihood (REML) and using standardized continuous predictors (final model R^2 marginal = 0.036 and R^2 conditional = 0.632). Separated by a line are the fixed effects that were dropped to fit the final model. To extract estimates and P values for main effects, two-way interactions were dropped. Reference level (intercept) for "Predation experiment" is 0 (natural). Random effects variance and significance estimated by LRTs are also presented.

Fixed effect	**Estimate**	**Std. error**	**2.5%**	**97.5%**	**Df**	**t**	***P***
(Intercept)	2.524	0.016	2.492	2.558	11.8	157.89	<0.001
Rainfall	0.020	0.012	-0.003	0.042	336.8	1.72	0.09
Number of helpers	-0.014	0.011	-0.035	0.007	483.4	-1.30	0.19
Predation experiment	0.013	0.014	-0.015	0.042	142.3	0.90	0.37
Tarsus length	0.059	0.020	**0.021**	**0.099**	235.7	2.99	**0.003**
Colony size	-0.027	0.019	-0.066	0.011	30.8	-1.40	0.17
Age	-0.022	0.016	-0.056	0.009	428.4	-1.36	0.18
Breeding attempt	0.014	0.012	-0.009	0.037	412.6	1.21	0.23
Clutch size	-0.002	0.010	-0.021	0.017	463.5	-0.22	0.83
No. helpers x Predation	-0.012	0.021	-0.053	0.030	428.8	-0.59	0.56
No. helpers x Rainfall	-0.022	0.019	-0.058	0.015	508.3	-1.17	0.24

Random effect	**Variance**	**Df**	**logLik**	***P***
(all)	-	-	936.2	-
Season (N=8)	0.0002	1	934.9	0.11
Colony ID (N=20)	0.001	1	935.6	0.28
Mother ID (N=253)	**0.019**	1	797.4	**<0.001**
Mother ID : Nest ID (N=614)	**0.003**	1	913.5	**<0.001**
Residual	0.014	-	-	-

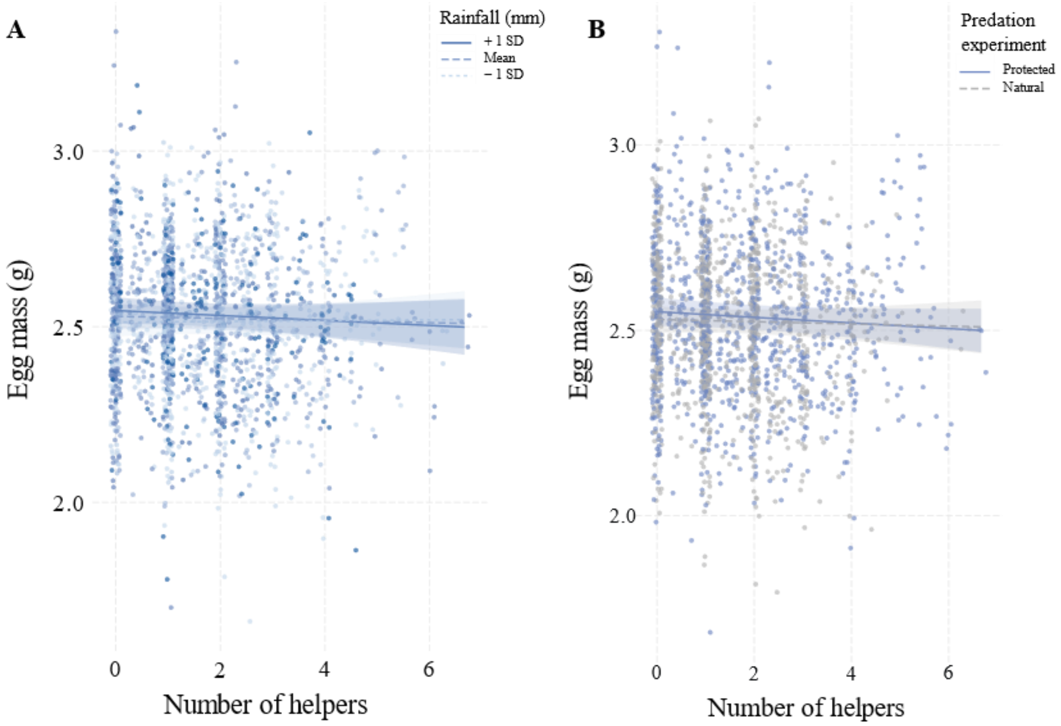


Figure S2. 2 Relationship between egg mass and number of helpers (A) depending on levels of total rainfall during the 30 days before the laying-date, (B) across predation experiment treatments. Dots represent raw values, solid and dashed lines represent the predicted values with 95% confidence intervals across different rainfall/predation conditions (see legends).

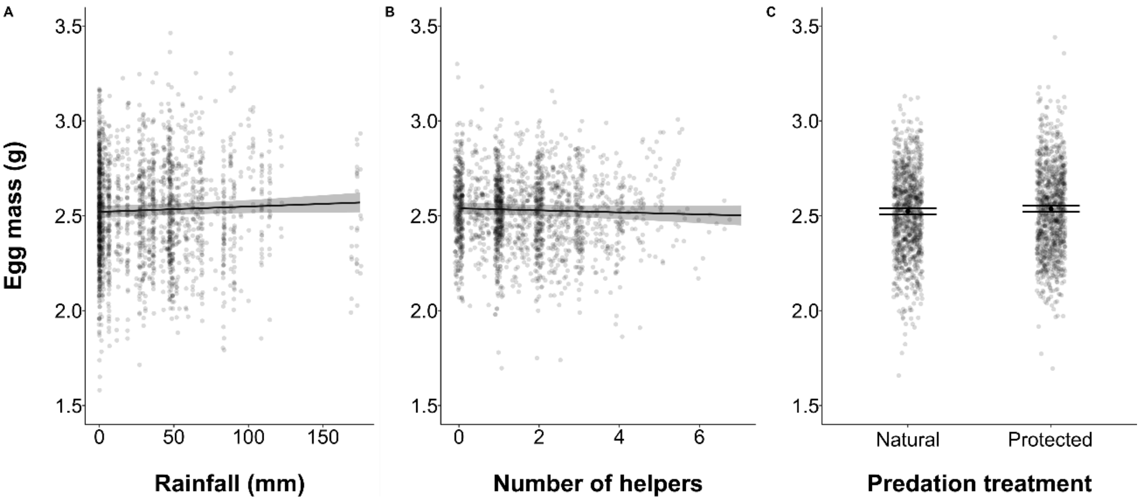


Figure S2. 3 Relationship between egg mass and (A) rainfall, (B) number of helpers and (C) predation experiment treatments. Dots represent raw values. In (A) and (B), lines show predicted values with 95% CI in grey reflecting variance in fixed effects. In (C), circles show the mean estimate of each category and bars represent the standard error.

Table S2. 6 Effect of climate, predation, number of helpers and other variables of the breeding environment on clutch size (N=569) when using a Normal distribution. Results from a LMM fitted with restricted maximum likelihood (REML) and *bobyqa* optimiser and using standardized continuous predictors (final model R^2 marginal = 0.074 and R^2 conditional = 0.246). Separated by a line are the fixed effects that were dropped to fit the final model. To extract estimates and P values for main effects, two-way interactions were dropped. Reference level (intercept) for "Predation experiment" is 0 (natural). Random effects variance and significance estimated by LRTs are also presented.

Fixed effect	**Estimate**	**Std. error**	**2.5%**	**97.5%**	**Df**	**T**	***P***
(Intercept)	3.229	0.093	3.047	3.424	7.0	34.67	<0.001
Rainfall	0.157	0.060	**0.038**	**0.273**	381.5	2.61	**0.01**
Predation experiment	0.137	0.059	**0.024**	**0.250**	55.7	2.31	**0.02**
Number of helpers	-0.017	0.053	-0.120	0.087	515.8	-0.32	0.75
Breeding attempt	0.211	0.059	**0.098**	**0.325**	499.0	3.61	**0.0003**
Mean egg mass	-0.079	0.050	-0.175	0.021	309.6	-1.58	0.12
Tarsus length	0.074	0.051	-0.026	0.172	189.3	1.46	0.15
Age	0.009	0.051	-0.092	0.108	240.9	0.17	0.86
Colony size	-0.007	0.062	-0.135	0.116	14.5	-0.11	0.91
No. helpers x Predation	0.141	0.102	-0.057	0.338	533.2	1.39	0.17
No. helpers x Rainfall	0.111	0.092	-0.068	0.290	553.6	1.20	0.23
Random effect	**Variance**				**Df**	**logLik**	***P***
(all)	-				-	-491.9	-
Season (N=8)	**0.044**				1	-496.5	**0.002**
Colony ID (N=19)	0.003				1	-492.2	0.47
Mother ID (N=246)	0.019				1	-493.1	0.12
Residual	0.287				-	-	-

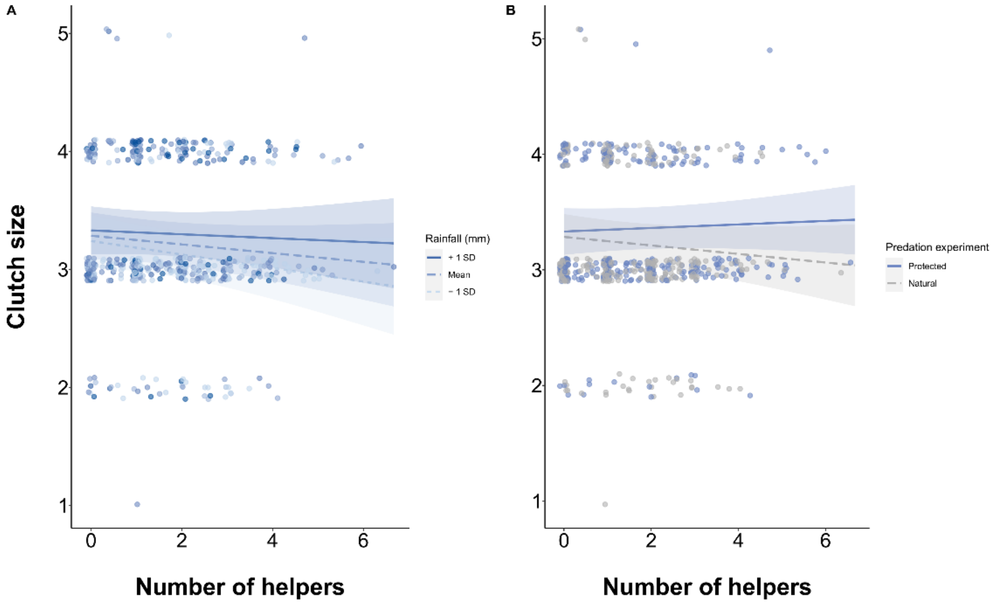


Figure S2. 4. Relationship between clutch size and number of helpers (A) depending on levels of total rainfall during the 30 days before the laying-date, (B) across predation experiment treatments. Dots represent raw values, solid and dashed lines represent the predicted values with 95% confidence intervals across different rainfall/predation conditions (see legends).

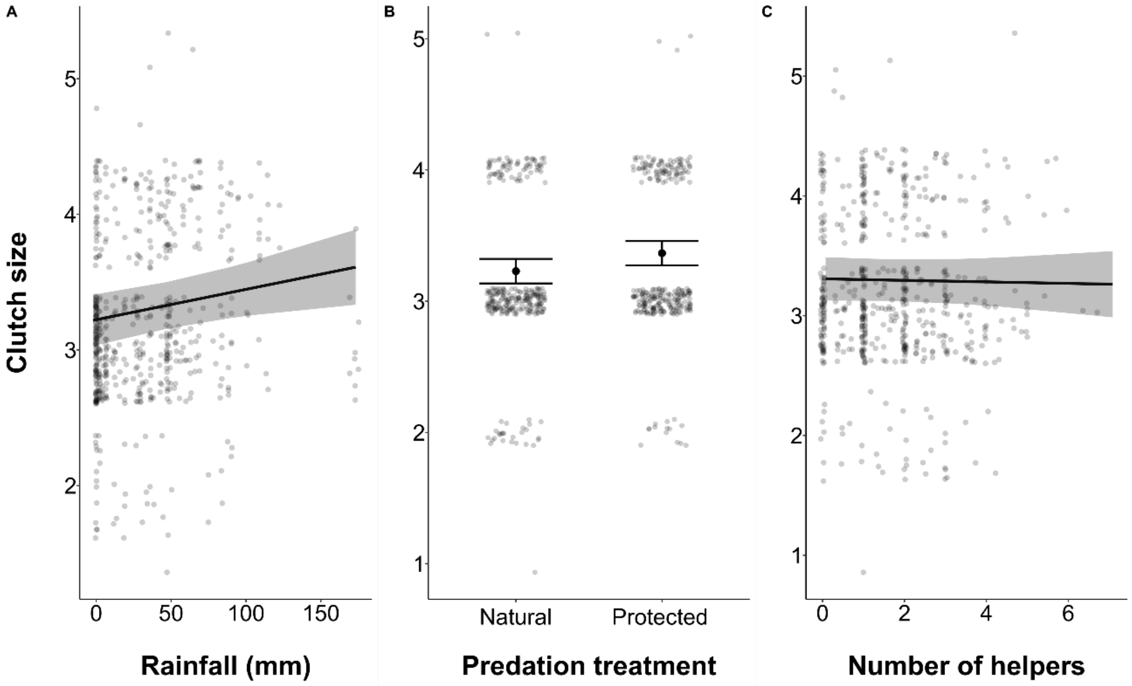


Figure S2. 5 Relationship between clutch size and (A) rainfall, (B) predation experiment treatments and (C) number of helpers. Dots represent raw values. In (A) and (C), lines show predicted values with 95% CI in grey reflecting variance in fixed effects. In (B), circles show the mean estimate of each category and bars represent the standard error.

Table S2. 7 Effect of climate, predation, number of helpers and other variables of the breeding environment on clutch size (N=569). Results from a CLMM fitted with the Laplace approximation, equidistant thresholds and standardized numerical inputs (conditional Hessian value = 27). Separated by a line are the fixed effects that were dropped to fit the final model. To extract estimates and P values for main effects, two-way interactions were dropped. The coefficient shown for "Predation experiment" is for protected colonies (1). Random effects variance and significance estimated by LRTs are also presented. Coefficients, std. errors and confidence intervals were exponentiated and are thus shown in the odds ratio scale.

Fixed effect	**Coef.**	**Std. error**	**2.5%**	**97.5%**	**z**	***P***
Rainfall	2.012	0.243	**1.250**	**3.239**	2.88	**0.004**
Predation experiment	1.709	0.227	**1.096**	**2.664**	2.37	**0.02**
Number of helpers	0.949	0.211	0.628	1.435	-0.25	0.80
Breeding attempt	2.309	0.235	**1.457**	**3.660**	3.56	**<0.001**
Mean egg mass	0.729	0.201	0.492	1.080	-1.58	0.12
Age	1.043	0.205	0.697	1.559	0.20	0.84
Tarsus length	1.349	0.201	0.910	2.000	1.49	0.14
Colony size	0.937	0.230	0.597	1.469	-0.28	0.78
Spacing	55.517	0.217	-	-	18.53	-
Threshold	0.001	0.520	-	-	-13.42	-
No. helpers x Predation	1.685	0.405	0.762	3.725	1.29	0.20
No. helpers x Rainfall	1.517	0.361	0.748	3.077	1.16	0.25

Random effect	**Variance**	**Df**	**logLik**	***P***
(all)	-	-	-470.5	-
Season (N=8)	**0.613**	1	-474.9	**0.003**
Colony ID (N=19)	0.010	1	-470.5	0.84
Mother ID (N=246)	0.276	1	-471.5	0.15

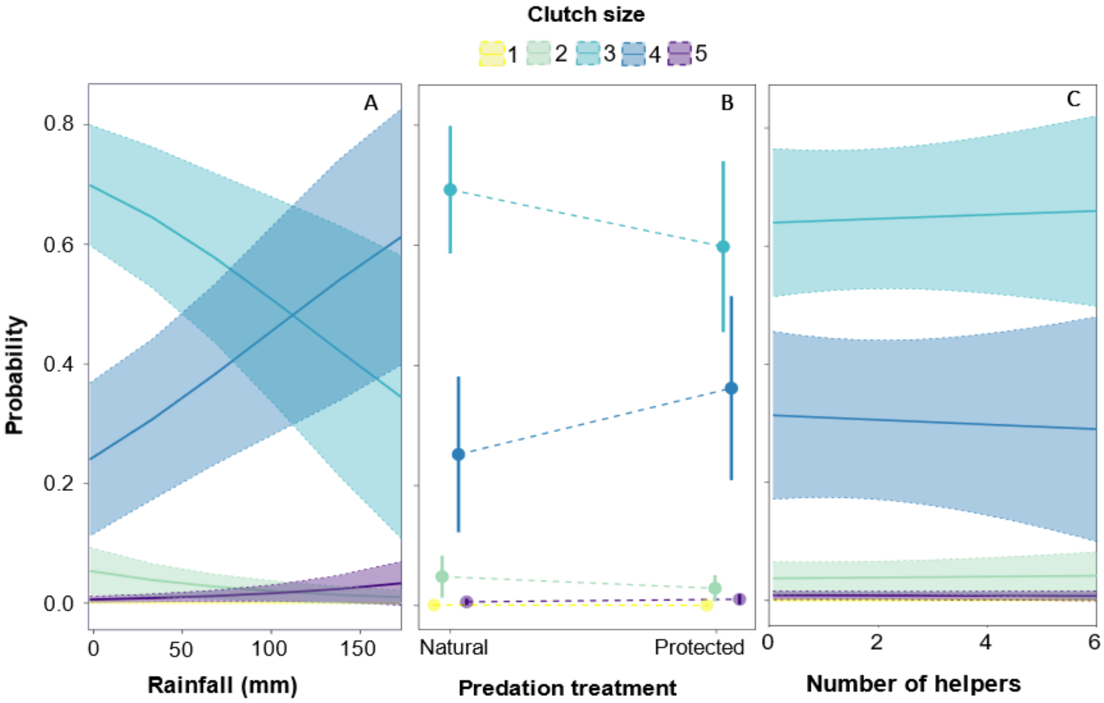


Figure S2. 6 Predicted probability of clutch size categories across (A) rainfall levels, (B) predation experiment treatments and (C) number of helpers. In (A) and (C), lines show CLMM predicted probabilities with 95% confidence bands. In (B), circles show CLMM predicted probabilities across treatments and vertical bars show 95% CI. Clutch size categories are represented by different colours. For a change of unit in rainfall (i.e.: 2 s.d. ~ 70 mm), the odds of laying larger clutches is 2.01 times higher (s.e.=0.243; 95% CI=[1.250,3.239]). The odds of laying more eggs in protected colonies were 1.7 times that of control colonies (i.e., 70% higher; s.e.=0.227, 95% CI = [1.096,2.664]).

Table S2. 8 Results of the bivariate model with egg mass and number of helpers as responses (N=1928). Posterior means and 95% credible intervals (HPD) are shown, together with effective samples sizes and pMCMC. The effect of mother ID and residuals was tested across both responses, but all other fixed and random effects were estimated for egg mas only. Reference level for predation experiment (Egg mass intercept) is 0 (natural).

Fixed effect	**Post. mean**	**Lower 95CI**	**Upper 95CI**	**Eff.samp**	**pMCMC**
Egg mass (Intercept)	2.532	2.487	2.585	2000	0.0005
Number of helpers (Intercept)	0.447	0.369	0.519	1635	0.0005
Predation experiment	0.007	-0.023	0.036	2000	0.647
Rainfall	0.018	-0.006	0.041	1802	0.139
Breeding attempt	0.017	-0.006	0.041	2000	0.172
Clutch size	-0.0004	-0.020	0.018	2000	0.961
Tarsus length	0.058	0.005	0.100	2000	0.014
Age	-0.020	-0.056	0.019	2000	0.289
Colony size	-0.016	-0.060	0.030	1832	0.45
Random effect					
Season	0.001	0.000	0.004	2000	-
Colony ID	0.002	0.0002	0.004	2000	-
Nest ID	0.003	0.001	0.004	2000	-
Mother ID (Egg mass)	0.030	0.024	0.036	1715	-
Mother ID (Egg mass:Number of helpers)	-0.008	-0.022	0.009	2000	-
Mother ID (Number of helpers)	0.339	0.274	0.411	2000	-
Residual (Egg mass)	0.016	0.015	0.017	2000	-
Residual (Egg mass:Number of helpers)	-0.003	-0.006	0.002	1858	-
Residuals (Number of helpers)	0.263	0.245	0.280	1823	-

Table S2. 9 Results of the bivariate model with clutch size and number of helpers as responses (N=569). Posterior means and 95% credible intervals (HPD) are shown, together with effective samples sizes and pMCMC. The effect of mother ID and residuals was tested across both responses, but all other fixed and random effects were estimated for clutch size only. Reference level for predation experiment (Clutch size intercept) is 0 (natural).

Fixed effect	**Post. mean**	**Lower 95CI**	**Upper 95CI**	**Eff.samp**	**pMCMC**
Clutch size (Intercept)	3.231	3.028	3.467	2131	0.0005
Number of helpers (Intercept)	0.506	0.431	0.579	2000	0.0005
Predation experiment	0.134	0.016	0.266	1864	0.043
Rainfall	0.157	0.042	0.282	1871	0.013
Breeding attempt	0.214	0.094	0.330	2000	0.002
Mean egg mass	-0.070	-0.182	0.041	2000	0.215
Tarsus length	0.063	-0.057	0.175	2000	0.284
Age	0.007	-0.110	0.119	2000	0.925
Colony size	-0.004	-0.138	0.154	2000	0.956
Random effect					
Season	0.061	0.001	0.165	1706	-
Colony ID	0.006	0.000	0.019	2000	-
Mother ID (Clutch size)	0.077	0.050	0.104	2000	-
Mother ID (Clutch size:Number of helpers)	0.005	-0.027	0.035	2000	-
Mother ID (Number of helpers)	0.171	0.108	0.233	2000	-
Residual (Clutch size)	0.271	0.238	0.309	2000	-
Residual (Clutch size:Number of helpers)	-0.006	-0.038	0.029	2000	-
Residuals (Number of helpers)	0.393	0.336	0.449	2000	-

F. Meta-analysis update

We used the code available at DOI:10.7717/peerj.4028/supp-4 and the data available at DOI:10.7717/peerj.4028/supp-5 to update the meta-analysis performed by Dixit, English, & Lukas (2017), replacing the two datapoints obtained from two previous studies in sociable weavers (dos Santos, 2016; Paquet, Covas, Chastel, Parenteau, & Doutrelant, 2013) with the effect size estimated from our study (which also includes the data from those studies). We estimated *r* (-0.0518) and Z (-0.0518) values and the variance (0.00052) using the same method referenced in Dixit et al. (2017; Jennions, Moller, & Petrie, 2001).

The overall effect size (study ID as random factor) is negative but not clearly different from zero (effect size=−0.1320; CI=[-0.2921;0.0281]; P=0.1061; Fig. S2.7).

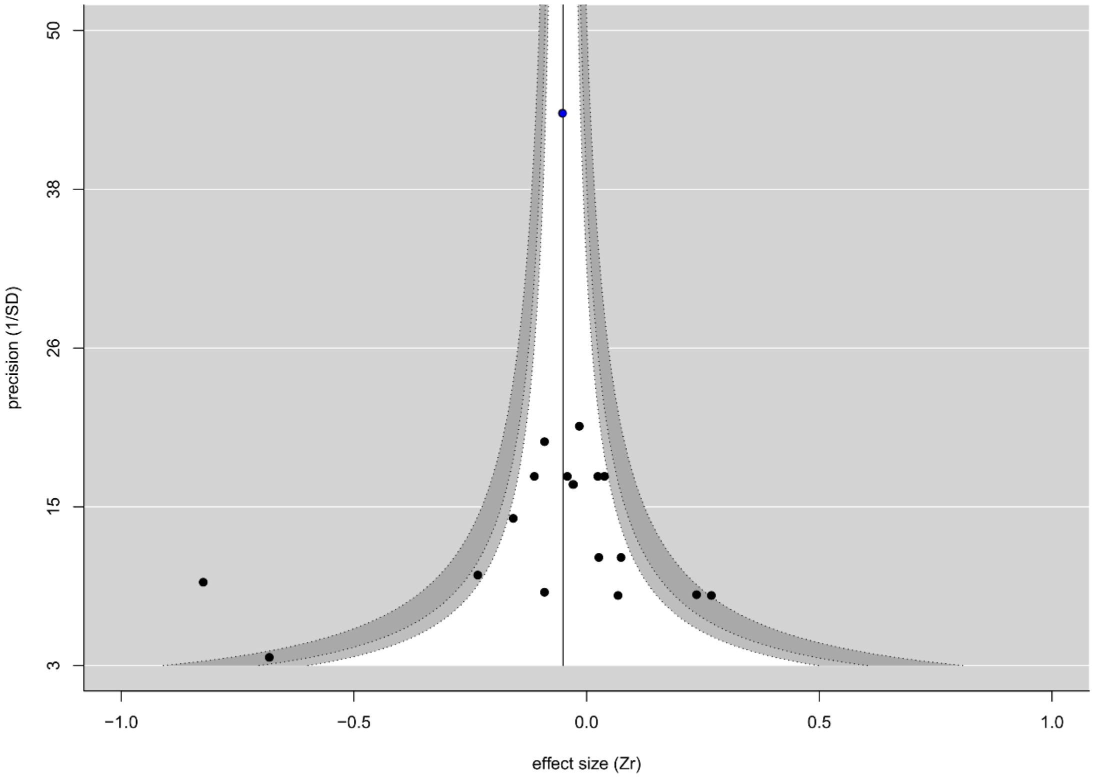


Figure S2. 7 Funnel plot of the meta-analysis performed by Dixit et al. (2017) updated with the effect size for sociable weavers estimated from our study (point in blue with highest precision value). The pooled mean estimate (solid line) is negative but not clearly different from zero.

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Chapter 3

Egg components and offspring survival vary with laying order and number of helpers in sociable weavers

Egg components and offspring survival vary with laying order and number of helpers in sociable weavers

Rita Fortuna[1,2,3,4], Matthieu Paquet[5,6], Clotilde Biard[7], Loïc Élard[7], André C. Ferreira[1,3,4], Sofia Jerónimo[1,3], Mathieu Leroux-Coyaux[7], Charline Parenteau[8], Liliana R. Silva[1,3], Franck Théron[1,3,4], Rita Covas[1,3,9] and Claire Doutrelant[4,9]

[1] CIBIO, Centro de Investigação em Biodiversidade e Recursos Genéticos, InBIO Laboratório Associado, Campus de Vairão, Universidade do Porto, 4485-661 Vairão, Portugal
[2] Departamento de Biologia, Faculdade de Ciências, Universidade do Porto, 4099-002 Porto, Portugal
[3] BIOPOLIS Program in Genomics, Biodiversity and Land Planning, CIBIO, Campus de Vairão, 4485-661 Vairão, Portugal
[4] CEFE, CNRS, Univ Montpellier, CNRS, EPHE, IRD, Montpellier, France
[5] Department of Ecology, Swedish University of Agricultural Sciences, Box 7044, SE-75007 Uppsala, Sweden
[6] Institute of Mathematics, University of Bordeaux, Talence, France
[7] Sorbonne Université, UPEC, Paris 7, CNRS, INRA, IRD, Institut d'Écologie et des Sciences de l'Environnement de Paris, iEES Paris, F-75005 Paris, France
[8] Centre d'Études Biologiques de Chizé, CNRS, Villiers-en-Bois, France
[9] Percy FitzPatrick Institute, DST-NRF Centre of Excellence, University of Cape Town, Cape Town, South Africa

Abstract

1. Prenatal allocation of resources to offspring can be influenced by mothers' breeding conditions and offspring value, consequently affecting offspring survival. In birds, egg components such as nutrients and hormones are an important pathway for maternal allocation strategies.
2. In cooperatively breeding systems, breeders can have a variable number of 'helpers' that provide offspring care. When breeding with helpers, females may vary resource allocation to eggs either by increasing their investment – 'differential allocation' hypothesis - or reducing it - 'load-lightening' hypothesis. To date, most studies focused on egg size, while helper effects on egg content were overlooked. Besides, although egg content and survival (i.e., offspring value) are known to vary with laying order, it is unknown how helpers' presence modulates laying order effects.
3. We investigated how maternal allocation varied with number of helpers and laying order in the cooperatively breeding sociable weaver (*Philetairus socius*). After finding that fledgling probability (i.e., offspring value) was negatively correlated with laying order, we estimated interactive effects of helpers and laying order on egg mass, yolk nutrients - yolk mass, proteins, lipids, carotenoids, vitamin A and vitamin E - and hormones - testosterone, androstenedione, and corticosterone.
4. Our results concurred with the 'differential allocation' predictions. Females with more helpers produced later-laid eggs with heavier yolks and more lipids, and laid eggs overall richer in lipids. In contrast, proteins, antioxidants, and hormones were not found to vary with helper number.
5. As a post-hoc analysis, we analysed how helper number modulated laying order effects on offspring survival. This revealed that eggs laid by females with more helpers were in general more likely to fledge, but females with more helpers did not specifically produce later-laid eggs with higher survival probability.
6. Overall, this study shows that some egg components (yolk mass, lipids) can vary according to females' breeding group size, which may improve offspring fitness. More studies are needed to understand if this association between egg nutrients and group size is caused by flexibly higher maternal allocation to offspring when breeding with more helpers and/or reflects differences in female quality/condition in larger groups.

Keywords: cooperative breeding, differential allocation, egg composition, helpers, hormones, laying order, load-lightening, nutrients

Introduction

Prenatal reproductive investment can vary with the breeding conditions experienced by females and may be adjusted to the expected fitness value of their current breeding event (Mousseau and Fox 1998). In oviparous species, the essential resources for embryonic development are accumulated in the eggs (Carey 1996). Mothers' condition or experience can lead to variation in the quantity and quality of these resources, which in turn can affect offspring growth, behaviour and survival ('maternal effects'; Bernardo 1996; Mousseau and Fox 1998; Krist 2011). In birds, variation in egg size has been shown to correlate with offspring quality (Williams 1994; Krist 2011) but eggs laid by the same female are often highly consistent in size across breeding attempts, indicating that females' ability to adjust egg size may be limited (Christians 2002; Fortuna et al. 2021). Alternatively, egg components such as nutrients and hormones appear to vary to a greater extent with females' prenatal environment (Groothuis et al. 2005; Eeva et al. 2011) and may thus be important alternative pathways for flexible maternal allocation (Saino et al. 2002; Williamson et al. 2006).

In cooperative breeders, females experience variable social conditions due to variation in the number of 'helpers' that assist with offspring care. Helpers can provide food and other types of care to the offspring (e.g. protection from predators), often resulting in a general positive correlation between number of helpers and offspring success and/or parental survival (Brouwer et al. 2005; Downing et al. 2020; Downing et al. 2021). Mothers could benefit from helpers' presence by adopting one of two opposite prenatal reproductive strategies: 1) load-lightening, whereby females save energy by investing less in eggs in the presence of helpers, who later compensate by providing additional food to the offspring, ultimately benefiting mothers' own survival and/or future reproduction (Russell et al. 2007; Taborsky et al. 2007; also called 'negative differential allocation' in Haaland et al. 2017), or 2) differential allocation, whereby females with helpers invest more in eggs, increasing current offspring survival (Cunningham and Russell 2000; Sheldon 2000; Russell and Lummaa 2009; Savage et al. 2015; Valencia et al. 2017; also called 'positive differential allocation' in Haaland et al. 2017). Prenatal 'load-lightening' or 'differential allocation' have been mostly investigated for egg size, with no overall consensus (meta-analysis from Dixit et al. 2017 updated in Fortuna et al. 2021). To date, only two studies investigated whether maternal allocation in egg components may vary with helper presence (Russell et al. 2007; Paquet et al. 2013).

Egg components are crucial for offspring development, with the major source of nutrients and energy being yolk lipids and proteins (Carey 1996). Moreover, yolk carotenoids and vitamins prime and shape the development of the embryo's antioxidant and immune systems (reviewed in Biard et al. 2009), and enhance antioxidant responses and immunity in adulthood (Olson and Owens 1998; Surai et al. 2001). Nutrient-rich eggs result in better-quality offspring (Saino et al. 2003; McGraw et al. 2005; Biard et al. 2007), but nutrients are limited for females in natural environments, leading to a trade-off between the resources allocated to current offspring and the ones retained for females' own survival and future reproduction (Erikstad et al. 1998; Blount et al. 2004). One study in superb fairy-wrens *Malurus cyaneus* analysed 17 clutches and reported evidence for maternal load-lightening in yolk mass, lipids and proteins in the presence of helpers (Russell et al. 2007). On the other hand, in sociable weavers *Philetairus socius*, no support was found for helper effects on egg carotenoid levels (of 84 clutches; Paquet et al. 2013).

In addition to nutrients, egg hormones may as well be influenced by mothers' social environment. Androgens, like testosterone and androstenedione (A4), enhance offspring competitive abilities, through faster development (Schwabl 1993; Eising et al. 2001) and stronger begging behaviour (e.g. Eising and Groothuis 2003), but may also affect offspring immune responses and survival (see reviews Groothuis et al. 2005; von Engelhardt and Groothuis 2011). In non-cooperatively breeding species, there is extensive work on how social factors influence female androgen levels, as well as corticosterone, and the concentration of these hormones in their eggs (Gil et al. 2007; Dentressangle et al. 2008; Safran et al. 2010; van Dijk et al. 2013; Bentz et al. 2016). In cooperative breeders, the only study that explored how helpers' presence may influence egg hormonal concentrations (Paquet et al. 2013) found that females without helpers laid eggs with more androgens, possibly to produce more competitive offspring (see also Cariello et al. 2006 for an example in join-nest species). Further studies are thus needed to understand hormonal maternal allocation in cooperative breeders (Russell and Lummaa 2009; Bebbington and Groothuis 2021).

Finally, an important but overlooked issue is whether helpers' presence affects how mothers distribute resources within clutches. Eggs' fitness value often varies with laying order and latter-laid eggs commonly have lower survival chances (Nager et al. 2000; Acevedo et al. 2020). In addition, variability in egg size and contents across the laying sequence is well demonstrated (Slagsvold et al. 1984; Schwabl 1993; Kozlowski and Ricklefs 2010) and costly components such as nutrients (Ojanen 1983; Williams 2005) often decrease with laying order (Royle et al. 1999; Saino et al. 2002; Kozlowski and Ricklefs 2010). This reduction may be a consequence of nutrient-depletion in female reserves and/or a strategy to allocate less resources to offspring that are less likely to survive (Slagsvold et al. 1984; Williams et al. 1993; Crean and Marshall 2009; Vedder et al. 2017). Since helpers may increase offspring survival (Covas and Du Plessis 2005; Downing et al. 2020; D'Amelio et al. 2021), the adaptive value of laying later-laid eggs poorer in nutrients could be modulated by helpers' presence (Fig.1), and it is therefore important to study how laying order and helpers' presence interact to shape egg composition and offspring survival.

Here, we tested whether maternal allocation, in terms of egg mass, yolk mass, yolk nutrients and hormones varied with females' breeding group size and laying order in the cooperatively breeding sociable weaver. First, we used data collected over seven breeding seasons to test how fledging probability varied with laying order, which allowed us to make predictions on how helper number could modulate laying-order effects. In sociable weavers, hatching is asynchronous, creating a size hierarchy among chicks, and later-laid eggs were found to have lower yolk mass and lower carotenoids and vitamin E concentrations (van Dijk et al. 2013). We therefore expected, and confirmed, that offspring from later-laid eggs have lower survival chances. We then examined how egg mass and content varied with laying order and group size. For egg mass analyses, we had data comprising eight breeding seasons. For egg content, we collected 59 clutches in two breeding seasons and measured nine egg components, representing three groups of compounds: yolk mass, lipids and proteins (macro-nutrients group), carotenoids, vitamin A and vitamin E (micro-nutrients group) and testosterone, A4 and corticosterone (hormones group). For nutrient allocation, we had opposite predictions according to the 'load-lightening' or the 'differential allocation' hypotheses (Fig 3.1).

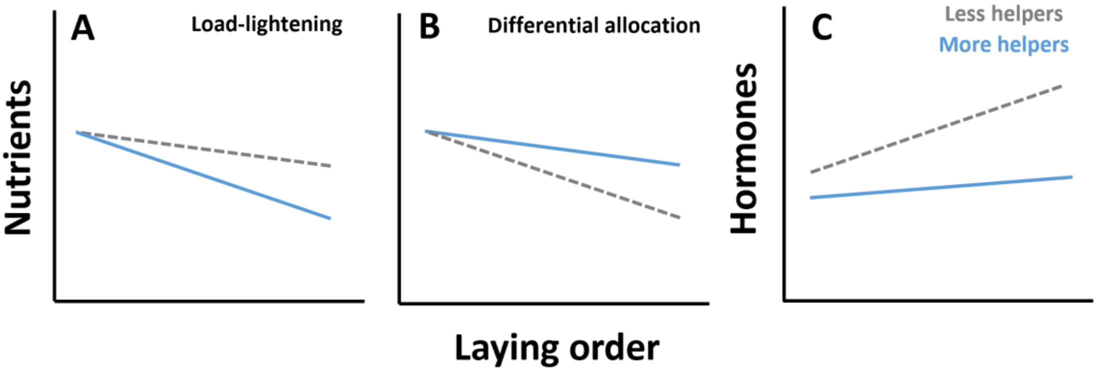

Figure 3. 1 Predictions for the effect of helper number (less helpers than average represented by grey dashed line, more helpers than average by blue solid line) on how nutrients (A and B) and hormones (C) vary with laying order. In A), the prediction is for 'load-lightening', whereby females with more helpers reduce nutrient allocation to eggs less likely to survive (i.e., latter-laid eggs). In B), the prediction is for 'differential allocation', whereby females with more helpers (i.e., higher chances of raising offspring successfully) allocate more resources towards later-laid eggs than females with less helpers. In both A and B, differences in nutrient allocation between females with more and less helpers than average should be more pronounced for latter-laid eggs (see Paquet et al. 2013). In C), the prediction is for hormone variation, similar under both load-lightening and differential allocation. Females with more helpers are expected to lay eggs with lower hormone levels (see Paquet et al. 2013). However, later-laid eggs are expected to have higher hormonal concentration than first eggs, to mitigate hatching asynchrony effects on offspring survival which should be more pronounced without helpers.

Methods

Study system and data collection

Sociable weavers are a cooperatively breeding passerine endemic to southern Africa. These birds build communal nests, or 'colonies', with several chambers where they roost and breed (Maclean 1973a). Breeding pairs can be assisted by one or several helpers with nestling feeding (Maclean 1973b), nest building and sanitation (Ferreira 2015). Helper number seems to be predictable by females at laying, since most helpers are previous offspring of the breeders (Covas et al. 2006; Fortuna et al. 2022), roosting group sizes before breeding were found to correlate with breeding group sizes (Paquet et al. 2016), and social bonds are stronger within breeding groups (Ferreira et al. 2020).

Sociable weavers breed for several months (Mares et al. 2017) and can have up to 11 breeding attempts per season (Maclean 1973c; Fortuna et al. 2021). Clutch size typically ranges between 2-4 eggs and females lay one egg per day (Covas and Du Plessis 2005; Fortuna et al. 2021). The incubation period lasts around 15 days and nestlings normally hatch asynchronously (Maclean 1973c; Covas and Du Plessis 2005), which creates an age-related hierarchy within broods. The subsequent nestling period lasts for 21-25 days (Maclean 1973c).

This work was conducted at Benfontein Nature Reserve, Northern Cape Province, South Africa (28°520 S, 24°500 E), under permission from landowners, provincial authorities and the UCT Ethics committee.

We monitored the breeding activity of 16 sociable weaver colonies during 8 breeding seasons (from 2010/2011 to 2017/2018) to obtain data on egg mass, egg laying order and fledging success (see Appendix A1 for details on data collection; D'Amelio et al. 2021; Fortuna et al. 2021). We obtained a final sample of 779 eggs (in 326 nests from 14 colonies) with known mass and position in the laying sequence, and for which mother identity, mother tarsus size and group size were identified (see below). Our sample of eggs that hatched and had known fate for the corresponding chick (fledged or not; see below), known egg mass and position in the laying sequence and known mother identity was of 419 (for 258 nests from 16 colonies; see below).

Egg content

In 2014 and in 2017, we collected 59 clutches for egg contents' assessment. In 2014, 129 eggs (43 full clutches) were collected between September and October and in 2017, 45 eggs (16 full clutches) were collected between October and December. Eggs were collected after weighing, two days after the first egg was found (most clutches have 3 eggs; 4th eggs were collected if found on the following day; Fortuna et al. 2021), and were stored whole by freezing at -20°C. From the 174 eggs collected, 170 were sent to the laboratories for analyses. Four eggs got damaged during transportation and therefore could not be analysed.

We measured 9 egg components, representing 3 groups of compounds: yolk mass, lipids and proteins (macro-nutrients group), carotenoids, vitamin A and vitamin E (micro-nutrients group) and testosterone, A4 and corticosterone (hormones group). Each batch of samples was analysed during the season in which they were collected, except corticosterone concentration of the 2014 samples which was measured at the same time as the 2017 samples. Hormonal assays for all eggs were conducted in the same laboratory (see Fanson et al. 2017).

Detailed methods of yolk contents' analyses are available in Appendix A2-6. Yolks were separated from the albumen while defrosting and weighed at the nearest 0.001g (Appendix A2). Yolk lipids' concentration was obtained by extraction with chloroform

(Appendix A3) and proteins' concentration by CHN (determination of carbon, nitrogen, and hydrogen content; Appendix A4). Fresh yolk carotenoid concentrations were determined by colorimetry in 2014 and, in 2017, carotenoid concentration as well as composition were determined by reverse phase high performance liquid chromatography (HPLC; Appendix A5; see Table S3.1 for description of carotenoid composition). Vitamin A (retinol) and vitamin E (sum of δ-, γ- and α-tocopherol) concentrations were determined by HPLC (Appendix A5; see Table S3.1). Yolk concentrations of testosterone, A4 and corticosterone were determined by radioimmunoassay (RIA) and enzyme linked immunosorbent assay (ELISA; Appendix A6). Sample sizes for each egg component can be found in Table S3.2. Correlations between egg components at the egg level and at the clutch level are given in Fig S3.1.

Group size and breeding females' identification

Individuals visiting the nests were identified using direct observations from 2010 to 2013/14, and by video recording nests for a minimum of 2h from 2014/15 on (see Silva et al. 2018).

Group size was calculated as the mean number of birds seen feeding the nestlings over all observations of each breeding attempt. Only birds that fed at least 3 times (in the same day or different days) were considered part of the group. Unringed birds were included in group size estimates (counted as 1 bird).

To identify nests' breeding females, we used a combination of criteria: incubation video recordings (for collected clutches, recorded before collection) and video recordings or direct observations of feeding visits in current and/or posterior breeding attempts in the same nest and colony. We then used information from genetic analysis from blood samples (Paquet et al. 2015) and field data (Silva et al. 2018) to attribute parentage to the birds seen (see Appendix A7 for details; Fortuna et al. 2021).

For the collected clutches, we identified the breeding female of 51 out of 59 clutches. The group size of these females was estimated from their subsequent breeding attempts and could be obtained for 46 out of 51 clutches. We expected that group size would not severely change in their next breeding attempt, as no juveniles were produced (since all eggs were collected) and most replacement clutches were laid within 2 months (see details in Appendix A8).

Statistical analyses

Data were analysed in R version 4.0.4 (R Development Core Team 2021).

Fledging probability

Before running egg mass and content models, we tested how fledging probability varied with laying order, and whether first and last eggs were more and less likely to fledge, respectively. This allowed us to make predictions on how helper number could modulate laying order effects (Fig 3.1). Details on this model can be found in Appendix A9. Results showed that, as expected, the probability of fledging was negatively correlated with the egg position in the laying sequence and can be found in Appendix B1 (Table S3.3; Fig S3.2).

Egg mass

To study whether group size interacted with laying order to explain egg mass variation, we fitted a GLMM with egg mass as response variable and laying order, group size, and their interaction as variables of interest. As covariates, we included clutch size and mother tarsus size, which was previously found to explain egg mass variation (Fortuna et al. 2021). The single effect of group size and covariates on egg mass will not be discussed here as a more powerful analysis has been performed in an extension of the dataset used here (i.e. not including laying order, N=1928; here N=779 see Fortuna et al. 2021). The random terms' structure included nest, breeding female, colony identity and season. Spearman rank correlation coefficients were never above 0.26.

This GLMM and all models described hereafter were run in a Bayesian framework using the MCMCglmm package (Hadfield 2010) because it better accommodated random terms with low estimated variance (see Tables S3.4-S3.15 in Appendix B). We used vague priors for all parameters (for details on model procedures, priors and diagnostics see Appendix A9). For each estimate, we present mean and 95% credible intervals of the posterior samples (or highest posterior densities intervals; 95CrI). We report effects as statistically credible when 95CrI do not overlap zero and discuss effects in which 95CrI slightly overlap zero.

Yolk mass and contents

To test if group size and laying order had interactive effects on egg content, we fitted separate GLMMs using each component as response variable: yolk mass, carotenoids concentration, lipids percentage, proteins percentage, concentrations of vitamin A, vitamin E, testosterone, A4 and corticosterone (see Appendix A9 for models' details). Two random terms representing colony and mother identity were included, as well as fixed covariates: clutch size, season (due to only having 2 levels), egg mass (for yolk mass model, see Appendix A9), and predator-protection status as a binary factor, since some eggs in 2014 were collected in colonies where a predator-exclusion experiment was running (0 for control colonies, 1 for protected colonies; see Fortuna et al. 2021 for information on the experiment). We did not expect interactive effects of group size and laying order to differ between predation treatments and therefore did not consider a three-way interaction. For the yolk components measured over a lower eggs' sample (vitamin A, vitamin E and A4 concentrations; 39 eggs from 14 clutches; see Table S3.2), fixed covariates were not added to the model to avoid overparameterization and results should thus be interpreted with caution (none of these clutches was collected in predator-protected colonies).

Helper effects on offspring survival: post-hoc test

Based on the egg content results showing that females with more helpers laid eggs richer in nutrients (i.e.: differential allocation; see below), we predicted that eggs laid by females with more helpers could have a higher survival probability than eggs laid by females with fewer helpers, and that this difference could be more pronounced for later-laid eggs (see below). Therefore, as a post-hoc analysis, we ran two models testing if group size and laying order had interactive effects on hatching and on fledging probability as binary response variables (0 if the chick did not hatch/fledge, 1 if it did). Models' structure was the same as in the fledging probability model (see above), only adding group size in interaction with laying order. Models were fitted in MCMCglmm using the 'categorical' family (logit link), with priors for fixed and random terms as described above but fixing the prior residuals' variance to 1 (Hadfield 2014). Latent variables were truncated to prevent under/overflow (Hadfield 2010). Number of iterations, burn-in and thinning intervals were adjusted to ensure minimum effective sample sizes of 1000. Plots show raw data and the predicted effects estimated using the 'predict' function in MCMCglmm

(Hadfield 2010). In the results, we present the means [and 95CrIs] from the posterior distributions of interest.

Results

Egg mass

We found no evidence for an interactive effect between group size and laying order on egg mass (-0.01 [-0.05;0.04]; p=0.602; N=779; Fig S3.3; Table S3.4), but later-laid eggs were heavier than first-laid eggs (0.19 [0.14;0.23]; p=0.001; Fig S3.3; Table S3.4).

Egg components

Macro-nutrients: yolk mass, lipids and proteins

Yolk mass varied differently with laying order depending on group size (interaction = 0.12 [0.02;0.24]; p=0.034; N=122; Figs. 3.2 and S3.4; Table S3.5). For females without helpers, fourth eggs' yolk was predicted to be on average 0.1g lighter than first eggs' yolk (4th egg= 0.59 [0.54;0.64]g; 1st egg=0.70 [0.65;0.73]g), representing a decrease of approximately 16%, while for females with a group size above average (approximately 4 helpers) this represented only a 1% decrease on average (4th egg= 0.68 [0.62;0.74]g; 1st egg=0.69 [0.64;0.74]g; Fig 3.2). There was no evidence for a group size effect on yolk mass (0.11 [-0.07;0.30]; p=0.276; Figs. 3.2 and S3.4; Table S3.5). Yolk mass, in terms of proportion of yolk in relation to egg mass, varied negatively with laying order (-0.16 [-0.27;-0.04]; p=0.004; Figs. 3.2 and S3.4; Table S3.5), while absolute changes in yolk mass followed a similar trend but not as clear statistically (Table S3.5).

For yolk lipids, a greater increase in relation to group size was observed for later-laid eggs than for earlier-laid eggs (interaction = 0.21 [0.01;0.39]; p=0.03; N=83; Fig 3.2; Table S3.6). Results showed that females without helpers were predicted to lay fourth eggs with around 17% less yolk lipids than first eggs (4th egg= 36 [24;48]%; 1st egg=53 [44;63]%), while females with group sizes above average (approximately 4 helpers) produced fourth eggs with on average 7% more yolk lipids than the first egg laid (4th egg= 63 [50;75]%; 1st egg=56 [46;65]%; Fig 3.2). In general, females with more helpers produced eggs richer in yolk lipids (0.34 [0.08;0.55]; p=0.012; Figs. 3.2 and S3.4; Table S3.6).

For yolk proteins, our results showed no evidence for effects of the interaction (0.04 [-0.13;0.21]; p=0.652; N=117; Figs. 3.2 and S3.4; Table S3.7) or for group size (0.07 [-

0.16;0.32]; p=0.58; Figs. 3.2 and S3.4; Table S3.7) and laying order (0.07 [-0.11;0.24]; p=0.462; Figs. 3.2 and S3.4; Table S3.7) as single terms.

Micro-nutrients: carotenoids, vitamin A and vitamin E

We found no evidence that group size interacted with laying order to explain variation in carotenoids (-0.05 [-0.14;0.06]; p=0.35; N=39; Figs. 3.2 and S3.4; Table S3.8), vitamin A (-0.09 [-0.37;0.22]; N=39; p=0.546; Figs. 3.2 and S3.4; Table S3.9) and vitamin E yolk concentrations (-0.15 [-0.40;0.12]; p=0.288; N=39; Figs. 3.2 and S3.4; Table S3.10).

We also found no evidence for a group size effect on carotenoid concentration (0.03 [-0.22;0.28]; p=0.812; Figs. 3.2 and S3.4; Table S3.8) and vitamin E in the yolk (-0.07 [-0.49;0.43]; p=0.768; Figs. 3.2 and S3.4; Table S3.10). However, there was a trend for a group size effect on vitamin A concentrations, suggesting that females with fewer helpers may have laid eggs richer in vitamin A (-0.36 [-0.73;0.01]; p=0.056; Figs. 3.2 and S3.4; Table S3.9).

Laying order correlated negatively with carotenoid concentration (-0.35 [-0.46;-0.25]; p=0.001 Figs. 3.2 and S3.4; Table S3.8) and vitamin E in the yolk (-0.34 [-0.59;-0.06]; p=0.016; Figs. 3.2 and S3.4; Table S3.10), but it did not clearly correlate with vitamin A (0.17 [-0.12;0.50]; p=0.256; Figs. 3.2 and S3.4; Table S3.9).

Hormones: testosterone, A4 and corticosterone

Our results showed no support for an effect of the interaction between group size and laying order on hormonal concentration, namely on testosterone (-0.03 [-0.16;0.08]; p=0.624; N=122; Figs. 3.2 and S3.4; Table S3.11), A4 (0.02 [-0.20;0.27]; p=0.864; N=39; Figs. 3.2 and S3.4; Table S3.12) and corticosterone (-0.02 [-0.13;0.11]; p=0.758; N=122; Figs. 3.2 and S3.4; Table S3.13). Contrary to expected, there were also no detectable effects of group size on testosterone (0.21 [-0.09;0.50]; p=0.146; Figs. 3.2 and S3.4; Table S3.11), A4 (-0.34 [-0.77;0.12]; p=0.138; Figs. 3.2 and S3.4; Table S3.12) or corticosterone (-0.08 [-0.34;0.22]; p=0.584; Figs. 3.2 and S3.4; Table S3.13). We found no evidence for laying order effects on testosterone (-0.07 [-0.20;0.05]; p=0.262; Figs. 3.2 and S3.4; Table S3.11). However, later-laid eggs had higher A4 (0.27 [0.04;0.50]; p=0.022; Figs. 3.2 and S3.4; Table S3.12) and corticosterone concentrations (0.16 [0.01;0.27]; p=0.014; Figs. 3.2 and S3.4; Table S3.13). The latter laying order effect on

A4 was not detected in absolute terms (when accounting for yolk mass differences; Table S3.13).

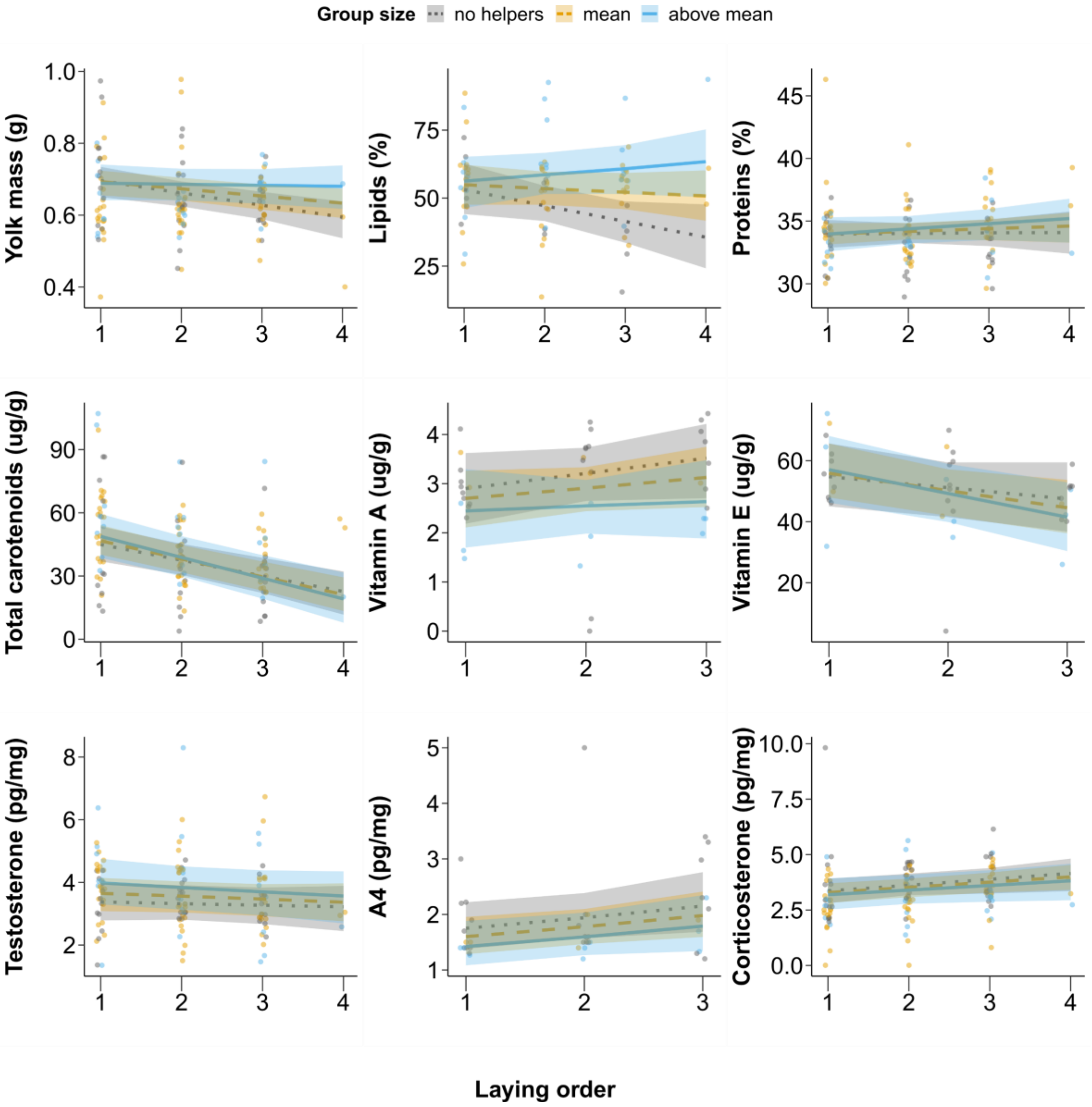

Figure 3. 2 Relationship between egg components and laying order for females with different group sizes. Lines represent the posterior predicted means and 95% credible intervals for three group size values: group size=2 (no helpers; grey dotted line), mean group size (between 2.6 and 4 depending on dataset; orange dashed line) and the average between mean and maximum group size (between 3.3 and 5.6; blue solid line). Points represent raw data and point colours represent observations for groups without helpers, groups between group size=2 and mean group size or group sizes above the mean (rounded to the nearest integer).

Hatching and fledging probability

Our post-hoc analyses showed no evidence for an interaction between laying order and group size on hatching (OR=0.92 [0.66;1.25]; p=0.62; N=331; Fig S3.5; Table S3.14) or fledging probabilities (OR=1.20 [0.56;2.52]; p=0.649; N=226; Fig 3.3; Table S3.15).

At hatching, there were no detectable group size effects (OR=1.02 [0.75;1.43]; p=0.88; Fig S3.5; Table S3.14), but later-laid eggs were less likely to hatch than earlier-laid ones (OR=0.48 [0.34;0.66]; p=0.0005; Fig S3.5; Table S3.14). Chicks' survival until fledging correlated positively with group size (OR=4.77 [1.51;16.26]; p=0.002; Fig 3.3; Table S3.15). Females without helpers were predicted to lay eggs with a fledging probability of 44% [25;63], while eggs from females with an average group size were estimated to survive until fledging 57% [39;75] of the times, and 73% [0.54;0.90] of the times when laid by females with a group size above average (Fig 3.3). In accordance with the first fledging probability model (larger dataset than here, see Appendix B1), later-laid eggs tended to have lower fledging probabilities (OR=0.53 [0.28;1.00]; p=0.047; Fig 3.3; Table S3.15).

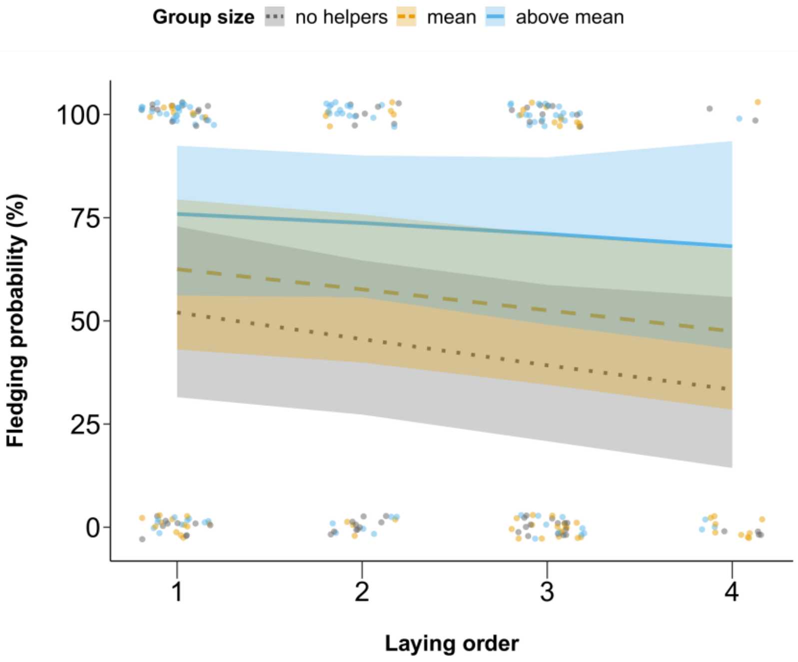

Figure 3. 3 Relationship between fledging probability and laying order for females of different group sizes. Lines represent the posterior predicted means and 95% credible intervals for three group size values: group size=2 (no helpers; grey dotted line), mean group size (3.3; orange dashed line) and the average between mean and maximum group size (5.2; blue solid line). Points represent raw data and point colours represent observations for groups without helpers, groups between group size=2 and mean group size or group sizes above the mean (all values rounded to the nearest integer).

Discussion

Here we tested whether maternal allocation, in terms of egg mass, yolk nutrients - yolk mass, lipids, proteins, carotenoids and vitamins – and hormones – testosterone, A4 and corticosterone - varied with group size and laying order in sociable weavers. Our aim was to understand if females could increase the offspring's and/or their own fitness by adopting different prenatal reproductive strategies as their number of helpers varies. We first showed that laying order was negatively associated with fledging success, implying that eggs' reproductive value varies within clutches. We then obtained two results concurring with the 'differential allocation' predictions, as later-laid eggs of females with more helpers had heavier yolks and more lipids when compared to females with fewer helpers and, overall, females with more helpers laid eggs richer in lipids. In contrast, remaining yolk nutrients and hormones were independent of females' group size. As expected, latter-laid eggs had lower antioxidant levels but were more concentrated in corticosterone and A4. Lastly, we ran a post-hoc test examining helper number and laying order effects on offspring hatching and fledging success. We predicted that eggs laid by females with more helpers could show higher survival partly due to the detected differences in yolk mass and lipids, and that this difference could be more pronounced for later-laid eggs. This analysis showed that females with more helpers laid eggs with a considerably higher fledging, but not hatching, probability, and that this was independent of laying order. This suggests that 'differential allocation' of some egg nutrients when females breed with more helpers could be improving offspring fitness overall but may not translate into a higher survival specific to later-laid eggs.

Helper effects on egg allocation

In this study population, nests with more helpers receive more food (Covas et al. 2008) and suffer less brood reduction (D'Amelio et al. 2021). Furthermore, here we found that an egg's position in the laying sequence negatively correlated with its fledging probability. Altogether, this implies that offspring rearing conditions and fitness vary with helper number and with laying order, and therefore that we could expect flexible maternal allocation strategies in relation to both group size and laying order.

When testing the effects of this interaction on variables representing maternal allocation to eggs, we found that two egg components, specifically yolk mass and lipid concentration, varied with egg laying order in different ways depending on the female's group size. Later-laid eggs of females with more helpers had heavier yolks and more lipids when compared to females with fewer helpers. These results concur with the predictions for a ‘differential allocation’ reproductive strategy in relation to helpers’ presence and laying order (Fig 3.1). The adaptive value of intra-clutch variation in egg investment has long been proposed, with some species suggested to follow a ‘brood-reduction strategy’ and others a ‘brood-survival strategy’ (Slagsvold et al. 1984). Based on our results, sociable weaver females might swing between these two strategies depending on their number of helpers (Russell and Lummaa 2009), via flexible allocation of yolk and lipids to their eggs. Offspring that develop from eggs with heavier yolks and with a higher lipid content should have access to more energy and nutrients, which are vital for embryonic tissue growth, and chicks should hatch with greater nutrient reserves that can be used for several days post-hatching (Noble and Cocchi 1990; Williams 1994; Carey 1996). Furthermore, some lipid constituents, namely fatty acids, have been reported to correlate with offspring hatching and fledging success (Mentesana et al. 2021). Therefore, in cooperative breeders, this ‘differential allocation’ strategy could be adaptive if a higher maternal investment in egg nutrients summed with the extra food provided by the helpers increases the survival probability of offspring from later-laid eggs, thus increasing the number of offspring reaching independence (D’Amelio et al. 2021). In contrast, when breeding with less helpers, females could benefit from a biased allocation of nutrients towards eggs with higher reproductive value (i.e., earlier-laid eggs), thus saving energy for their own survival or future reproduction if brood reduction is likely to occur through later-hatched chicks’ mortality (Williams et al. 1993; Royle et al. 1999; Crean and Marshall 2009; Vedder et al. 2017). It should be noted though that the differences observed here for yolk mass do not appear to result from variation in yolk lipids or proteins, as these variables were not clearly correlated with yolk mass, and may instead represent an increase in water content or other minor dry components, as minerals and carbohydrates (Nys and Guyot 2011).

Importantly, we found that females with more helpers laid eggs richer in lipids also independently of laying order, which implies that mothers may be allocating more nutrients to all eggs when breeding with more helpers. The idea that sociable weaver females invest more when breeding in better conditions concurs with previous results in this species showing that females laid larger clutches in better climatic conditions and in colonies protected from nest predation (however, no change in egg mass or number was found when expecting to breed with more helpers: Fortuna et al. 2021). ‘Differential allocation’ was first proposed as a beneficial strategy when females mate with attractive partners (Burley 1986; Cunningham and Russell 2000; Sheldon 2000), but was later suggested to explain cases in which females provided more care when breeding with more helpers (Russell and Lummaa 2009; Savage et al. 2015). However, evidence that ‘differential allocation’ has evolved as a prenatal strategy in cooperative breeders is scarce and limited to egg size, having been reported only once in Iberian magpies *Cyanopica cooki* (Valencia et al. 2017; see also Woxvold and Magrath 2005; Lejeune et al. 2016 for reports of positive helper effects on clutch size). Moreover, results supporting the opposite strategy, ‘load-lightening’, via egg size and nutritional content are, respectively, ambiguous (Dixit et al. 2017; Fortuna et al. 2021) and rare (Russell et al. 2007). More studies are needed before concluding on the generality of ‘differential allocation’ through egg components across cooperative breeders. However, theoretical work by Savage et al. (2015) predicts that females should take advantage of better rearing conditions by increasing prenatal investment, if this investment leads to lasting benefits for offspring and allows them to receive more post-birth care. In sociable weavers, there is some evidence that prenatal investment may affect offspring begging behaviour (Paquet et al. 2015) and thus the rate at which nestlings are fed (Fortuna et al. 2022), suggesting that it may prime offspring to receive more postnatal care. Yet, ‘differential allocation’ is not expected when early investment is unimportant or interchangeable with postnatal investment (Savage et al. 2015), and it would therefore be relevant to better assess the effects of prenatal maternal allocation on offspring quality and survival in this species (see also below).

Instead of an active resource allocation strategy, the differences in egg nutrients observed here could be explained by female quality/condition, if better females can lay eggs, or later-laid eggs, with more nutrients (Ardia et al. 2006) and also have more helpers. The link between female quality/condition and helper number in sociable weavers is not clear. For example, not all females with more helpers seem to survive better, but only the younger ones (Paquet et al. 2015). Even though we tried to account for female quality and condition in our models by using proxies such as clutch size and egg mass (Fortuna et al. 2021), we cannot conclude whether the ‘differential allocation’ pattern found here is a passive consequence of females being in better state or an active adjustment of egg content to helpers’ presence (Cockburn et al. 2008; Russell and Lummaa 2009). An experimental manipulation of helper number in females’ groups could help to disentangle female quality/condition from helper effects (but see Cockburn 1998). Otherwise, this could be achieved with longitudinal studies that follow females as their group size varies (Fortuna et al. 2021). The latter could also provide valuable insights on how prenatal allocation strategies may be moderated by other conditions of the females' environment (Hatchwell 1999; Langmore et al. 2016).

We found no evidence that egg mass and remaining yolk nutrients – proteins, carotenoids, vitamin A, vitamin E - varied in relation to the group size alone or in interaction with laying order (see also Fortuna et al. 2021). Egg mass was positively correlated with laying order, as previously found is this population (van Dijk et al. 2013) and other species (Howe 1976; Zach 1982; Slagsvold et al. 1984; Rutkowska and Cichon 2005). Our results also show that, even though heavier eggs had heavier yolks, later-laid eggs were heavier but had proportionally lighter yolks and lower carotenoids and vitamin E concentrations. Moreover, we did not detect relationships between egg mass and the amount of yolk lipids, proteins or hormones in the eggs, which suggests that studying egg mass may provide only partial insights on egg quality (see also Hadfield et al. 2013).

Surprisingly, we found no effect of females' group size on eggs' hormonal content. This contradicts previous findings in this species, where the first egg of the clutches was found to be more concentrated in testosterone and A4 when females had no helpers (Paquet et al. 2013). Instead, our results indicate that females without helpers may not benefit from allocating more hormones to offspring, or specifically to chicks from later-laid eggs, that could enhance their competitive abilities. However, the contrasting results obtained here and before (Paquet et al. 2013) also suggest that other unaccounted environmental or social factors might affect eggs' hormones. Moreover, we also observed a positive effect of laying order on A4 concentration, which was not found in a previous study in this same population (van Dijk et al. 2013). Discrepancies in hormonal effects are frequently detected and maternal hormone transfers have been suggested to depend on social and environmental contexts (Groothuis et al. 2019; Bebbington and Groothuis 2021), which could explain the inconsistencies found in our system. Discrepancies between studies can also be attributed to inter-laboratory variation (Fanson et al. 2017). Nevertheless, the positive relationships between A4 and corticosterone concentrations and laying order observed here concur with literature reporting higher hormonal levels in later-laid eggs (Royle 2001; Kozlowski and Ricklefs 2010; Müller and Groothuis 2013). This could function as a 'cheap' mitigation strategy (Groothuis and Schwabl 2008) to enhance the competitive abilities of chicks from later-laid eggs, which hatch later and have less access to carotenoids and vitamin E during embryo development and at hatching (Royle 2001; this study).

‘Differential allocation’ and nestling survival

We then assessed if producing eggs with heavier yolks and richer in lipids when breeding with more helpers (i.e., ‘differential allocation’) could be associated with increased offspring survival. For this, we used our long-term dataset to test the interactive effect of group size and laying order on hatching and fledging success. Our analyses showed no effect of this interaction on nestling survival, which suggests that chicks hatching from later-laid eggs that are raised with more helpers do not appear to have an advantage in terms of fledging success.

There are several possible explanations for the lack of detectable interactive effects between laying order and group size on hatching and fledging success. First, variation in yolk mass and lipids in relation to laying order without subsequent differences in hatching/fledging success may suggest that egg nutrients play a role in survival at other stages, for instance during the first days after hatching or even post-fledging, or contribute instead to offspring morphological traits as body mass or size (Moore et al. 2019). Second, any positive effects of increased allocation towards later-laid eggs may be undetectable at fledging if, for instance, they are masked by postnatal care. A third possibility is that environmental factors are mediating maternal allocation strategies in relation to group size (Langmore et al. 2016). Under this scenario, the way mothers distribute resources within clutches depends not only on their number of helpers, but also on other environmental factors that differ between years (Langmore et al. 2016), resulting in undetectable general effects on offspring survival over the seven breeding seasons included in this analysis. Therefore, at this stage, we cannot fully dismiss that ‘differential allocation’ when breeding with more helpers has positive effects on offspring from later-laid eggs in this species, and further work focusing on offspring phenotypic traits and survival at different stages, as well as on seasonal variation in egg composition, would be necessary to assess these effects.

Nevertheless, our findings that group size is positively correlated both with eggs’ lipid content and with chicks’ fledging success suggests that ‘differential allocation’ may be contributing to higher offspring survival, independently of laying order. Therefore, females may be benefiting from the improved breeding conditions provided by helpers and increasing their reproductive output (Sheldon 2000; Russell and Lummaa 2009). Here, females with a helper number above average laid eggs with almost 30% more fledging chances than females without helpers. In accordance, previous analyses showed positive helper effects on fledging mass and success under adverse conditions (Covas et al. 2008), and more recent long-term analyses in this population showed that pairs with more helpers have a higher probability of fully-fledging their broods (D’Amelio et al. 2021). It would now be important to specifically address whether these benefits result from ‘additive’ effects of increased maternal allocation and helper care or solely from the postnatal contributions of helpers (Covas et al. 2008; Paquet et al. 2016).

Conclusion

We have shown that maternal allocation strategies in relation to helpers’ number may be detected for some egg components that are important for offspring development and survival. When breeding with more helpers, sociable weaver females laid eggs richer in lipids and their offspring had higher fledging success, which suggests that larger breeding groups represent improved breeding conditions for females. Moreover, females with more helpers produced later-laid eggs with heavier yolks and more lipids. This implies that helpers’ presence modulates resource distribution within clutches and opens new lines of research. First, future research focusing on the mechanisms leading to such ‘differential allocation’ to clarify whether this is a passive consequence of better female quality/condition or a strategy taking advantage of the presence of more helpers. Second, studies across cooperatively breeding species and spanning a larger number of years are necessary to assess general patterns in maternal allocation of egg components. Finally, it is important to explore if an increase in allocation to yolk mass and lipids when breeding with more helpers has any fitness advantage for the offspring.

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Appendix

Contents

A. Methods

1. Captures and breeding monitoring

Individuals were captured once or twice a year at the colonies using mist nests since 1999 (Covas 2002). Birds were ringed with a uniquely coded aluminium ring and a unique colour-ring combination, allowing individual visual identification, and blood samples were collected for genetic sexing and determination of parentage relationships (see below). Nest contents were inspected every 3 days from mid-September. First eggs were marked with a pencil and nests were inspected every day to mark every subsequently laid egg. Two days after clutch initiation, we weighed the eggs to the nearest 0.001 g with a digital Pesola scale. Nests were checked the following day to weigh a possible 4th egg. We did not intentionally look for 5th eggs because five eggs' clutches are rare (4% of the clutches; Fortuna et al. 2021), but all nests were routinely inspected every 3 days and 5th eggs were weighed whenever found.

Nests were monitored until hatching and, when possible, we marked chicks according to their egg of origin (if two chicks hatched in the same day, egg of origin was unknown). When the first nestling was 9 days old, nestlings were weighed and ringed with a unique numbered aluminium ring and a blood sample was taken. When the first chick was 17 days of age (day 17 of the nest; the last day nests can be visited without increasing the chances of inducing fledging), nestlings' wing, tarsus, and weigh were measured. The fate and fate date of each egg and chick were registered and if the chicks survived until day 17 they were considered as having fledged.

2. Yolk mass

The yolks were separated from the albumen while defrosting, weighed at the nearest 0.001g and kept at -80°C until analyses. Albumen mass was estimated as the difference between egg mass (before freezing, weighed in the field at collection) and wet yolk mass, since wet egg mass could not be reliably estimated due to frequent albumen leaks through eggshell cracks caused by freezing and transportation.

3. Yolk lipids

For lipids estimation, yolks were then dried at 60ºC for about 24-48 hours. We introduced 180 mg of dried yolk into tubes resistant to chloroform (type Sarstedt 15 mL). Then, 3 mL of deionized (DI) water, 6 mL of methanol and 3 mL of chloroform were added to the samples (Bligh and Dyer 1959). Afterwards, the samples were vortexed (30 seconds at 2400 rpm), 3 mL of DI water and 3 mL of chloroform were added and then vortexed again and centrifuged (10 minutes at 4500 rpm). Samples were biphasic, the water and methanol were positioned on the top, the chloroform and lipids on the bottom and one thin layer of proteins divided the two phases. The chloroform and lipids were extracted with a Pasteur pipette into a glass tube previously weighed and were reserved. Then, 3 mL of chloroform were added again to the sample, which was vortexed and centrifuged. We did a second extraction of the chloroform and added it to the previous extraction. The tubes with the extractions were put in heating plates (60ºC) and when all chloroform evaporated, tubes containing the lipids were weighed.

4. Yolk proteins

Yolks were dried at 60ºC for about 24-48 hours. The nitrogen concentration of the samples was determined with an elemental analyser Thermo-Finnigan, Flash EA 1112 Series. Protein content was calculated from the nitrogen values using a conversion factor of 6.25. About 2 mg of dried yolk was weighed in a microbalance (Sartorius MC5) in a tin capsule, sealed and placed in an auto sampler, from which it was dropped into a combustion chamber. As the sample entered, the combustion chamber oxygen was injected into the carrier gas (He), which flowed through the combustion tube. The temperature raised up to 1800°C, which insured complete combustion of the sample. Inter and intra variations were never above 5.10% and 2.34%, respectively.

5. Yolk carotenoids and vitamins

Carotenoids' concentration of the samples collected in 2014 was determined by colorimetry following procedures in Paquet et al. (2013). For carotenoid extraction, 60 mg of egg yolk was diluted with acetone (1µg of acetone for 0.1mg of yolk). Samples were vortexed, kept overnight at 20°C and then centrifugated (10 minutes at 13000g, at 4ºC). We extracted 125 µL of supernatant for each sample and determined the optic density (OD) at 450nm in a microplate photometer (Victor3 1420 Multilabel Plate Reader, Perkin-Elmer). Commercial solution of lutein (xanthophylls Sigma X-6250) was used for serial dilution and to obtain a standard curve to determine the relationship between the OD value and carotenoid concentration in yolk eggs, expressed as µg/g yolk. We used the mean of the two closest values obtained for the three replicates as the carotenoid concentration in fresh yolk eggs.

Carotenoid composition and concentration, as well as vitamin A and vitamin E concentrations, of the samples collected in 2017 were determined by reverse phase high performance liquid chromatography (HPLC), using a Jasco equipment (PU-2089 Quaternary Gradient HPLC pump, AS-2057 auto sampler, MD-2018 Diode-array Detector and FP-2020 fluorescence detector; monitored through ChromNAV software; Jasco France), following procedures adapted from Biard et al. (2005; 2009).

Lipid-soluble antioxidants were extracted from eggs using half the yolk (mean yolk mass used ± s. e. = 0.35 ± 0.06 g). Yolk samples were homogenised with 0.7 mL NaCl 5% and 1 mL ethanol with an IKA T10 Basic Ultra Turrax tool (Fisher Scientific). Antioxidants were extracted adding 2 mL hexane and further homogenisation, centrifugation and collection of the hexane phase (extraction repeated twice for all samples and three times for nine samples when yolk was still visible in the tubes after the second extraction). Hexane extracts were pooled and evaporated in a block heater at 37°C under nitrogen flow. The residue was dissolved in 0.4 mL dichloromethane and 0.4mL methanol. Sample extracts were filtered through Whatman NYL 0.45 µm syringe filter (Sigma Aldrich). Carotenoid composition was determined by injecting 40µL of extract onto a VENUSIL AQ C18 5µm C18 reverse-phase column, 25 cm×4.6 mm (Agela). An isocratic HPLC at a flow rate of 2 mL min^{-1} with a mobile phase of acetonitrile-methanol (60:40) for 8 minutes was used with a change within 1 minutes to acetonitrile-methanol-dichloromethane (60:20:20) and running for the next 11 minutes, followed with re-equilibration with the first mobile phase for the next 5 minutes, using detection by absorbance at 445 nm. Peaks were identified and concentrations calculated by comparison with the retention times and dilution curves of a range of carotenoid standards (Sigma Aldrich). Total carotenoid concentration was also determined by injecting 40µL of extract onto a PROMOSIL 50µm NH2 reverse-phase column (25 cmx4.6 mm, Agela) with a mobile phase of methanol and HPLC grade distilled water (97 : 3), at a flow rate of 1.5 mL.min^{-1}. Lutein was used for calibration (Sigma Aldrich). The correlation between total carotenoid concentration and the sum of the concentration of all peaks identified was of 0.95 (95%CI=[0.91, 0.97]; P-value<0.001; N=41) and thus the sum of all identified peaks was used as measure of total carotenoid concentration.

Concentrations of vitamins A (retinol) and vitamin E (δ-, γ- and α-tocopherol) were determined by injection of 40µL of extracts onto a UNISOL 3µm C18 reverse-phase column, 15 cm × 4.6 mm (Agela) with a mobile phase of methanol, at a flow rate of 1.5 mL min^{-1} using fluorescence detection by excitation and emission wavelength of 295 and 330 nm, respectively, for vitamin E and UV detection at 325 nm for vitamin A. Peaks were identified and concentrations calculated by comparison with the retention times and dilution curves of standards of retinol, δ-, γ- and α-tocopherol (Sigma Aldrich). All concentrations are expressed as μg/g yolk. Concentrations rather than quantities of antioxidants were used as dependent variables in subsequent analyses because concentration is the main factor determining physiological action of antioxidants at the level of tissues (Biard et al. 2009).

Table S3. 1 Composition of egg yolk in carotenoid and vitamin E compounds, as mean concentration (± SD), mean proportion (% ± SD) and proportion of samples (out of N=45) in which they were detected.

		Mean concentration ± SD	**Mean % of total ± SD**	**Proportion of samples (%)**
Individual carotenoids (μg/g yolk)	Lutein	11.55 ± 5.61	54.9 ± 6.1	100
	Zeaxanthin	2.29 ± 0.99	11.4 ± 2.3	100
	Cis-lutein	1.81 ± 1.11	8.35 ± 2.61	96
	Cis-Zeaxanthin	1.61 ± 0.66	8.19 ± 2.44	98
	β-Carotene	0.51 ± 0.4	2.47 ± 1.71	89
	Cryptoxanthin	1.34 ± 0.61	7.62 ± 5.04	96
	Unidentified carotenoids	1.44 ± 0.63	7.07 ± 1.62	100
Vitamin E compounds (μg/g yolk)	α-tocopherol	33.3 ± 10.49	64.65 ± 11.26	100
	δ-tocopherol	17.56 ± 7.79	33.52 ± 11.19	100
	γ-tocopherol	1.01 ± 0.91	1.83 ± 1.43	98

6. Yolk testosterone, androstenedione (A4) and corticosterone

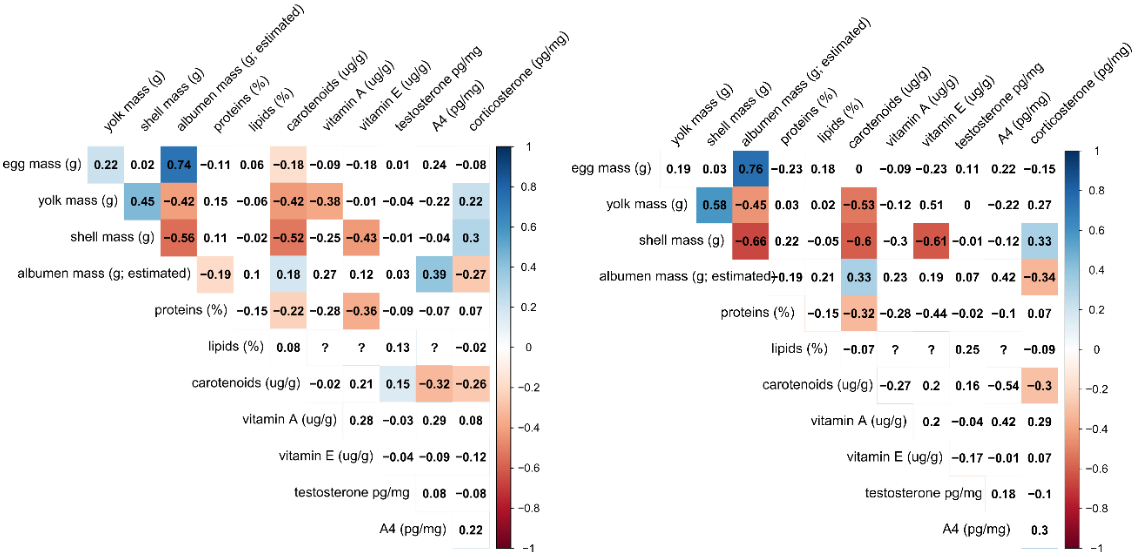
The yolks were separated from the albumen while defrosting, weighed at the nearest 0.001g and kept at -20°C until analyses. Testosterone, androstenedione, and corticosterone of eggs collected in the two breeding seasons were assayed with RIA and ELISA methods (radioimmunoassay and enzyme linked immunosorbent assay, respectively).

In detail, 100 mg of each sample were homogenised in 1 mL of distilled water and three to four glass beads, using a vortex. Steroids were extracted by adding 3 mL of diethyl-ether to 300 μL of the mixture, vortexing and centrifuging (5 minutes at 2000 rpm, at 4°C). The diethyl-ether phase containing steroids was decanted and poured off after snap freezing the tube in an alcohol bath at minus 40°C. This was done twice for each yolk, and the solvent was then evaporated at 37°C. The dried extracts were re-dissolved in 800 µL of phosphate 0.01 M pH 7.4 buffer each hormone was assayed in duplicate. Then, for testosterone and corticosterone (in 2014 and 2017 samples) measured with RIA method, 100 µL of extract were incubated overnight at 4°C with 4000 cpm of the appropriate H^3-steroid (Perkin Elmer, US) and polyclonal rabbit antiserum. Anti-testosterone was provided by Dr. Picaper (médecin nucléaire, CHU La Source, Orléans, France), anti-corticosterone antiserum was supplied by Merck. The bound fraction was then separated from free fraction by addition of dextran-coated charcoal and activity was counted on a tri-carb 2810 TR scintillation counter (Perkin Elmer, US). Androstenedione, in 2017 samples, was assayed with an ELISA kit supplied by IBL International. Some tests were performed to validate the hormone assays on egg yolk samples. Yolk extracts were serially diluted in the assay buffer and their displacement curves were parallel to the standard curve, for the three steroids. Inter- and intra-assay variations were respectively 12.43% and 5.80% for testosterone, 12.53% and 10.84% for corticosterone, and 7.27% and 8.70% for androstenedione. Testosterone, corticosterone and androstenedione lowest detectable concentrations in yolk extracts were respectively 50.5 pg/mL, 56.3 pg/mL and 40 pg/mL. The assay specificity was evaluated by spiking extracts with the three steroids: recovery was 97.8% for testosterone, 113.3% for corticosterone and 100.67% for androstenedione.

Cross-reactions of testosterone antiserum were as follows : androsterone (63%), progesterone (1.45%), 17-β-estradiol (0.176%), corticosterone (0.41%), estrone (0.03%), aldosterone (<0.01%), cortisone (<0.01%). Cross-reactions of corticosterone antiserum were as follows : 11-dehydrocosticosterone (0.67%), deoxycorticosterone (1.5%), 18–hydroxy-deoxycorticosterone (<0.01%), cortisone (<0.01%), cortisone (<0.01%), progesterone (0.004%), aldosterone (0.2%). Cross-reactions of androstenedione antiserum were as follows: DHEA (1.8%), testosterone (0.20%), estrone (<0.1%), estradiol (<0.1%), progesterone (<0.1%), 17-OH-progesterone (<0.1%), 5α-dihydrotestosterone (<0.1%), cortisol (<0,01%) and DHEA-S (<0.01%).

Table S3. 2 Mean, range (min/max), standard deviation (sd) and sample sizes for each egg component measured in the eggs collected in 2014 and/or in 2017. The last row represents the sample size of each model, after excluding eggs with missing information for the response variable or covariates included in the models. Shell mass and albumen mass were measured but not included in the statistical analysis. The sample size of eggs analysed for each component varied due to the capacity to assess some components only during one season (i.e.: lipids only in 2014 and vitamins and A4 only in 2017) or because the laboratory process failed for specific samples.

	Yolk mass (g)	**Egg mass (g)**	**Shell mass (g)**	**Albumen mass (g)**	**Lipids (% yolk)**	**Proteins (% yolk)**	**Carotenoids (ug/g wet yolk)**	**Vitamin A (ug/g wet yolk)**	**Vitamin E (ug/g wet yolk)**	**Testosterone (pg/mg wet yolk)**	**A4 (pg/mg wet yolk)**	**Corticosterone (pg/mg wet yolk)**
Mean	0.64	2.51	0.19	1.69	53.35	33.94	43.59	2.94	51.86	3.64	1.84	3.2
Min	0.37	2.04	0.12	0.97	9	28.95	9.65	0	4.14	1.35	1.2	0.01
Max	0.98	3.16	0.71	2.36	93.68	46.31	118.21	4.43	75.46	8.3	5	9.82
SD	0.1	0.2	0.09	0.23	15.13	2.33	22.03	0.98	13.26	1.12	0.73	1.3
N eggs	167	170	169	163	122	162	170	45	45	170	45	170
N clutches	59	58	59	58	43	57	59	16	16	59	16	59
N colonies	8	8	8	8	7	8	8	4	4	8	4	8
N seasons	2	2	2	2	1	2	2	1	1	2	1	2
N eggs model	122	-	-	-	83	117	119	39	39	122	39	122



	yolk mass (g)	shell mass (g)	albumen mass (g; estimated)	proteins (%)	lipids (%)	carotenoids (ug/g)	vitamin A (ug/g)	vitamin E (ug/g)	testosterone pg/mg	A4 (pg/mg)	corticosterone (pg/mg)
egg mass (g)	0.22	0.02	0.74	−0.11	0.06	−0.18	−0.09	−0.18	0.01	0.24	−0.08
yolk mass (g)		0.45	−0.42	0.15	−0.06	−0.42	−0.38	−0.01	−0.04	−0.22	0.22
shell mass (g)			−0.56	0.11	−0.02	−0.52	−0.25	−0.43	−0.01	−0.04	0.3
albumen mass (g; estimated)				−0.19	0.1	0.18	0.27	0.12	0.03	0.39	−0.27
proteins (%)					−0.15	−0.22	−0.28	−0.36	−0.09	−0.07	0.07
lipids (%)						0.08	?	?	0.13	?	−0.02
carotenoids (ug/g)							−0.02	0.21	0.15	−0.32	−0.26
vitamin A (ug/g)								0.28	−0.03	0.29	0.08
vitamin E (ug/g)									−0.04	−0.09	−0.12
testosterone pg/mg										0.08	−0.08
A4 (pg/mg)											0.22

	yolk mass (g)	shell mass (g)	albumen mass (g; estimated)	proteins (%)	lipids (%)	carotenoids (ug/g)	vitamin A (ug/g)	vitamin E (ug/g)	testosterone pg/mg	A4 (pg/mg)	corticosterone (pg/mg)
egg mass (g)	0.19	0.03	0.76	−0.23	0.18	0	−0.09	−0.23	0.11	0.22	−0.15
yolk mass (g)		0.58	−0.45	0.03	0.02	−0.53	−0.12	0.51	0	−0.22	0.27
shell mass (g)			−0.66	0.22	−0.05	−0.6	−0.3	−0.61	−0.01	−0.12	0.33
albumen mass (g; estimated)				−0.19	0.21	0.33	0.23	0.19	0.07	0.42	−0.34
proteins (%)					−0.15	−0.32	−0.28	−0.44	−0.02	−0.1	0.07
lipids (%)						−0.07	?	?	0.25	?	−0.09
carotenoids (ug/g)							−0.27	0.2	0.16	−0.54	−0.3
vitamin A (ug/g)								0.2	−0.04	0.42	0.29
vitamin E (ug/g)									−0.17	−0.01	0.07
testosterone pg/mg										0.18	−0.1
A4 (pg/mg)											0.3

Figure S3. 1 Pearson correlation coefficients between egg components at the egg-level on the left (N=174) and at the clutch-level (mean per clutch) on the right (N=59), estimated using the Hmisc package (Harrell 2020). Blue squares represent positive correlations and red squares represent negative correlations with p<0.05. White squares represent non-significant correlations. Correlations that could not be estimated are represented by a question mark (when two components were not assessed in the same egg/clutch). The strongest correlation among components used as response variables (see Statistical analyses) was between yolk mass and yolk carotenoids concentration (cor=-0.42; p<0.001). No clear correlations were detected between hormones. Hormones showed significant, but weak (and mainly negative) correlations with carotenoids concentration. There are no qualitative differences between the correlations at the egg and at the clutch levels.

7. Identification of breeding females

The sex of the birds seen visiting the nests was genetically determined from blood samples (Paquet, Doutrelant, et al. 2015). Breeders of each nest were genetically identified using full-likelihood parentage inference (Paquet, Doutrelant, et al. 2015; Fortuna et al. 2021). When no genetic data was available, parentage was determined based on the birds' biology (e.g., age or pedigree; for details on parentage attribution see Supplementary materials in Fortuna et al., 2021).

8. Group size of females from collected clutches

Group size of females whose clutches had been collected was expected to be similar in their next breeding attempt, as no juveniles had been produced and most replacement clutches were laid within 2 months' time. In any case, we used a long-term group identification database to test if the group size of breeding females in two consecutive breeding attempts was correlated. For this, we estimated the correlation between groups of the same breeding females in consecutive breeding attempts separated in time by a maximum of 3 months (only 4 out of the 51 following breeding attempts of females with collected clutches had a difference above 3 months). We only compared nests with their next breeding attempt when no chicks had fledged in the first attempt, and therefore no juveniles became part of the group. Mean group size was calculated as previously described and the Spearman's rank correlation coefficient was assessed using the package 'RVAideMemoire' which estimates confidence intervals by bootstrapping (we used default number of replicates; Hervé 2021). We found a mean correlation of 0.57 (95CI=[0.33;0.75]; p<0.001; N=50) between the size of two consecutive groups of the same breeding female. We thus considered that previous knowledge of the system on the composition of the groups (i.e., mostly offspring of the breeding pair) and our estimation of a moderate to high correlation between group sizes of consecutive breeding attempts validates the use of this variable as a proxy of the breeding females group size at the time they laid the collected clutches.

9. Statistical analyses

Fledging probability model

To test how fledging probability varied with laying order, and whether first and last eggs were more and less likely to fledge, respectively, we fitted three binomial general linear mixed models (GLMM) with 'fledged' as a binary response variable (0 if the chick did not fledge, 1 if it did) and, in each separate model, either laying order (as a continuous variable), or first egg or last egg (both as categorical variables scored as 0/1) as variables of interest. We controlled for clutch size and egg mass as fixed effects and fitted nest identity nested in breeding female identity as random terms, as well as colony identity and season, to account for non-independence. This GLMM was fitted using the lme4 package (Bates et al. 2015). Numerical independent variables were centred and scaled by subtracting their mean and dividing by one standard deviation (Schielzeth 2010). Spearman rank correlation coefficients between variables were never above 0.31. We report effects as statistically significant when 95% confidence intervals (95CI) do not overlap zero. Plots show raw data and the predicted effects were estimated using the ggeffects package (Lüdecke 2018). To decide which variable to use (laying order, first egg or last egg) to test how maternal allocation varies with egg position in the laying sequence, we compared the three fledging probability models using Akaike Information Criteria (AIC) scores and used the variable included in the model with lowest AIC.

Egg mass, yolk mass and contents models

Since ‘last egg’ and ‘laying order’ were equally supported in the fledging probability analysis (see Table S3.3), for each dependent variable we fitted one model with laying order as a continuous variable and a second model replacing laying order by the ‘last egg’ binary variable (1 if it was the last egg, 0 if not). Results from both models are available below but only laying order models are described in the main text, after confirming these had higher R^2 and lower DIC (deviance information criterion) in most cases (see Tables S3.4-S3.13).

For all models, numerical independent variables were scaled and centred as previously described and numerical response variables were scaled by dividing by one standard deviation. Models of egg mass and contents were fitted assuming a normal error distribution, with default priors for fixed effects and vague priors for random terms and the residuals, with the degree-of-belief parameter (nu) set to 0.002 and variance (V) set to 1. We assessed residuals’ normal distribution and deviation from posterior predicted values based on 1000 model simulations using the DHARMa package (Hartig 2021). Three chains were run, and model convergence was assessed visually through trace plots and by calculating Gelman–Rubin statistic (all values <1.1; Gelman & Rubin, 1992).

For each chain of the egg mass model, 200,000 iterations were run, with samples taken every 195 iterations and the first 5,000 removed as burn-in, resulting in 1000 samples and ensuring low autocorrelation among thinned samples (<0.1). Effective sample size was ≥1000 for all parameters.

For egg content variables, when data distribution seemed closer to a normal distribution when on the log scale (only the case for A4), that response variable was fitted as well using log scale and the normality of the residuals of the two models was visually compared prior to looking at the results. The model with a residuals’ distribution closer to normal was used for inference.

Since yolk and egg mass vary with laying order in this species (van Dijk et al. 2013; this study, see below) and yolks with similar weight could be differently rich in nutrients or hormones, each model was also fitted including yolk mass and egg mass as covariates (only yolk mass for vitamins and A4 models). For the response variables that represent concentrations (all but yolk mass), this allowed to test how the absolute level of a component varied with laying order and group size. For the yolk mass model, including egg mass allowed to test how the proportion of yolk mass relative to egg mass correlated with the variables of interest, and excluding it showed effects on the absolute yolk mass of the eggs. Plots show results on the relative amount of each egg component. Results on absolute terms are described in the Results when the effects of the variables of interest differed from the model on relative terms, and all results can be found below (see Results).

Regarding correlations between variables included in the models, absolute values of Spearman rank correlation coefficients between predation treatment and season were high in some datasets (up to 0.59). Similarly, wet yolk mass and season were correlated (up to 0.56) possibly due to differences in defrosting stage, as more time was needed to weigh the samples in 2014 (larger sample size). In the lipids' dataset, clutch size and predation treatment showed a strong correlation (-0.54). However, these covariates were kept in the models since these were not variables of interest and a correlated variable may still explain some additional variation. All remaining correlation coefficients were below 0.42.

Egg content models were run following the same steps and using the same priors as described before, but number of iterations, burn-in (always ≥ 5,000) and thinning intervals were set to higher values in some models to ensure an effective sample size ≥1000 for all parameters.

For all models, we present scaled coefficients of numerical variables, together with marginal and conditional R^2 (variance explained only by fixed effects and by both fixed and random effects, respectively), calculated using code adapted from Nakagawa and Schielzeth (2013), and pMCMC (p). Plots show raw data and the predicted effects estimated using the ggeffects package (Lüdecke 2018).

B. Results

1. Fledging probability

The probability of fledging was negatively correlated with the egg position in the laying sequence (Fig S3.2). Nestlings from later-laid eggs had lower chances of fledging than the ones from earlier-laid eggs (N=419; Odds ratio OR=0.56; 95CI=[0.39;0.81]; p=0.002; Table S3.3), independently of egg mass, and a similar result was observed when looking specifically at the last eggs in a clutch (OR=0.29; 95CI=[0.14;0.62]; p=0.001; Fig S3.2; Table S3.3), which had on average half the chances of fledging than the remaining ones (30% 95CI=[11;60] chances of fledging for last eggs, 60% 95CI=[31;83] for remaining eggs). The most supported model for fledging probability was the one including the 'last egg' variable, but its AIC score was not clearly different from the score of the model including ‘laying order’ as a continuous variable (ΔAIC = 1.4; Table S3.3). In contrast, being the first egg in the laying sequence did not show a clear effect on the likelihood of fledging (OR=1.57; 95CI=[0.81;3.05]; p=0.181; Fig S3.2; Table S3.3) and this model was the least supported one when comparing AIC scores (ΔAIC = 10.3 more than model with ‘last egg’ variable; Table S3.3).

Table S3. 3 Standardised estimates of the models testing the effect of egg position in the laying sequence on fledging probability (N=419). Results from binomial GLMMs including ‘laying order’, ‘ first egg’ (Y/N) or ‘last egg (Y/N) as variables of interest. Statistically supported effects are presented in bold. Reference level (intercept) for “first egg” and ‘last egg’ is 0 (no). Random effects variance, AIC and R^2 (Nakagawa and Schielzeth 2013) are also presented for each model.

	Model with laying order			**Model with first egg**			**Model with last egg**		
Fixed effect	**Log-Odds**	**95CI**	**p**	**Log-Odds**	**95CI**	**p**	**Log-Odds**	**95CI**	**p**
Fledged (Intercept)	-0.04	-1.11 1.04	0.947	-0.19	-1.22 0.83	0.710	0.40	-0.78 1.57	0.51
Laying order	**-0.58**	**-0.95 -0.21**	**0.002**	-	-	-	-	-	-
First egg (Y)	-	-	-	0.45	-0.21 1.12	0.181	-	-	-
Last egg (Y)	-	-	-	-	-	-	**-1.22**	**-1.96 -0.48**	**0.001**
Clutch size	-0.24	-0.71 0.23	0.322	-0.35	-0.81 0.11	0.137	**-0.58**	**-1.08 -0.08**	**0.02**
Egg mass	0.01	-0.40 0.42	0.950	-0.05	-0.46 0.35	0.797	-0.06	-0.47 0.36	0.79
Random Effect									
Mother ID:Nest ID (N=258)	1.93			1.78			1.98		
Mother ID (N=176)	2.06			2.09			2.19		
Colony ID (N=16)	0.57			0.54			0.69		
Season (N=8)	1.37			1.12			1.59		
Residuals	3.29			3.29			3.29		
AIC	526.3			535.2			524.9		
Marginal R^2 / Conditional R^2	0.05 / 0.661			0.023 / 0.635			0.054 / 0.68		

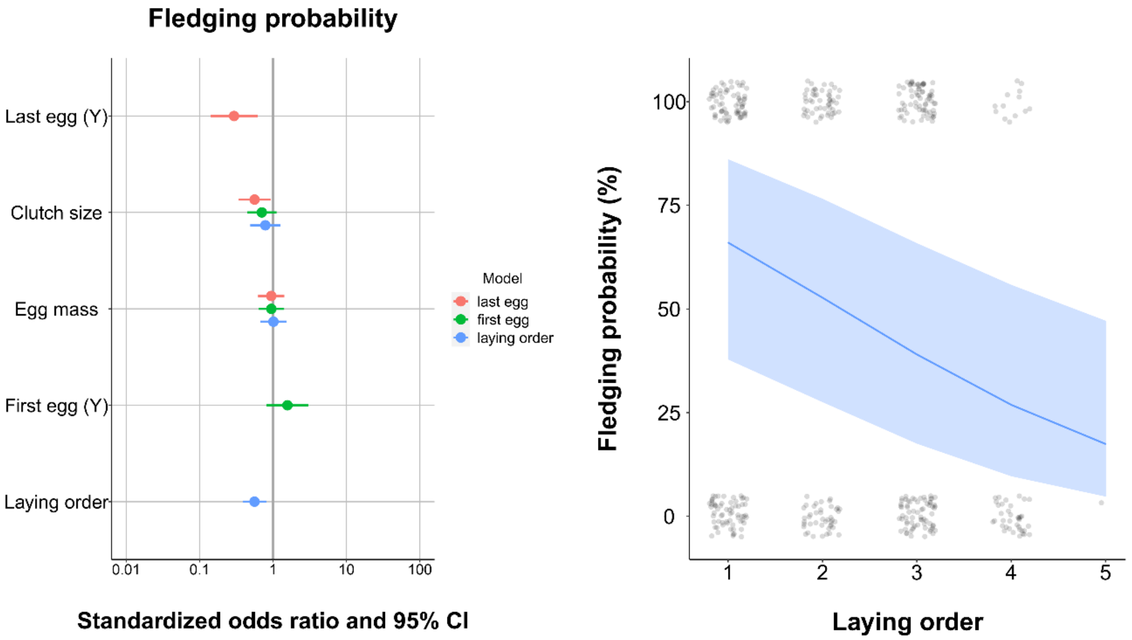


Figure S3. 2 On the left, standardised model coefficients and 95CI for the three models testing the effects of egg position on fledging probability. The legend shows to which model corresponds each model estimate (model including last egg, first egg or laying order as variables of interest). The reference level for the first and last egg categorical variables is ‘No’. On the right, raw data (N=419) and predicted slope (with 95CI) of the model on fledging probability in relation to laying order.

2. Egg mass

Table S3. 4 Standardised estimates of the models with egg mass as response variable (N=779). Posterior means and 95CrI for each variable are shown, as well as pMCMC (p) when applicable (all effective sample sizes ≥ 1000). Model marginal and conditional R^2 (R^2m and R^2c, respectively) and DIC are given below. Statistically supported effects are presented in bold. The response variable was scaled before model fitting (SD= 0.20). Reference level (intercept) for 'last egg' is 0 (not last egg).

	Model with laying order				**Model with last egg**			
Fixed effect	**Post. mean**	**95CrI**		**p**	**Post. mean**	**95CrI**		**p**
Intercept	12.67	12.49	12.83	0.001	12.63	12.45	12.83	0.001
Group size:laying order	-0.01	-0.05	0.04	0.602	-	-	-	-
Group size	-0.06	-0.15	0.02	0.21	-0.03	-0.12	0.07	0.528
Laying order	**0.19**	**0.14**	**0.23**	**0.001**	-	-	-	-
Group size:last egg	-	-	-	-	-0.06	-0.16	0.03	0.19
Last egg 1	-	-	-	-	**0.17**	**0.07**	**0.26**	**0.001**
Clutch size	-0.07	-0.15	0.02	0.102	0.002	-0.07	0.09	0.994
Tarsus size	0.07	-0.05	0.18	0.268	0.07	-0.04	0.19	0.202
Random effect								
Mother ID:Nest ID N=326	0.16	0.08	0.24		0.13	0.03	0.20	
Mother ID N=192	0.47	0.34	0.62		0.48	0.34	0.64	
Colony ID N=14	0.01	0.0002	0.04		0.01	0.0002	0.04	
Season N=7	0.01	0.0002	0.05		0.02	0.0002	0.07	
Residuals	0.33	0.29	0.37		0.36	0.32	0.41	
R^2 m	0.05	0.02	0.07		0.02	0.006	0.05	
R^2 c	0.7	0.56	0.84		0.67	0.53	0.83	
DIC	1566.4				1641.2			

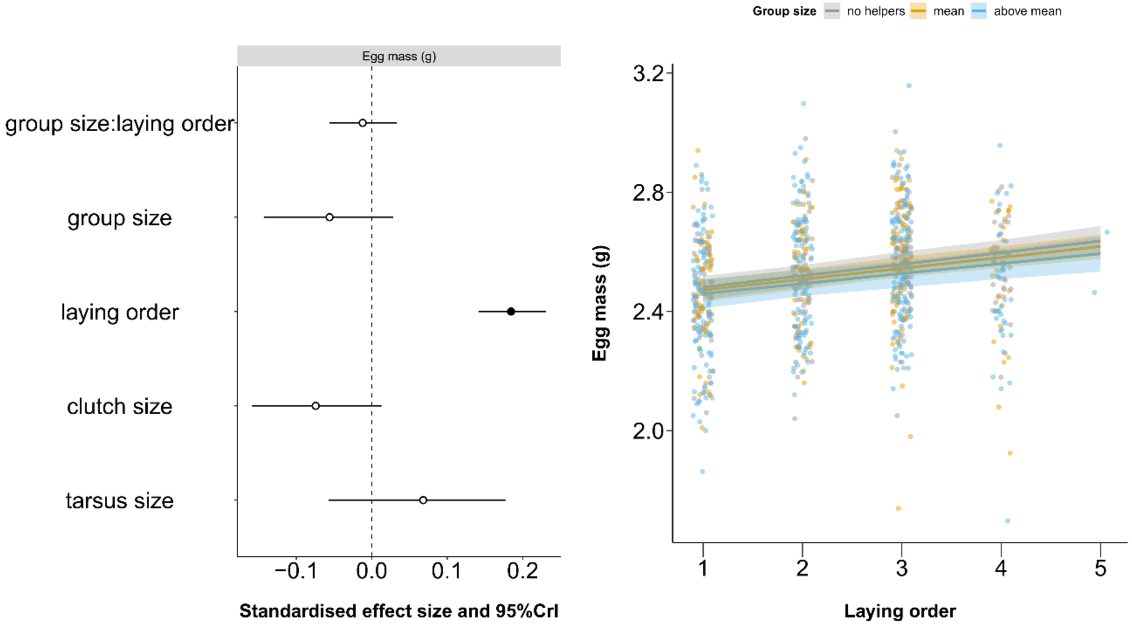


Figure S3. 3 On the left, egg mass model standardised coefficients and 95CrI. On the right, predicted relationship between egg mass and laying order for females with different group sizes. Lines represent the predicted values for the correlation between egg mass and laying order for three group size values: group size=2 (no helpers), mean group size (3.5) and the average between mean and maximum group size (5.5). Points represent raw data and point colours represent observations for groups without helpers, groups between group size=2 and mean group size or group sizes above the mean (all values rounded to the nearest integer).

3. Egg contents

Yolk mass, lipids and proteins

Table S3. 5 Standardised estimates of the models with yolk mass (g) as response variable (N=122). Posterior means and 95CrI for each variable are shown, as well as pMCMC (p) when applicable (all effective sample sizes ≥ 1000). Model marginal and conditional R2 (R2m and R2c, respectively) and DIC are given below. Statistically supported effects are presented in bold. The response variable was scaled before model fitting (SD= 0.10). Reference level (intercept) for 'last egg', 'protected' and 'season' is 0 (not last egg, not protected, and 2014/2015, respectively).

	Model with laying order (change in proportion of yolk)				**Model without egg mass (absolute change)**				**Model with last egg (change in proportion of yolk)**			
Fixed effect	**Post. mean**	**95CrI**		**p**	**Post. mean**	**95CrI**		**p**	**Post. mean**	**95CrI**		**p**
Intercept	5.38	4.92	5.91	0.001	5.42	4.9	6.01	0.001	5.49	4.98	6.00	0.001
GS:l.order	**0.12**	**0.02**	**0.24**	**0.034**	**0.11**	**0.01**	**0.24**	**0.068**	-	-	-	-
Group size	0.11	-0.07	0.30	0.276	0.11	-0.09	0.32	0.304	0.06	-0.15	0.27	0.570
Lay. order	**-0.16**	**-0.27**	**-0.04**	**0.004**	-0.12	-0.23	0.01	0.064	-	-	-	-
GS:last e.	-	-	-	-	-	-	-	-	0.16	-0.09	0.40	0.204
Last egg 1	-	-	-	-	-	-	-	-	**-0.25**	**-0.50**	**-0.01**	**0.056**
Egg mass	**0.29**	**0.14**	**0.44**	**0.001**	-	-	-	-	**0.28**	**0.12**	**0.44**	**0.001**
Clutch size	-0.03	-0.20	0.14	0.678	-0.08	-0.26	0.10	0.35	-0.08	-0.25	0.10	0.336
Protected 1	0.43	-0.10	1.00	0.126	0.42	-0.22	1.06	0.204	0.42	-0.15	0.94	0.140
Season 1	**1.69**	**1.18**	**2.23**	**0.001**	**1.56**	**0.99**	**2.11**	**0.001**	**1.69**	**1.17**	**2.17**	**0.001**
Random effect												
Colony ID N=7	0.10	0.0002	0.38		0.09	0.0003	0.39		0.09	0.0002	0.36	
Mother ID N=42	0.13	0.0002	0.29		0.18	0.0007	0.35		0.15	0.0003	0.32	
Residuals	0.40	0.27	0.54		0.43	0.30	0.60		0.42	0.27	0.55	
R^2 m	0.46	0.29	0.59		0.39	0.28	0.53		0.45	0.3	0.59	
R^2 c	0.65	0.5	0.79		0.61	0.45	0.77		0.64	0.49	0.77	
DIC	260.1				269.7				264.3			

Table S3. 6 Standardised estimates of the models with lipids (%) as response variable (N=83). Posterior means and 95CrI for each variable are shown, as well as pMCMC (p) when applicable (all effective sample sizes ≥ 1000). Model marginal and conditional R^2 (R^2m and R^2c, respectively) and DIC are given below. Statistically supported effects are presented in bold. The response variable was scaled before model fitting (SD=15.5). Reference level (intercept) for 'last egg' and 'protected' is 0 (not last egg, not protected, respectively).

	Model with laying order (changes in concentration)				**Model with egg/yolk mass (absolute change)**				**Model with last egg (changes in concentration)**			
Fixed effect	**Post. mean**	**95CrI**		**p**	**Post. mean**	**95CrI**		**p**	**Post. mean**	**95CrI**		**p**
Intercept	3.38	2.65	4.11	0.001	3.37	2.63	4.23	0.001	3.36	2.63	4.25	0.001
GS:l.order	**0.21**	**0.01**	**0.39**	**0.03**	0.23	-0.01	0.41	0.038	-	-	-	-
Group size	**0.33**	**0.1**	**0.56**	**0.01**	**0.34**	**0.08**	**0.55**	**0.012**	0.27	-0.02	0.54	0.056
Lay. order	-0.08	-0.28	0.11	0.446	-0.09	-0.30	0.14	0.398	-	-	-	-
GS:last e.	-	-	-	-	-	-	-	-	0.21	-0.24	0.58	0.336
Last egg 1	-	-	-	-	-	-	-	-	-0.18	-0.60	0.29	0.428
Yolk mass	-	-	-	-	-0.07	-0.34	0.17	0.606	-	-	-	-
Egg mass	-	-	-	-	0.06	-0.17	0.31	0.578	-	-	-	-
Clutch size	0.16	-0.09	0.43	0.222	0.15	-0.14	0.42	0.306	0.15	-0.13	0.42	0.328
Protect. 1	0.14	-0.65	1.03	0.724	0.15	-0.80	1.01	0.692	0.24	-0.62	1.13	0.542
Random effect												
Colony ID N=6	0.04	0.0001	0.18		0.04	0.0004	0.19		0.04	0.0002	0.18	
Mother ID N=28	0.03	0.0003	0.11		0.03	0.0002	0.13		0.03	0.0002	0.11	
Residuals	0.84	0.58	1.12		0.86	0.61	1.16		0.88	0.59	1.16	
R^2 m	0.23	0.1	0.37		0.25	0.12	0.39		0.2	0.08	0.34	
R^2 c	0.28	0.12	0.44		0.3	0.14	0.46		0.25	0.1	0.42	
DIC	229.5				233				232.8			

Table S3. 7 Standardised estimates of the models with proteins (%) as response variable (N=117). Posterior means and 95CrI for each variable are shown, as well as pMCMC (p) when applicable (all effective sample sizes ≥ 1000). Model marginal and conditional R^2 (R^2m and R^2c, respectively) and DIC are given below. Statistically supported effects are presented in bold. The response variable was scaled before model fitting (SD= 2.49). Reference level (intercept) for 'last egg', 'protected' and 'season' is 0 (not last egg, not protected, and 2014/2015, respectively).

	Model with laying order (changes in concentration)				**Model with egg/yolk mass (absolute change)**				**Model with last egg (changes in concentration)**			
Fixed effect	**Post. mean**	**95CrI**		**p**	**Post. mean**	**95CrI**		**p**	**Post. mean**	**95CrI**		**p**
Intercept	13.68	13.09	14.23	0.001	13.86	13.13	14.47	0.001	13.60	13.00	14.18	0.001
GS:l.order	0.06	-0.13	0.21	0.504	0.04	-0.13	0.21	0.652	0.16	-0.23	0.50	0.428
Group size	0.07	-0.16	0.32	0.58	0.05	-0.23	0.30	0.692	0.02	-0.23	0.30	0.912
Lay. order	0.07	-0.11	0.24	0.462	0.13	-0.06	0.30	0.184	-	-	-	-
GS:last e.	-	-	-	-	-	-	-	-	-	-	-	-
Last egg 1	-	-	-	-	-	-	-	-	0.24	-0.14	0.64	0.242
Yolk mass	-	-	-	-	0.24	-0.03	0.53	0.096	-	-	-	-
Egg mass	-	-	-	-	-0.21	-0.43	0.01	0.074	-	-	-	-
Clutch size	-0.05	-0.28	0.18	0.65	-0.05	-0.30	0.18	0.654	-0.01	-0.25	0.22	0.922
Protect. 1	-0.15	-0.8	0.52	0.614	-0.23	-1.00	0.37	0.496	-0.14	-0.79	0.54	0.63
Season 1	0.25	-0.31	0.86	0.384	-0.18	-0.99	0.57	0.626	0.28	-0.37	0.89	0.328
Random effect												
Colony ID N=7	0.03	0.0002	0.14		0.04	0.0002	0.15		0.04	0.0002	0.15	
Mother ID N=40	0.11	0.0003	0.36		0.17	0.0003	0.47		0.12	0.0003	0.38	
Residuals	0.94	0.67	1.26		0.88	0.62	1.19		0.94	0.67	1.25	
R^2 m	0.08	0.01	0.15		0.13	0.04	0.23		0.0.9	0.02	0.18	
R^2 c	0.2	0.02	0.4		0.29	0.07	0.52		0.21	0.03	0.43	
DIC	341.3				337.6				339.6			

Total carotenoids, vitamin A and vitamin E

Table S3. 8 Standardised estimates of the models with total carotenoids (ug/g) as response variable (N=119). Posterior means and 95CrI for each variable are shown, as well as pMCMC (p) when applicable (all effective sample sizes ≥ 1000). Model marginal and conditional R^2 (R^2m and R^2c, respectively) and DIC are given below. Statistically supported effects are presented in bold. The response variable was scaled before model fitting (SD=20.7). Reference level (intercept) for ‘last egg’, ‘protected’ and ‘season’ is 0 (not last egg, not protected, and 2014/2015, respectively).

	Model with laying order (changes in concentration)				**Model with egg/yolk mass (absolute change)**				**Model with last egg (changes in concentration)**			
Fixed effect	**Post. mean**	**95CrI**		**p**	**Post. mean**	**95CrI**		**p**	**Post. mean**	**95CrI**		**p**
Intercept	2.34	1.68	2.93	0.001	2.22	1.63	2.91	0.001	2.53	1.88	3.13	0.001
GS:l.order	-0.05	-0.14	0.06	0.35	-0.03	-0.13	0.06	0.522	-	-	-	-
Group size	0.03	-0.22	0.28	0.812	0.06	-0.16	0.34	0.61	0.02	-0.22	0.31	0.912
Lay. order	**-0.35**	**-0.46**	**-0.25**	**0.001**	**-0.34**	**-0.45**	**-0.23**	**0.001**	-	-	-	-
GS:last e.	-	-	-	-	-	-	-	-	0.02	-0.24	0.24	0.89
Last egg 1	-	-	-	-	-	-	-	-	**-0.51**	**-0.75**	**-0.26**	**0.001**
Yolk mass	-	-	-	-	**-0.17**	**-0.35**	**-0.01**	**0.046**	-	-	-	-
Egg mass	-	-	-	-	**-0.19**	**-0.36**	**-0.02**	**0.036**	-	-	-	-
Clutch size	0.15	-0.04	0.36	0.15	0.13	-0.06	0.34	0.216	0.04	-0.17	0.23	0.73
Protect. 1	0.04	-0.65	0.66	0.884	0.11	-0.60	0.76	0.72	0.01	-0.67	0.66	0.95
Season 1	**-1.04**	**-1.70**	**-0.36**	**0.004**	**-0.87**	**-1.51**	**-0.11**	**0.014**	**-1.06**	**-1.73**	**-0.42**	**0.001**
Random effect												
Colony ID N=7	0.08	0.0002	0.34		0.09	0.0003	0.38		0.08	0.0003	0.37	
Mother ID N=41	0.33	0.13	0.55		0.32	0.13	0.52		0.31	0.10	0.52	
Residuals	0.32	0.22	0.42		0.29	0.20	0.37		0.41	0.29	0.54	
R^2 m	0.38	0.23	0.54		0.42	0.25	0.57		0.32	0.15	0.48	
R^2 c	0.72	0.6	0.82		0.76	0.65	0.85		0.65	0.51	0.79	
DIC	233.8				222.9				261			

Table S3. 9 Standardised estimates of the models with vitamin A (ug/g) as response variable (N=39). Posterior means and 95CrI for each variable are shown, as well as pMCMC (p) when applicable (all effective sample sizes ≥ 1000). Model marginal and conditional R^2 (R^2m and R^2c, respectively) and DIC are given below. Statistically supported effects are presented in bold. The response variable was scaled before model fitting (SD=1.03). Reference level (intercept) for 'last egg' is 0 (not last egg).

	Model with laying order (changes in concentration)				**Model with egg/yolk mass (absolute change)**				**Model with last egg (changes in concentration)**			
Fixed effect	**Post. mean**	**95CrI**		**p**	**Post. mean**	**95CrI**		**p**	**Post. mean**	**95CrI**		**p**
Intercept	2.81	2.37	3.24	0.001	2.70	2.14	3.25	0.001	2.74	2.27	3.23	0.001
GS:l.order	-0.09	-0.37	0.22	0.546	-0.11	-0.29	0.12	0.276	-	-	-	-
Group size	-0.36	-0.73	0.01	0.056	-0.23	-0.73	0.37	0.354	-0.34	-0.75	0.10	0.144
Lay. order	0.17	-0.12	0.50	0.256	0.07	-0.20	0.30	0.552	-	-	-	-
GS:last e.	-	-	-	-	-	-	-	-	-0.01	-0.66	0.59	0.986
Last egg 1	-	-	-	-	-	-	-	-	0.19	-0.38	0.86	0.534
Yolk mass	-	-	-	-	**-0.37**	**-0.70**	**-0.07**	**0.022**	-	-	-	-
Random effect												
Colony ID N=4	0.16	0.0003	0.64		0.07	0.0002	0.32		0.08	0.0001	0.31	
Mother ID N=14	0.64	0.0007	1.48		0.16	0.0003	0.58		0.14	0.0003	0.55	
Residuals	0.42	0.19	0.83		0.86	0.45	1.35		0.91	0.47	1.42	
R^2 m	0.25	0.04	0.46		0.18	0.006	0.36		0.15	0.01	0.32	
R^2 c	0.7	0.4	0.94		0.34	0.08	0.63		0.3	0.04	0.57	
DIC	81.7				111.5				113.3			

Table S3. 10 Standardised estimates of the models with vitamin E (ug/g) as response variable (N=39). Posterior means and 95CrI for each variable are shown, as well as pMCMC (p) when applicable (all effective sample sizes ≥ 1000). Model marginal and conditional R^2 (R^2m and R^2c, respectively) and DIC are given below. Statistically supported effects are presented in bold. The response variable was scaled before model fitting (SD=13.4). Reference level (intercept) for ‘last egg’ is 0 (not last egg).

	Model with laying order (changes in concentration)				**Model with egg/yolk mass (absolute change)**				**Model with last egg (changes in concentration)**			
Fixed effect	**Post. mean**	**95CrI**		**p**	**Post. mean**	**95CrI**		**p**	**Post. mean**	**95CrI**		**p**
Intercept	3.79	3.18	4.33	0.002	3.69	2.81	4.50	0.001	3.92	3.18	4.70	0.002
GS:l.order	-0.15	-0.40	0.12	0.288	-0.15	-0.32	0.02	0.086	-	-	-	-
Group size	-0.07	-0.49	0.43	0.768	0.04	-0.61	0.85	0.936	0.01	-0.63	0.66	0.986
Lay. order	**-0.34**	**-0.59**	**-0.06**	**0.016**	**-0.42**	**-0.61**	**-0.22**	**0.001**	-	-	-	-
GS:last e.	-	-	-	-	-	-	-	-	-0.12	-0.63	0.33	0.6
Last egg 1	-	-	-	-	-	-	-	-	**-0.61**	**-1.08**	**-0.15**	**0.016**
Yolk mass	-	-	-	-	**-0.27**	**-0.52**	**-0.02**	**0.034**	-	-	-	-
Random effect												
Colony ID N=4	0.22	0.0002	0.47		0.37	0.0002	1.18		0.28	0.0002	0.98	
Mother ID N=14	0.40	0.0008	1.08		1.43	0.32	2.98		1.14	0.0008	2.64	
Residuals	0.70	0.31	1.20		0.27	0.13	0.48		0.42	0.16	0.82	
R^2 m	0.17	0.01	0.32		0.16	0.03	0.31		0.12	0.002	0.27	
R^2 c	0.48	0.14	0.84		0.86	0.7	0.98		0.73	0.35	0.98	
DIC	105.5				68.06				82.3			

Testosterone, A4 and corticosterone

Table S3. 11 Standardised estimates of the models with testosterone (pg/mg) as response variable (N=122). Posterior means and 95CrI for each variable are shown, as well as pMCMC (p) when applicable (all effective sample sizes ≥ 1000). Model marginal and conditional R^2 (R^2m and R^2c, respectively) and DIC are given below. Statistically supported effects are presented in bold. The response variable was scaled before model fitting (SD=1.13). Reference level (intercept) for 'last egg', 'protected' and 'season' is 0 (not last egg, not protected, and 2014/2015, respectively).

	Model with laying order (changes in concentration)				**Model with egg/yolk mass (absolute change)**				**Model with last egg (changes in concentration)**			
Fixed effect	**Post. mean**	**95CrI**		**p**	**Post. mean**	**95CrI**		**p**	**Post. mean**	**95CrI**		**p**
Intercept	3.17	2.43	3.93	0.001	3.02	2.27	3.86	0.001	3.21	2.48	4.01	0.001
GS:l.order	-0.03	-0.16	0.08	0.624	-0.01	-0.13	0.10	0.798	-	-	-	-
Group size	0.21	-0.09	0.50	0.146	0.23	-0.10	0.52	0.132	0.25	-0.05	0.59	0.11
Lay. order	-0.07	-0.20	0.05	0.262	-0.09	-0.21	0.04	0.166	-	-	-	-
GS:last e.	-	-	-	-	-	-	-	-	-0.12	-0.39	0.13	0.346
Last egg 1	-	-	-	-	-	-	-	-	-0.11	-0.36	0.14	0.39
Yolk mass	-	-	-	-	-0.17	-0.38	0.04	0.112	-	-	-	-
Egg mass	-	-	-	-	0.02	-0.24	0.22	0.882	-	-	-	-
Clutch size	-0.09	-0.35	0.12	0.412	-0.10	-0.34	0.12	0.442	-0.12	-0.36	0.12	0.298
Protect. 1	0.00	-0.80	0.79	0.986	0.10	-0.81	0.90	0.778	0.03	-0.76	0.91	0.922
Season 1	-0.06	-0.84	0.77	0.848	0.21	-0.65	1.07	0.628	-0.06	-0.85	0.70	0.852
Random effect												
Colony ID N=7	0.19	0.0005	0.61		0.21	0.0003	0.73		0.18	0.0003	0.58	
Mother ID N=42	0.48	0.19	0.82		0.50	0.17	0.85		0.49	0.22	0.86	
Residuals	0.46	0.32	0.59		0.45	0.31	0.59		0.46	0.32	0.61	
R^2 m	0.11	0.01	0.23		0.13	0.03	0.25		0.12	0.02	0.23	
R^2 c	0.62	0.44	0.78		0.64	0.47	0.82		0.62	0.44	0.77	
DIC	285.5				285.1				285.2			

Table S3. 12 Standardised estimates of the models with A4 (pg/mg) as response variable (N=39). Posterior means and 95CrI for each variable are shown, as well as pMCMC (p) when applicable (all effective sample sizes ≥ 1000). Model marginal and conditional R^2 (R^2m and R^2c, respectively) and DIC are given below. Statistically supported effects are presented in bold. The response variable was used in the log scale and was scaled before model fitting (SD log=0.33). Reference level (intercept) for 'last egg' is 0 (not last egg).

	Model with laying order (changes in concentration)				**Model with yolk mass (absolute change)**				**Model with last egg (changes in concentration)**			
Fixed effect	**Post. mean**	**95CrI**		**p**	**Post. mean**	**95CrI**		**p**	**Post. mean**	**95CrI**		**p**
Intercept	1.74	1.18	2.29	0.002	1.74	1.22	2.25	0.001	1.54	0.96	2.17	0.004
GS:l.order	0.02	-0.20	0.27	0.864	0.03	-0.22	0.26	0.778	-	-	-	-
Group size	-0.34	-0.77	0.12	0.138	-0.37	-0.82	0.12	0.132	-0.35	-0.84	0.15	0.15
Lay. order	**0.27**	**0.04**	**0.50**	**0.022**	0.23	-0.07	0.50	0.106	-	-	-	-
GS:last e.	-	-	-	-	-	-	-	-	0.12	-0.37	0.59	0.618
Last egg 1	-	-	-	-	-	-	-	-	**0.56**	**0.13**	**1.05**	**0.026**
Yolk mass	-	-	-	-	-0.05	-0.37	0.30	0.758	-	-	-	-
Random effect												
Colony ID N=4	0.33	0.0003	0.78		0.14	0.0002	0.59		0.28	0.0002	0.77	
Mother ID N=14	0.44	0.0004	1.05		0.37	0.0003	1.00		0.46	0.0007	1.09	
Residuals	0.52	0.23	0.88		0.59	0.25	1.00		0.49	0.21	0.89	
R^2 m	0.2	0.01	0.4		0.23	0.02	0.42		0.19	0.01	0.39	
R^2 c	0.59	0.23	0.85		0.55	0.23	0.87		0.6	0.28	0.88	
DIC	95.5				93.2				93.1			

Table S3. 13 Standardised estimates of the models with corticosterone (pg/mg) as response variable (N=122). Posterior means and 95CrI for each variable are shown, as well as pMCMC (p) when applicable (all effective sample sizes ≥ 1000). Model marginal and conditional R^2 (R^2m and R^2c, respectively) and DIC are given below. Statistically supported effects are presented in bold. The response variable was scaled before model fitting (SD=1.25). Reference level (intercept) for ‘last egg’, ‘protected’ and ‘season’ is 0 (not last egg, not protected, and 2014/2015, respectively).

	Model with laying order (changes in concentration)				**Model with egg/yolk mass (absolute change)**				**Model with last egg (changes in concentration)**			
Fixed effect	**Post. mean**	**95CrI**		**p**	**Post. mean**	**95CrI**		**p**	**Post. mean**	**95CrI**		**p**
Intercept	2.54	1.90	3.19	0.001	2.64	1.93	3.30	0.001	2.45	1.82	3.16	0.001
GS:l.order	-0.02	-0.13	0.11	0.758	-0.02	-0.14	0.10	0.754	-	-	-	-
Group size	-0.08	-0.34	0.22	0.584	-0.08	-0.37	0.22	0.574	-0.05	-0.36	0.24	0.722
Lay. order	**0.16**	**0.01**	**0.27**	**0.014**	**0.18**	**0.04**	**0.31**	**0.004**	-	-	-	-
GS:last e.	-	-	-	-	-	-	-	-	-0.07	-0.34	0.17	0.574
Last egg 1	-	-	-	-	-	-	-	-	0.24	-0.03	0.49	0.076
Yolk mass	-	-	-	-	0.12	-0.11	0.30	0.278	-	-	-	-
Egg mass	-	-	-	-	-0.11	-0.31	0.10	0.332	-	-	-	-
Clutch size	0.08	-0.16	0.30	0.512	0.07	-0.17	0.28	0.546	0.13	-0.12	0.33	0.318
Protect. 1	-0.12	-0.79	0.66	0.724	-0.16	-0.86	0.58	0.702	-0.13	-0.86	0.56	0.73
Season 1	0.66	0.002	1.38	0.056	0.44	-0.29	1.26	0.286	0.67	-0.07	1.32	0.064
Random effect												
Colony ID N=7	0.04	0.0002	0.16		0.04	0.0003	0.19		0.04	0.0002	0.15	
Mother ID N=42	0.45	0.16	0.74		0.47	0.19	0.82		0.45	0.18	0.74	
Residuals	0.47	0.33	0.61		0.47	0.34	0.64		0.48	0.33	0.63	
R^2 m	0.2	0.07	0.34		0.21	0.08	0.35		0.2	0.05	0.33	
R^2 c	0.6	0.45	0.77		0.62	0.46	0.77		0.59	0.43	0.76	
DIC	286.7				287.5				289.5			

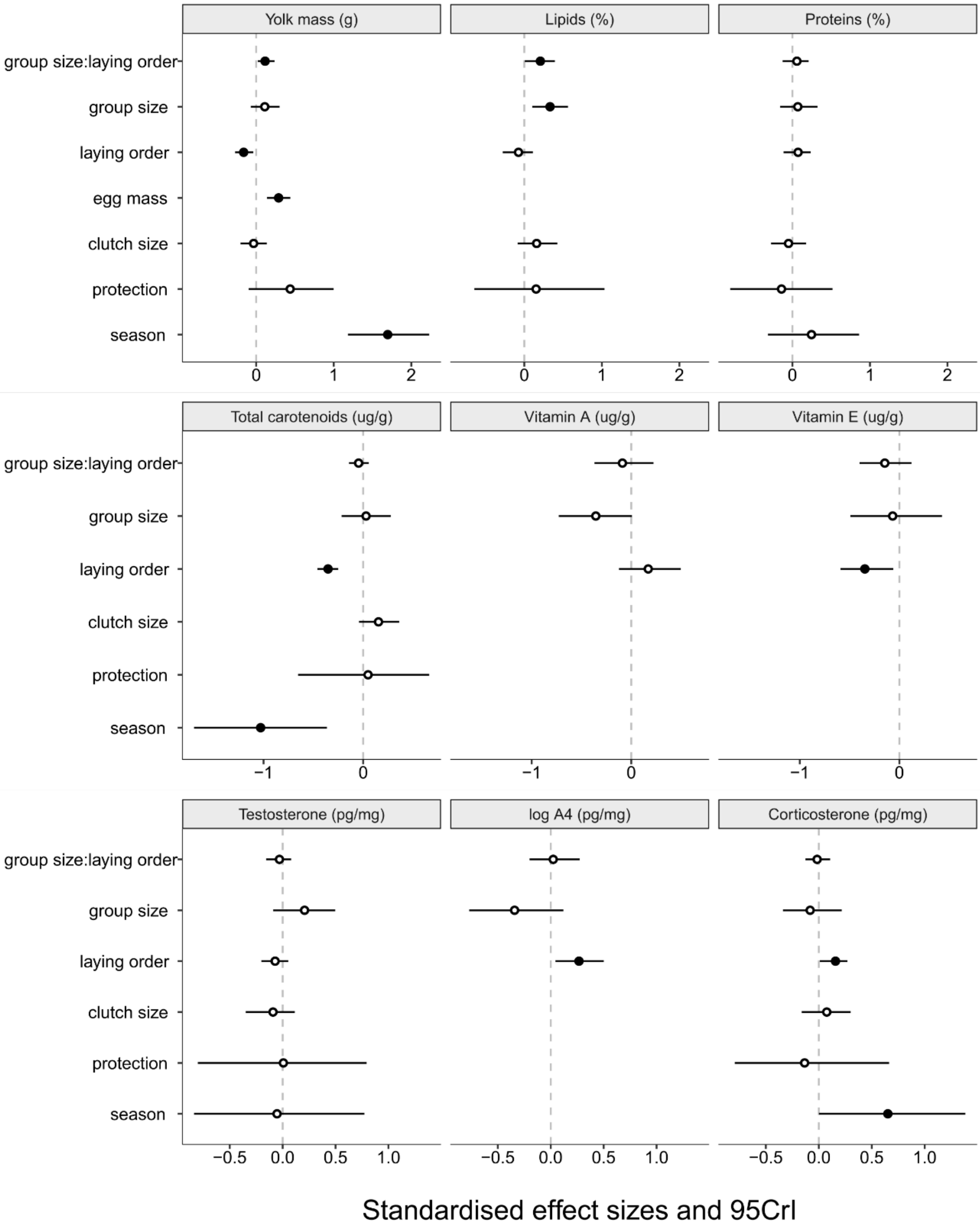


Figure S3. 4 Standardised posterior means represented by circles and 95CrI represented by bars of the variables of interest (interaction group size:laying order and its single terms) and covariates included in the model for each response variable. Filled circles show statistically credible effects.

4. Helper effects on hatching and fledging success

Table S3. 14 Standardised posterior log odds' means of the categorical GLMM testing the effect of the interaction between egg laying order and group size on **hatching probability** (N=331). Random effects variance are also presented. Statistically supported effects are in bold.

	Model with laying order			
Fixed effect	**Log-Odds**	**95CrI**		**p**
Hatched (Intercept)	1.06	0.66	1.49	0.0005
Group size:laying order	-0.08	-0.41	0.23	0.62
Group size	0.02	-0.29	0.36	0.88
Laying order	**-0.74**	**-1.08**	**-0.41**	**0.0005**
Clutch size	-0.04	-0.39	0.28	0.814
Egg mass	**0.59**	**0.28**	**0.94**	**0.001**
Mother ID:Nest ID (N=196)	0.22	0.0002	1.11	
Mother ID (N=144)	0.09	0.0003	0.42	
Colony ID (N=13)	0.07	0.0002	0.27	
Season (N=7)	0.08	0.0002	0.35	
Residuals	1	1	1	

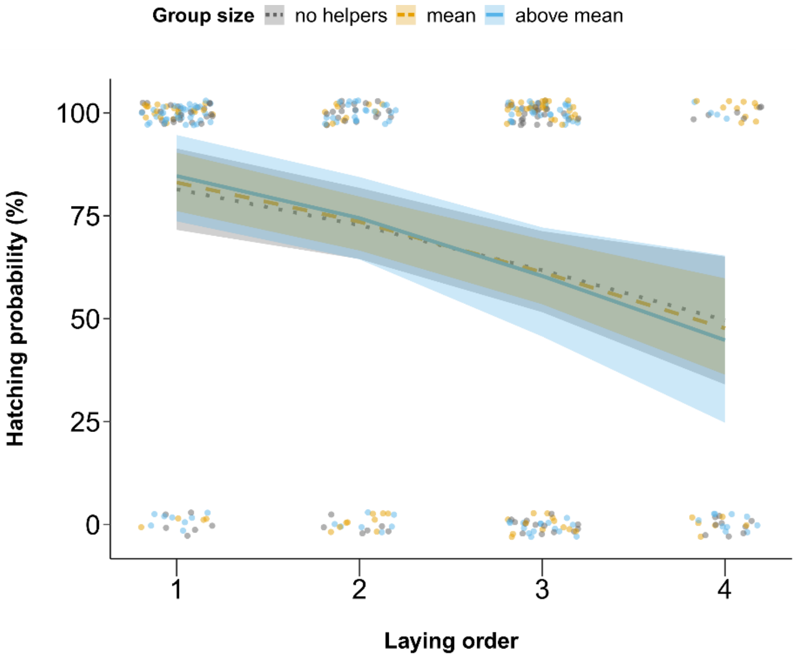


Figure S3. 5 Relationship between hatching probability and laying order for females of different group sizes. Lines represent the posterior predicted means and 95% credible intervals for the correlation between fledging probability and laying order for three group size values: group size=2 (no helpers; grey dotted line), mean group size (3.3; orange dashed line) and the average between mean and maximum group size (5.2; blue solid line). Points represent raw data and point colours represent observations for groups without helpers, groups between group size=2 and mean group size or group sizes above the mean (all values rounded to the nearest integer).

Table S3. 15 Standardised posterior log odds' means of the categorical GLMM testing the effect of the interaction between egg laying order and group size on fledging probability (N=226). Random effects variance are also presented. Statistically supported effects are in bold.

	Model with laying order			
Fixed effect	**Log-Odds**	**95CrI**		**p**
Fledged (Intercept)	0.83	-1.44	3.64	0.428
Group size:laying order	0.18	-0.59	0.93	0.649
Group size	**1.56**	**0.41**	**2.79**	**0.002**
Laying order	-0.63	-1.29	0.003	0.047
Clutch size	-0.69	-1.78	0.25	0.144
Egg mass	-0.32	-1.18	0.44	0.425
Mother ID:Nest ID (N=150)	11.11	0.0005	26.88	
Mother ID (N=120)	1.64	0.0002	7.52	
Colony ID (N=13)	0.97	0.0004	4.43	
Season (N=7)	7.91	0.0006	26.01	
Residuals	1	1	1	

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Chapter 4

Predator playbacks affect maternal egg allocation regardless of group size in a cooperatively breeding bird

Predator playbacks affect maternal egg allocation regardless of group size in a cooperatively breeding bird

Rita Fortuna[a,b,c,d], Rita Covas[a,c,e], Pietro B. D'Amelio[d], Liliana R. Silva[a,c], Louis Bliard[f], Fanny Rybak[g] , Claire Doutrelant[d] and Matthieu Paquet[h]

[a] CIBIO, Centro de Investigação em Biodiversidade e Recursos Genéticos, InBIO Laboratório Associado, Campus de Vairão, Universidade do Porto, Vairão, Portugal
[b] Departamento de Biologia, Faculdade de Ciências, Universidade do Porto, Porto, Portugal
[c] BIOPOLIS Program in Genomics, Biodiversity and Land Planning, CIBIO, Campus de Vairão, Vairão, Portugal
[d] CEFE, CNRS, Univ Montpellier, EPHE, IRD, Montpellier, France
[e] Percy FitzPatrick Institute, DST-NRF Centre of Excellence, University of Cape Town, Cape Town, South Africa
[f] University of Zurich, Department of Evolutionary Biology & Environmental Studies, Winterthurerstrasse 190, CH-8057 Zurich, Switzerland
[g] Institut des Neurosciences Paris-Saclay, Université Paris-Saclay, CNRS (UMR 9197), Saclay, France
[h] Institute of Mathematics, University of Bordeaux, Talence, France

Abstract

Predation affects individuals not only through mortality, but also through indirect effects of predation risk, which influence behaviour, reproductive investment, and ultimately fitness. For example, mothers under high predation risk were found to produce smaller clutches and lay eggs with higher corticosterone levels. These ‘fear’ effects on maternal allocation may affect offspring phenotype and compromise reproductive success. In cooperatively breeding birds, helpers assist breeders by feeding the nestlings, maintaining the nest, and groups often forage and roost together before and during breeding. Helpers’ presence may therefore affect female condition, stress levels or predation risk and influence prenatal allocation strategies in response to predators. Yet, whether helper number modulates effects of predation risk on maternal allocation remains unstudied. Here, we tested how perceived predator presence affected maternal allocation to clutch size, egg mass, yolk mass and yolk corticosterone in cooperatively breeding sociable weavers *Philetairus socius*, and whether helper number modulated the effects of predation risk. To simulate predator presence, we broadcasted playbacks of the main predator of sociable weaver adults, Gabar goshawk *Micronisus gabar* before egg laying. Predator-exposed females reduced the amount of resources allocated to offspring by laying eggs with lighter yolks but, contrary to other studies, predator exposure did not affect clutch size, egg mass or corticosterone concentration. Predator effects on yolk mass were not influenced by group size, suggesting that helpers do not buffer negative predation risk effects on maternal allocation. The observed predator-induced changes in maternal allocation may reduce nutrients’ availability to embryos and recently hatched nestlings, and therefore have detrimental effects on offspring phenotype and fitness.

Keywords: clutch size, cooperative breeding, corticosterone, egg mass, maternal allocation, playback experiment, predation risk, yolk mass

Introduction

Predation is amongst the most important selective pressures, affecting density and population trends (Hanski et al., 1993; Krebs et al., 1995; McNamara & Houston, 1987). Predators can affect individuals not only through direct consumption, but also by perceived risk (or ‘fear’), which can affect the behaviour, reproductive strategies and social interactions of prey (Allen et al., 2022; Dudeck et al., 2018; Lima, 1998). Antipredator behavioural responses may entail fitness costs which are as important as lethal effects (Creel & Christianson, 2008) because the need to avoid immediate predation may lead to a decrease in long-term survival, growth and/or reproductive investment (Cresswell, 2008; LaManna & Martin, 2016; Lima, 1998, 2009).

Antipredator responses have been primarily studied in relation to individuals’ foraging behaviour, which can be compromised under high predation risk, and cause a reduction in their body condition (Abbey-Lee et al., 2016; Lima, 1986; Macleod et al., 2005). Individuals may also trade-off the time spent foraging with vigilance behaviour (Creel et al., 2014; Sansom et al., 2008), and decrease nest provisioning rates (Ghalambor & Martin, 2000; Tilgar et al., 2011), sometimes at an evident cost to the offspring (Dudeck et al., 2018; Scheuerlein & Gwinner, 2006). Moreover, predators’ presence or perception has been found to cause physiological stress responses and lead to increased levels of circulating glucocorticoids (Clinchy et al., 2004, 2013). Since predation can affect individuals’ condition, stress levels and reproductive success, it can be expected to influence the amount of energy and resources allocated to reproduction.

Accordingly, female birds were found to allocate less resources to reproduction by laying less eggs per clutch (e.g.: in Eastern bluebirds *Sialia sialis*; Hua et al., 2014; but see Coslovsky & Richner, 2011). Moreover, females under high predation risk were found to lay eggs with higher corticosterone levels and lower testosterone levels (Coslovsky et al., 2012; Saino et al., 2005; but see Morosinotto et al., 2016). These changes in hormonal levels can have detrimental effects on offspring growth (Henriksen, Rettenbacher, et al., 2011; Pitk et al., 2012; Saino et al., 2005) but, simultaneously, potentiate their flight performance (Chin et al., 2009), which can allow nestlings to better survive in riskier environments (Coslovsky & Richner, 2011; Morales et al., 2018; Mousseau & Fox, 1998; Sheriff & Love, 2013; Storm & Lima, 2010). Altogether, this suggests that predator effects on maternal allocation may not simply be passive consequences of females’ adaptations to high predation risk, but reproductive strategies that might increase females’ fitness by saving energy for future reproduction, or increase offspring fitness by better preparing them to survive in high-risk environments (i.e.: selfish and anticipatory maternal effects, respectively; see Marshall & Uller, 2007; MacLeod et al., 2021; Morales et al., 2018; Sheriff & Love, 2013).

There is strong evidence that being part of a group can limit negative effects of predation, as it reduces the chances of being depredated while exposed (Bertram, 1978; Foster & Treherne, 1981; Hamilton, 1971; Rasa, 1989). In social systems with cooperative breeding, helpers and breeders form breeding groups that provide care to the young. Helpers may also provide help with nest building, protecting offspring from predators, and often forage and roost with the breeders before and during reproduction (Dickinson & Koenig, 2016). There are several reasons to hypothesise that breeders with more helpers may be at an advantage in high predation risk environments. First, foraging in larger groups may lead to reduced predation risk through dilution effects or higher efficacy at detecting predators (Sorato et al., 2012). In the cooperatively breeding chestnut-crowned babbler *Pomatostomus ruficeps*, for instance, larger groups were found to have a lower probability of being attacked by avian predators and individuals' predation risk was estimated to be lower in larger groups (Sorato et al., 2012). Moreover, parents often reduce their feeding rates when they have helpers (i.e.: 'load-lightening'; J. L. Brown, 1978; Covas et al., 2008; Crick, 1992), and may therefore reduce their own exposure to predators by feeding offspring less often when breeding with more helpers. Being part of a large group may also generally improve females' condition before egg-laying, as groups that forage together are thought to have higher foraging efficiency (Bednarz, 1988; Bertram, 1978) and individuals can gain thermoregulation benefits from communal roosting (du Plessis & Williams, 1994; Hatchwell et al., 2009). Helper number can thus influence females' behaviour and stress levels in response to predation risk, and their energy expenditure (see above), and may therefore mitigate predator-induced changes in reproductive allocation. However, interactive effects of helper number and predation risk on maternal allocation strategies have not been, to our knowledge, explored in cooperative systems (but see Antunes & Taborsky, 2020 on how social and predation conditions during female rearing determine their reproductive strategies later on).

In this study, we tested how experimentally increased perceived adult predation risk affected prenatal maternal allocation to clutch size, egg mass, yolk mass and yolk corticosterone in the cooperatively breeding sociable weaver (*Philetairus socius*). Furthermore, we considered the role of breeding group sizes as a social factor that may modulate maternal allocation strategies. Sociable weavers are facultative cooperative breeders and helpers provision food to the offspring and help with nest building and maintenance (A. Ferreira, 2015; Maclean, 1973a). Helper number is thought to be predictable by females at egg-laying, because most helpers are previous offspring of the breeders (Covas et al., 2006; Fortuna et al., 2022), roosting group sizes before breeding were found to correlate with breeding group sizes (Paquet et al., 2016) and individuals from the same breeding group have stronger social bonds (A. C. Ferreira et al., 2020). Besides, both parents reduce their nest feeding visits when breeding with more helpers (Covas et al., 2008), which suggests that having more helpers may reduce breeders' predation risk during rearing. Moreover, females with more helpers allocate more resources to egg components, namely yolk lipids and yolk mass of later-laid eggs, which indicates that females in larger groups might be in better condition before egg laying (Chapter 3).

We therefore predicted that females exposed to higher perceived predator presence would lay less eggs per clutch, as females may be in lower condition due to stress/reduced foraging, or strategically produce less offspring to save energy and reduce postnatal exposure to predators. Yet, females in smaller breeding groups should show a stronger tendency to reduce the number of eggs laid, as these should be the ones incurring higher predation risk. Females were as well expected to lay lighter eggs and/or with less nutritional content (lighter yolks) in response to increased predator presence, again due to poorer condition or to 'selfish' reductions in maternal investment in adverse conditions. As before, this association was expected to be stronger for females with less helpers. Lastly, females under increased perceived predation risk were expected to lay eggs with higher corticosterone concentration, which could be a passive consequence of higher circulating levels of corticosterone in females, or a way of programming offspring to better survive in high-risk environments, particularly so for females breeding in small groups.

Methods

Study system

This experiment was performed from January to March 2020 in a population of sociable weavers that has been the target of a long-term study at Benfontein Nature Reserve, Northern Cape Province of South Africa (28°520 S, 24°500E). The study area is located at the southeastern edge of the distribution range of the species and consists of an open *Acacia erioloba* savanna environment.

Sociable weavers build communal nests or ‘colonies’ containing independent chambers where breeding pairs or groups raise the chicks during breeding, and individuals show communal roosting throughout the year (Maclean, 1973b). These colonies were captured annually since 1999 for colony size estimates, ringing and blood sample collection, which allowed birds’ posterior identification in video recordings. Helpers cooperate primarily by provisioning food to offspring, but can also mob nest predators (Rat, 2015) and assist with nest building (A. Ferreira, 2015).

Manipulation of perceived predation risk

We simulated the presence of one of the main sociable weaver adults’ predator, the Gabar goshawk (*Micronisus gabar;* Christie & Ferguson-Lees, 2010; Maclean, 1973d). Gabar goshawks can seize in flight both adult and post-fledgling juvenile sociable weavers (Maclean, 1973d). In the presence of this bird of prey, sociable weavers are observed seeking refuge in trees or hiding in the colony’s nest chambers (authors pers. obs.). Playback experiments have been found to elicit antipredator responses in numerous studies (Abbey-Lee & Dingemanse, 2019; Hua et al., 2014; Zanette et al., 2011). We thus used playbacks to simulate the regular presence of a Gabar goshawk near the breeding colonies before egg laying. In control colonies, we broadcasted the calls of ringed-necked doves (*Streptopelia capicola*), a harmless bird for sociable weavers that is commonly found around the colonies.

To create the playback tracks, we extracted recordings of four adult Gabar goshawks and four ringed-necked doves the online repository *xeno-canto* (www.xeno-canto.org). Recordings from xeno-canto were processed in Audacity v.2.3.2 (available at https://www.audacityteam.org/; Audacity, 2019) to minimize background noise, applying high or low pass filters and noise reduction according to the requirements of each recording. Each playback session lasted two hours at a ratio of sound to silence of 1:1.5 (i.e.: 48 minutes of signal and 72 minutes of silence in two hours; see Zanette et al., 2011). We built four 2-hour playback tracks of goshawks and four 2-hour playback tracks of doves (each including calls from just one individual). For this, we assembled predator playback calls lasting one minute, which was the natural maximum duration of an adult goshawk call sampled from the files collected in the online repository. Within each 1-minute call, we combined six bouts of approximately 3 seconds belonging to the same individual with a distribution of silence breaks that was randomly sampled from the natural distribution of breaks estimated between 13 bouts of 5 different individuals (range from 2 to 18 seconds, mean ± standard deviation or sd = 6.8 ± 4.6 seconds). Signal bouts were faded in and out. Each 1-minute call was then separated by silence intervals of different durations (30 seconds, 1 minute, 1 minute and a half and 3 minutes), to minimise predictability of calls. The order of appearance of these four silence intervals between the 1-minute calls was randomised each 10 minutes. Playbacks were broadcasted at a volume of approximately 90dB at 1m distance from the speaker (Abbey-Lee & Dingemanse, 2019). Control playback tracks were built using the same design as predator tracks, and we confirmed with observations that birds did not show any unusual behavioural reaction to this possibly abnormal ringed-necked dove call pattern.

We conducted this experiment in 6 study colonies, splitting them into predator (3 colonies, N=163 birds) and control (3 colonies, N=172 birds) treatments. The predator and control-treatment colonies were chosen based on similar mean colony sizes that season, and a mixed distribution across the study site to minimise effects of spatial autocorrelation (Fig. 4.1).

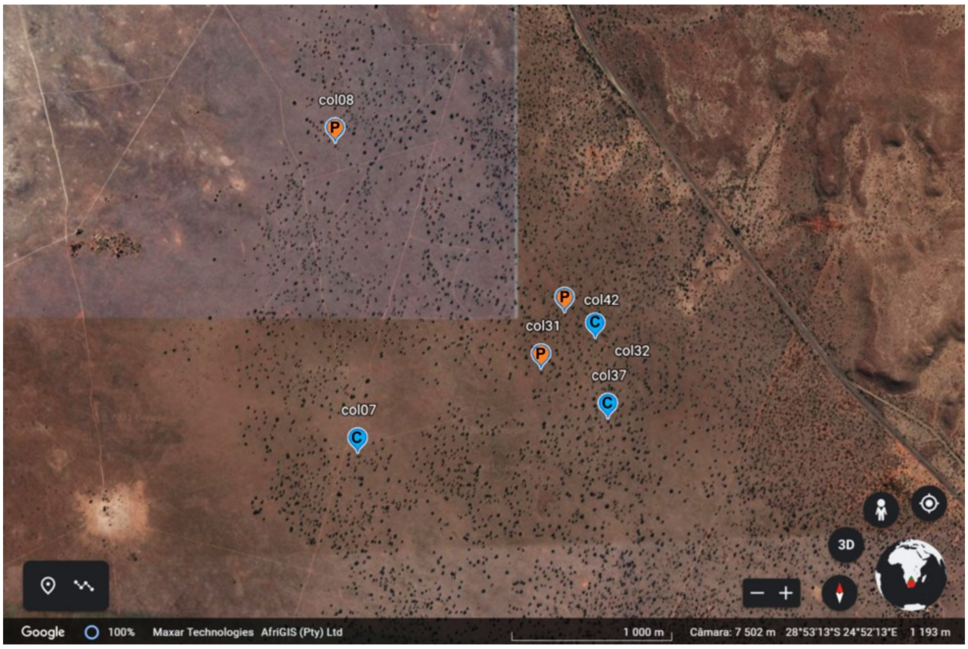

Figure 4. 1. Distribution of control (C) and predator-exposed (P) colonies in the study area.

The experiment started on 26 January 2020 and stopped when the first chick of each colony hatched (last colony stopped on 14 March 2020). We used an Anker Soundcore Motion+ speaker (Soundcore, United States, https://www.soundcore.com/) placed inside a cardboard box wrapped in plastic. Speakers were installed on a tree close to each colony attached to the tree branches with ropes, approximately 1.5 m high (distance from tree to colony varied between 28 and 40 m; average distance in predator colonies was 34.7 m and in control colonies was 33 m). Playbacks automatically started 20 minutes before sunrise and, for this, each speaker was connected to a single-board computer (Raspberry pi 3, model B, Raspberry Pi Foundation, United Kingdom, https://www.raspberrypi.org/) attached to a digital-to-analog sound converter board (PIFI DAC+ v2.0, China, https://www.kubii.fr/) and both the speaker and the single-board computer were powered by portable batteries. Computer and battery were kept in a plastic camouflaged box on the ground next to the tree with the speaker box. To minimise the risk of habituation, we broadcasted playbacks every other day at each colony. All material was moved every day from three colonies to the other three, except the speaker cardboard boxes that were kept at the colonies throughout the playback experiment. Every treatment colony was exposed to all four playback-sessions of predator calls in different days and every control colony was exposed to all four playback tracks of dove calls in different days. Two people verified that playbacks at one colony could not be heard from other experimental colonies.

To track possible automatic-playback failures due to batteries/cables malfunctions caused by wildlife or weather conditions, we additionally installed audio recorders with a microphone to be able to detect the playbacks in sound files. When playbacks failed at sunrise, or heavy rain was predicted during night-time or at sunrise, playbacks were broadcasted in the scheduled day but during late morning/early afternoon (34 out of 115 playback sessions), except when heavy rains did not cease in which case playback sessions were cancelled (re-starting two days after). In total, 115 two-hours playback-sessions were broadcasted, 57 in control colonies and 58 in treatment colonies.

Breeding monitoring procedures

From the start of the experiment, we checked nests every 2 days at the 6 colonies. After the playback broadcast was over each morning, nests were checked for new clutches. Sociable weavers usually lay one egg per day, in the morning, and start incubating before the clutch is complete (Maclean, 1973c). When the first egg of a clutch was found, the nest was visited every day to mark new eggs (with a soft blunt pencil) and weigh them to the nearest 0.001 g with a digital Pesola balance. Weighing of all eggs was done at the third laying day, since most sociable weaver clutches have 3 eggs (Fortuna et al., 2021). Furthermore, the third-laid egg of each clutch was collected after weighing and kept frozen at -20ºC to measure yolk mass and corticosterone concentration. For ethical and practical reasons, we chose to collect only one egg. Specifically collecting the third egg minimised the risk of collecting eggs while the laying process was occurring (as most clutches have 3 eggs) with the additional benefit that the 3rd egg was collected in the same morning it was laid, and thus little incubated. Nests were also checked on the next day to weigh possible 4th eggs. Clutches of 5 eggs are very rare (Fortuna et al., 2021) but were also weighted whenever found (N=1). We still weighed and collected eggs from clutches that started being laid the day just after the playbacks stopped at a colony. Some females re-laid clutches after failed breeding attempts during the experimental period, but only one of the clutches laid in each nest was considered (the one with more complete data for the variables tested was chosen). During the experimental period, we thus quantified the clutch size of 90 clutches, weighed 281 eggs from 82 clutches (only eggs with known laying order were weighed) and collected 77 third-laid eggs (only collected eggs from clutches with at least 3 eggs).

We did not prevent real predation but conducted surveys at the colonies after playback mornings to assess the presence of actual Gabar goshawks during the experiment. For 5 minutes, all Gabar goshawk sightings or calls were recorded, by inspecting all trees and skyline around the colonies. Gabar goshawks were detected in 3 of 165 surveys, twice near a treatment colony and once near a control colony, indicating that our playbacks did not seem to attract this predator to the colonies. All encounters with Gabar goshawks near the colonies at any moment during the experimental period (ca. 2 months) were also recorded. Gabar goshawks were spotted once perching at the colony tree of a treatment colony and once attacking a weaver at a control colony.

Yolk mass and corticosterone measurements

Yolks were separated from the albumen while defrosting and wet yolk was weighted at the nearest 0.001g. Corticosterone was assayed via radioimmunoassay (RIA) in two runs.

In detail, 100 mg of each sample were homogenised in 1 mL of distilled water and three to four glass beads, using a vortex. Steroids were extracted by adding 3 mL of diethyl-ether to 300 µL of the mixture, vortexing and centrifuging (5 minutes at 2000 rpm, at 4°C). The diethyl-ether phase containing steroids was decanted and poured off after snap freezing the tube in an alcohol bath at minus 40°C. This was done twice for each yolk, and the solvent was then evaporated at 37°C. The dried extracts were re-dissolved in 800 µL of phosphate 0.01 M pH 7.4 buffer each hormone was assayed in duplicate. Then, 100 µL of extract were incubated overnight at 4°C with 4000 cpm of the appropriate H3-steroid (Perkin Elmer, US) and polyclonal rabbit antiserum. Anti-corticosterone antiserum was supplied by Merck. The bound fraction was then separated from free fraction by addition of dextran-coated charcoal and activity was counted on a tri-carb 2810 TR scintillation counter (Perkin Elmer, US). Some tests were performed to validate the hormone assays on egg yolk samples. Yolk extracts were serially diluted in the assay buffer and their displacement curves were parallel to the standard curve. Inter- and intra-assay variations were respectively 10.42% and 8.91%. Corticosterone lowest detectable concentrations in yolk extracts was 56.3 pg/mL. The assay specificity was evaluated by spiking extracts and recovery was 113.3%. Cross-reactions of corticosterone antiserum were as follows : 11-dehydrocosticosterone (0.67%), deoxycorticosterone (1.5%), 18–hydroxy-deoxycorticosterone (<0.01%), cortisone (<0.01%), progesterone (0.004%), aldosterone (0.2%).

Group size and breeder identity

Nests were video recorded to obtain breeding group sizes and the identity of the breeders and helpers visiting the nests based on their colour rings (Silva et al., 2018). Video-cameras were placed on tripods under the colonies pointing to the entry of the target nests (Silva et al., 2018). During the incubation period, two 2h-videos were recorded, one between the 2nd-3rd laying day before collecting the egg and another between 8-10 days after laying the first egg. During the nestling period, two 2h-videos were recorded, one between days 8-12 after hatching started, and another between days 9-15.

Breeding group sizes could only be estimated in 24 out of 90 nests due to nestlings' mortality before chicks reached 8-12 days of age (for 24 nests, mean group size ± sd = 3.125 ± 1.262). As helpers visit the nests during incubation, we used instead the number of birds seen during this period as the group size for further analyses, which could be obtained for 89 nests (mean incubation group size ± sd = 3.438 ± 1.495; Spearman's rank correlation coefficient between incubation group size and feeding rate group size = 0.54; P=0.006; N=24 comparisons). All individuals seen visiting, building and/or feeding were considered part of the groups, except individuals that were attacked by a member of the group when trying to enter the nests.

Statistical analyses

To test how experimentally increased adult predation risk affected maternal allocation strategies, and whether this effect was conditional on breeding group sizes, we built four linear mixed models (LMM) including each maternal allocation measure as a dependent variable – clutch size, egg mass, yolk mass and yolk corticosterone - and an interaction between treatment and group size as independent variables of interest. Treatment was included as a binary factor (0 for control, 1 for predator playbacks). All analyses were conducted using the R software v.4.0.4 (R Core Team, 2021). All models were fitted assuming a normal error distribution by restricted maximum likelihood in lme4 (Bates et al., 2015). Clutch size models were under-dispersed using a Poisson error and therefore a normal distribution was also assumed. However, we confirmed that results were qualitatively similar when using a cumulative link mixed model that considers clutch size a categorical ordered variable (see below).

In the egg mass model, we controlled for non-independence by fitting nest identity and colony identity as random terms. In the clutch size, yolk mass and yolk corticosterone models there was only one value per nest, hence we only included colony identity as a random term. Additionally, in the yolk mass model, we included egg mass (mean ± sd = 2.56 ± 0.21) as a predictor of yolk mass (Chapter 2), but also tested if results were the same in absolute terms, i.e.: when removing this variable. Similarly, effects on corticosterone concentration were tested as well when including egg mass and yolk mass (mean ± sd = 0.51 ± 0.06) in the model, thus testing for an absolute change in corticosterone levels.

Response variables were scaled by subtracting the mean and diving by one standard deviation (Schielzeth, 2010). Collinearity among predictors was assessed by calculating Spearman rank correlation coefficients (all <0.4). Model diagnostics were assessed using the performance package (Lüdecke et al., 2020). Type-II Wald X^2 tests were used to estimated P values. No model simplification was performed.

We fitted a cumulative link mixed model (CLMM) with clutch size as an ordinal categorical variable for comparison with the LMM following a normal distribution, both yielding similar results (see Table S4.7; Fortuna et al., 2021). In this case, clutch size was fitted as an ordinal variable with 4 categories (2-5 eggs) using the logit link function in the ordinal package (Christensen, 2019b). Distance between the levels of clutch size was set as equidistant (e.g.: assuming that distance from 2 to 3 eggs is the same as from 3 to 4 eggs) and estimates were obtained via maximum likelihood with Laplace approximation. The proportional odds assumption (i.e.: the relationship between each pair of outcome groups is the same) was confirmed to be met, and the empirical identifiability of the CLMM is also reported through the condition number of the Hessian matrix (values over 10^4 indicate ill-defined models; Christensen, 2019a). P values and 95% confidence intervals were estimated via Wald tests.

Effects were considered statistically significant when confidence intervals did not overlap 0 and P values were lower than 0.05. Results are presented as estimated means [and 95% confidence intervals].

Results

There was no clear effect of the interaction between treatment and group size on clutch size (0.197 [-0.048,0.459]; P=0.128; Table S4.1). Clutch size was also not significantly affected by playback treatment (-0.072 [-0.478,0.346]; P=0.735) and did not significantly vary with group sizes (-0.112 [-0.307,0.066]; P=0.928; Table S4.1). Qualitatively equivalent results were obtained when analysing clutch size as a categorical variable (see Table S4.2).

For egg mass, we did not detect an interaction between group size and treatment (0.015 [-0.059,0.090]; P=0.694; Table S4.3). Egg mass was also not detectably affected by playback treatment as a single term (-0.016 [-0.102,0.060]; P=0.690) or significantly associated to group size (-0.022 [-0.075,0.031]; P=0.465; Table S4.3).

Yolk mass of the third-laid egg was not clearly affected by an interaction between treatment and group size (-0.015 [-0.036,0.005]; P=0.146; Table S4.4). However, yolks in predator-exposed nests were on average 5% [1-9%] lighter than egg yolks in control nests (-0.024 [-0.045,-0.004]; P=0.023; Table S4.4). A significant effect of similar strength was still observed when testing for absolute yolk mass changes (i.e.: excluding egg mass as covariate; see Table S4.5). We furthermore tested whether treatment differences were only driven by one very low yolk mass value in treatment colonies (0.282g; see Fig. 4.2). Treatment effect size was of similar magnitude after excluding this datapoint, and the effect was still statistically significant. There was no evidence that yolk mass varied with group sizes (0.013 [-0.001,0.028]; P=0.271; Table S4.4).

Lastly, we detected no effects of the interaction between treatment and group size on corticosterone concentration of third-laid eggs (0.119 [-0.190,0.415]; P=0.448; Table S4.6). Corticosterone concentration was not clearly affected by the treatment (-0.143 [-0.448,0.156]; P=0.39) and did not clearly vary with group size (-0.002 [-0.208,0.216]; P=0.475; Table S4.6). Qualitatively similar results were obtained in terms of corticosterone absolute changes (i.e.: including egg mass and yolk mass in the model; see Table S4.7).

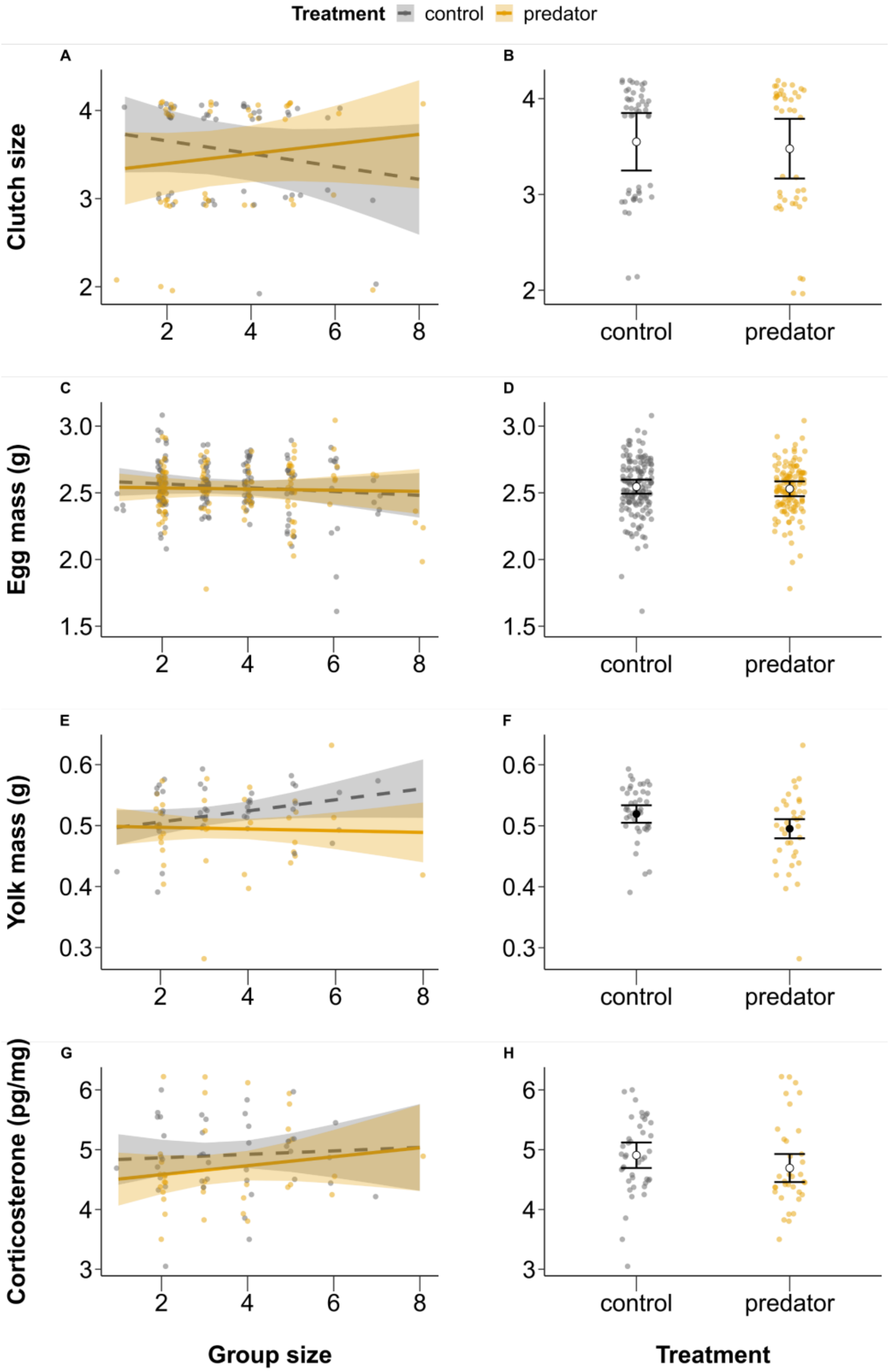

Figure 4. 2. Predicted effect of the interaction between treatment (control playback – grey points and dashed line – and predator playback – orange points and solid line) and group size (A,C,E,G), and predicted effect of treatment as a single term (B,D,F,H) on clutch size (A,B), egg mass (C,D), yolk mass (E,F), and corticosterone (G,H). Lines (left) or circles (right) show mean predicted effects and bands (left) or bars (right) show effect confidence intervals. Full circles represent statistically supported differences between treatments. Points show observed values.

Discussion

In this study, we experimentally increased perceived predator presence in a cooperatively breeding system to estimate predation risk effects on maternal reproductive allocation and whether number of helpers buffered potential predator effects. We predicted that females in smaller cooperatively breeding groups would show a stronger reduction in resource allocation to reproduction – clutch size, egg mass and yolk mass – than females with more helpers. We also predicted that predator-exposed females with fewer helpers would produce eggs more concentrated in corticosterone. Our results showed that predator-exposed mothers laid eggs with lighter yolks, but this effect was independent of females' group size, suggesting that helper number does not mitigate predation risk effects on reproductive allocation. On the other hand, the predator treatment did not evidently affect clutch size, egg mass, and egg corticosterone concentration. This suggests that simulated predator presence did not cause major changes in females' allocation to eggs, but the reduction in yolk mass documented here may have fitness consequences for females and offspring.

No interactive effects of helpers and predation risk

We did not detect interactive effects of group size and predator-induced changes in maternal allocation. We expected number of helpers to mitigate predator-induced effects on females' behaviour, condition, and reproductive success (Hua et al., 2014; Sorato et al., 2012), and therefore to influence how predation risk affects maternal allocation. Furthermore, as number of helpers during rearing seems predictable at the time of laying (A. C. Ferreira et al., 2020; Paquet et al., 2016) and breeders reduce feeding rates when they have helpers (Covas et al., 2008), this could allow strategic prenatal adjustments in reproductive investment in relation to group size and predation risk (Morales et al., 2018; Mousseau & Fox, 1998; Sheriff & Love, 2013; Stearns, 1992).

Instead, we found that the predator treatment similarly affected females regardless of their group size, which indicates that females with more helpers under high predation risk environments may not be at an advantage. The reduced exposure to predation risk as number of helpers increases has never been addressed in sociable weavers, and this would help clarifying whether group size confers protection to individuals before and during rearing. There is however some indication suggesting that individuals in larger colonies have higher survival, which has been interpreted as evidence for anti-predator benefits in relation to this social factor (C. R. Brown et al., 2003). It is also possible that even though females in larger groups have benefits in terms of reduced predation risk/lower stress/better condition, this does not influence maternal allocation strategies in relation to predation risk. On the other hand, our sample may not be large enough to detect statistically supported effects of this interaction. This is also indicated by the non-statistically supported trend for positive group size effects on yolk mass of the egg collected (the third-laid egg), even though this effect was detected in a previous and more powerful study (Chapter 3, N=122 eggs; here N=77).

Predator-induced changes in maternal allocation

Existing empirical work on the effects of adult predators on maternal allocation to reproduction showed that females laid less eggs per clutch in response to higher perceived predation risk (Hua et al., 2014; see also Thomson et al., 2006; Zanette et al., 2011). Here, clutch size was not affected by predator playbacks, even though clutch size appears to vary with other environmental factors in this system, like rainfall levels and nest predation risk (Fortuna et al., 2021). In addition, our predation risk manipulation did not affect egg mass (but see Zanette et al., 2011), concurring with previous findings in this system indicating lack of egg mass adjustments to environmental variables (Fortuna et al., 2021). Egg corticosterone levels were also not affected by the predation treatment. Even though there are reports of increased corticosterone in eggs of females exposed to predators (Saino et al., 2005), other investigations suggest that the transfer of circulating plasma corticosterone into eggs can be low (Rettenbacher et al., 2005), which may explain why we did not detect differences between the treatments.

Instead, here we found that predator-exposed females laid eggs with lighter yolks. A previous investigation of predator effects in pied flycatchers *Ficedula hypoleuca* has shown that predator-exposed females laid eggs with higher immunoglobin levels, potentially improving offspring immune capacity, but no differences in yolk mass or egg mass were detected (Morosinotto et al., 2013). Yolks contain the major source of nutrients and energy for embryo development (Carey, 1996), and these reserves can be used for several days after hatching (Williams, 1994). Therefore, yolk mass reductions, besides possibly representing energy savings for the female (Carey, 1996; Stearns, 1992), may also represent a decrease in the amount of vital nutritional resources available to the offspring, which can have detrimental effects on offspring fitness (McGraw et al., 2005; Mentesana et al., 2021). However, it is important to note that yolk mass was only measured in the third-laid egg of the clutches, and in sociable weavers there is a tendency for decreasing yolk mass with laying order (see Chapter 3), so we cannot determine whether this adjustment was similar for the remaining eggs or exclusive to third-laid ones. Nevertheless, not having collected the remaining eggs will allow future analyses on hatching success, nestling survival rates and mass differences between treatments, which could shed light on how the differences observed here in maternal allocation might have affected offspring fitness.

In terms of the mechanism that led females to produce eggs with lighter yolks, several non-exclusive scenarios are possible. First, predator playbacks were broadcasted before egg laying, which may have affected females' foraging behaviour (Abbey-Lee et al., 2016; Lima & Dill, 1990) and hence the amount of nutrients they had available to allocate to offspring (Blount et al., 2004). Second, predator playbacks may have been a stressor for females and thus increase their plasma circulating corticosterone (Clinchy et al., 2013), which has been in turn found to cause reductions in egg mass and yolk mass in captive birds (Henriksen, Groothuis, et al., 2011). On the other hand, this could be a strategy to reduce investment in current reproduction and instead save energy for survival or future reproduction once conditions improve (Stearns, 1992). Females' incubation behaviour has been recorded while the playbacks were broadcasted and future analyses on incubation patterns could provide information on the mechanism behind laying lighter-yolk eggs, if for instance females' foraging behaviour is found to be affected in predator treatments. Moreover, other measures representing prenatal reproductive investment that have been found to be affected by predation risk, such as delaying or forgoing reproduction (Scheuerlein et al., 2001; Thomson et al., 2006), could be assessed in the future to better understand potential trade-offs between current and future reproduction/survival in sociable weavers.

Conclusion

This work shows that helper number did not buffer predator-induced reductions in maternal allocation to yolk mass in sociable weavers. Even though larger groups are expected to mitigate predation risk effects on females' behaviour, physiological state and condition, this apparent advantage does not appear to translate into a higher allocation of resources to reproduction when breeding with more helpers under high predation risk. Predator-induced reductions in maternal allocation to yolk mass may have fitness consequences for mothers and their offspring, as these may represent a reduction in nutrients' availability to embryos and recently hatched nestlings, and energy savings for the female.

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Author's contributions

R.F., M.P., C.D. and R.C. designed the study; R.F., P.B.D. and L.B. collected field data; R.F., P.B.D. and F.R. created the playback files; L.R.S. analysed the videos; R.F. performed the statistical analyses; R.F. wrote the manuscript with input from all authors. All authors contributed to revisions.

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Appendix

Table S4. 1. Results from GLMM on effect of playback treatment and group size (mean=3.4; sd=1.5) on clutch size (N=89). Estimates, confidence intervals and significance test results are presented. Reference level for “Treatment” is control.

Fixed effect	**Estimate**	**Std. error**	**2.5%**	**97.5%**	**Chisq**	**Df**	**Pr(>Chisq)**
(Intercept)	3.55	0.151	3.259	3.833	-	-	-
Group size x Treatment	0.197	0.129	-0.048	0.459	2.312	1	0.128
Group size	-0.112	0.095	-0.307	0.066	0.008	1	0.928
Treatment	-0.072	0.218	-0.478	0.346	0.114	1	0.735
Random effect	**Variance**						
Colony ID (N=6)	0.045						
Residual	0.352						

Table S4. 2. Results from CLMM on effect of playback treatment and group size (mean=3.4; sd=1.5) on clutch size as a categorical ordinal variable (N=89). Estimates (log-odds-ratio), confidence intervals and significance test results are presented. Reference level for “Treatment” is control. Model conditional Hessian value = 19.

Fixed effect	**Estimate**	**Std. error**	**2.5%**	**97.5%**	**z**	**Pr(>|z|)**
Group size x Treatment	1.953	0.478	0.765	4.984	1.401	0.161
Group size	0.703	0.339	0.362	1.366	-1.040	0.299
Treatment	0.750	0.756	0.171	3.299	-0.381	0.704
Spacing	11.893	0.433	-	-	5.714	-
Threshold	0.048	0.659	-	-	-4.598	-
Random effect	**Variance**					
Colony ID (N=6)	0.522					

Table S4. 3. Results from GLMM on effect of playback treatment and group size (mean=3.5; sd=1.5) on egg mass (g; N=281). Estimates, confidence intervals and significance test results are presented. Reference level for “Treatment” is control.

Fixed effect	**Estimate**	**Std. error**	**2.5%**	**97.5%**	**Chisq**	**Df**	**Pr(>Chisq)**
(Intercept)	2.546	0.027	2.493	2.6	-	-	-
Group size x Treatment	0.015	0.039	-0.059	0.09	0.155	1	0.694
Group size	-0.022	0.027	-0.075	0.031	0.535	1	0.465
Treatment	-0.016	0.039	-0.102	0.06	0.159	1	0.69
Random effect	**Variance**						
Colony ID (N=6)	0						
Nest ID (N=82)	0.027						
Residual	0.013						

Table S4. 4. Results from GLMM on effect of playback treatment and group size (mean=3.5; sd=1.5) on yolk mass (g; N=77). Estimates, confidence intervals and significance test results are presented. Statistically significant results are in bold. Reference level for "Treatment" is control.

Fixed effect	Estimate	Std. error	2.5%	97.5%	Chisq	Df	Pr(>Chisq)
(Intercept)	0.519	0.007	0.506	0.533	-	-	-
Group size x Treatment	-0.015	0.011	-0.036	0.005	2.112	1	0.146
Group size	0.013	0.007	-0.001	0.028	1.211	1	0.271
Treatment	-0.024	0.011	**-0.045**	**-0.004**	5.159	1	**0.023**
Egg mass	0.029	0.005	**0.018**	**0.039**	28.635	1	**<0.001**
Random effect	**Variance**						
Colony ID (N=6)	0						
Residual	0.002						

Table S4. 5. Results from GLMM on effect of playback treatment and group size (mean=3.5; sd=1.5) on yolk mass (g; N=77) excluding egg mass from model (i.e.: absolute yolk mass change). Estimates, confidence intervals and significance test results are presented. Statistically significant results are in bold. Reference level for "Treatment" is control.

Fixed effect	Estimate	Std. error	2.5%	97.5%	Chisq	Df	Pr(>Chisq)
(Intercept)	0.523	0.008	0.507	0.54	-	-	-
Group size x Treatment	-0.012	0.012	-0.036	0.012	0.869	1	0.351
Group size	0.011	0.009	-0.006	0.028	0.684	1	0.408
Treatment	-0.032	0.012	**-0.058**	**-0.008**	6.71	1	**0.01**
Random effect	**Variance**						
Colony ID (N=6)	0						
Residual	0.003						

Table S4. 6. Results from GLMM on effect of playback treatment and group size (mean=3.5; sd=1.5) on yolk corticosterone concentration (pg/mg; N=77). Estimates, confidence intervals and significance test results are presented. Reference level for "Treatment" is control.

Fixed effect	Estimate	Std. error	2.5%	97.5%	Chisq	Df	Pr(>Chisq)
(Intercept)	4.874	0.112	4.672	5.08	-	-	-
Group size x Treatment	0.119	0.157	-0.19	0.415	0.575	1	0.448
Group size	-0.002	0.11	-0.208	0.216	0.511	1	0.475
Treatment	-0.143	0.166	-0.448	0.156	0.74	1	0.39
Random effect	**Variance**						
Colony ID (N=6)	0.005						
Residual	0.464						

Table S4. 7. Results from GLMM on effect of playback treatment and group size (mean=3.5; sd=1.5) on yolk corticosterone concentration (pg/mg; N=77) accounting for egg and yolk mass (i.e. absolute change in yolk corticosterone). Estimates, confidence intervals and significance test results are presented. Reference level for "Treatment" is control.

Fixed effect	**Estimate**	**Std. error**	**2.5%**	**97.5%**	**Chisq**	**Df**	**Pr(>Chisq)**
(Intercept)	4.907	0.107	4.69	5.116	-	-	-
Group size x Treatment	0.068	0.159	-0.234	0.37	0.183	1	0.668
Group size	0.042	0.112	-0.171	0.255	0.943	1	0.332
Treatment	-0.214	0.163	-0.529	0.114	1.779	1	0.182
Egg mass	0.085	0.093	-0.093	0.262	0.821	1	0.365
Yolk mass	-0.161	0.097	-0.346	0.025	2.727	1	0.099
Random effect	**Variance**						
Colony ID (N=6)	0						
Residual	0.462						

Chapter 5

Begging and feeding responses vary with relatedness and sex of provisioners in a cooperative breeder

Begging and feeding responses vary with relatedness and sex of provisioners in a cooperative breeder

Rita Fortuna[a,b,c,d], Pietro B. D'Amelio[d,e], Claire Doutrelant[d,e], André C. Ferreira[a,c,d], Clothilde Lecq[d,f], Liliana R. Silva[a,c], Rita Covas[a,c,e], Fanny Rybak[f] and Matthieu Paquet[g]

[a] CIBIO, Centro de Investigação em Biodiversidade e Recursos Genéticos, InBIO Laboratório Associado, Campus de Vairão, Universidade do Porto, Vairão, Portugal
[b] Departamento de Biologia, Faculdade de Ciências, Universidade do Porto, Porto, Portugal
[c] BIOPOLIS Program in Genomics, Biodiversity and Land Planning, CIBIO, Campus de Vairão, Vairão, Portugal
[d] CEFE, CNRS, Univ Montpellier, EPHE, IRD, Montpellier, France
[e] Percy FitzPatrick Institute, DST-NRF Centre of Excellence, University of Cape Town, Cape Town, South Africa
[f] Institut des Neurosciences Paris-Saclay, Université Paris-Saclay, CNRS (UMR 9197), Saclay, France
[g] Department of Ecology, Swedish University of Agricultural Sciences, Uppsala, Sweden

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Abstract

Begging behaviour can provide information on offspring hunger levels and be used by parents to adjust food provisioning efforts. In cooperative breeders, helpers also provide care by feeding the young. However, how helpers of different sex and relatedness to the offspring respond to begging behaviour has rarely been studied in cooperatively breeding species, which limits our understanding of the indirect and/or direct benefits that helpers may obtain by responding to offspring demand. Here, we used a cooperatively breeding bird, the sociable weaver, *Philetairus socius*, to investigate how nest intervisit intervals of breeders and different types of helpers, distinguished by sex and relatedness, varied with acoustic begging. Moreover, we tested whether these different classes of provisioners experienced distinct levels of begging. Our results show that only breeding males, but not breeding females or helpers of any sex and relatedness to the nestlings, returned faster to the nest to feed after experiencing more begging calls. When contrasted directly, we confirmed a statistically supported difference in responses to begging between male and female breeders. Surprisingly, second-order relatives experienced more begging calls than the other classes of more related helpers and breeders. These results show that we might find differences in how provisioners respond to begging levels when classifying group members according to their potential fitness gains. In sociable weavers, the benefits and costs of adjusting feeding efforts to begging seem to differ with sex and life history stage. Experimental and more detailed investigations on begging–feeding interactions are necessary to understand the origin and prevalence of these differences across cooperatively breeding systems.

Keywords: begging, cooperative breeding, feeding responses, helpers, parent–offspring interactions, sociable weaver

Introduction

When offspring depend on food provisioning from breeders, parent–offspring communication signals are crucial to maximize the fitness of parents and their progeny (Trivers, 1974). Food demand through begging displays influences parental provisioning and thus it has been central in the study of parent–offspring interactions (Kilner & Johnstone, 1997). Begging has been described across taxa and usually involves the performance of visual and/or acoustic displays (e.g. birds: Wright and Leonard 2002; mammals: Brotherton 2001; insects: Mas and Kölliker 2008; amphibians: Yoshioka et al. 2016). In birds, nestlings extend their body and may display brightly coloured gapes, while repeatedly performing acoustic begging calls (Kilner, 2002). Several studies have shown that begging can contain information about offspring hunger levels (Brotherton, 2001; Leonard & Horn, 2001a; Yoshioka et al., 2016). In food deprivation experiments, nestlings were seen to increase begging rate and duration (Leonard & Horn, 2001a; Ogawa et al., 2015; Sacchi, 2002). The relationship between begging intensity and hunger levels supports the hypothesis that begging is an honest signal of nestlings' need (Kilner and Johnstone 1997; Fresneau et al. 2018; but see Mock et al., 2011 and Royle et al., 2002). In addition, studies reporting growth and immunity costs associated with exaggerated begging suggest that these displays may be costly and condition dependent (Moreno-Rueda & Redondo, 2011, 2012).

Parents, accordingly, seem responsive to increases in offspring demand. Breeders were found to increase feeding behaviour in response to increased begging rate and duration in several biparental care systems (Bowers et al., 2019; Leonard & Horn, 1996; Leonard & Horn, 2001b; Ottosson et al., 1997). Recognizing honest and condition-dependent signals of hunger may allow parents to provide care when it is most needed (Grodzinski & Lotem, 2007), while avoiding exploitation from the offspring (Godfray, 1991; Kilner & Johnstone, 1997).

Males and females can provide distinct levels of care and, in some species, only one sex is found to respond to begging (reviewed in Müller et al. 2007). For instance, in great tits, *Parus major*, male breeders increased feeding in response to begging while females did not (Tanner et al., 2008). In another study using begging playbacks in superb fairy-wrens, *Malurus cyaneus*, breeding males but not females increased food provisioning (MacGregor & Cockburn, 2002). In contrast, responses to begging intensity from breeding females but not males have been also been detected, for example in canaries, *Serinus canaria* (Kilner, 2002) and in Manx shearwaters, *Puffinus puffinus*

(Quillfeldt et al., 2004). These discrepancies between the sexes are often explained by the trade-off between parental care and other sex-specific costs of reproduction (e.g. gamete production or investing in attracting mates; Siefferman and Hill 2008). Therefore, the sexes may have different investment optimums, defined by the fitness benefits and costs of responding to begging stimuli.

In cooperatively breeding systems, ‘helpers’ cooperate with the breeders to provide food to the young. By providing care to offspring that are not their own, helpers can also experience different benefits and costs than breeders and may hence have evolved distinct food allocation strategies. When helpers share kin relationships with the offspring, the costs of helping may be compensated by indirect fitness gains (Green et al., 2016; Hamilton, 1964). Indirect benefits are greater for individuals with higher levels of relatedness to the recipients of help, which could explain why, in some cases, helpers that are more closely related to the offspring provision at higher rates than less related individuals (Barati et al., 2018; Green et al., 2016; Griffin & West, 2003; Nam et al., 2010; Wright et al., 2010; but see Kay et al. 2020). Breeders’ and helpers’ responses to offspring needs have been studied in several cooperatively breeding species, and most studies have found that helpers, like parents, increase their feeding effort when offspring demand is higher (see Table 5.1). Interestingly, experimental manipulations of begging caused parents and helpers to increase provisioning in Arabian babblers, *Turdoides squamiceps* (Wright, 1998), where most helpers are highly related to the offspring, but also in red-winged fairy wrens, *Malurus elegans* (MacLeod & Brouwer, 2018) and bell miners, *Manorina melanophrys* (McDonald et al., 2009), where groups often include less related individuals. It is often the case that these distinct types of helpers are present within species, which provides a good opportunity to understand which indirect and/or direct fitness benefits may explain helpers’ responses to offspring demand for food. Specifically, helpers’ response can be expected to vary proportionally to the degree of indirect fitness benefits they will obtain from maximizing their relatives’ survival (Emlen & Wrege, 1988; Komdeur, 1994; Nam et al., 2010). Furthermore, in cooperative systems, different sexes usually have distinct reproductive strategies, with one sex dispersing to breed and the other being philopatric (Koenig & Haydock, 2004). The philopatric sex should benefit more from increasing the survival chances of the offspring, since young are often recruited as new group members (Clutton-Brock et al. 2002). Therefore, if helpers respond to offspring demand to obtain direct fitness benefits through group augmentation (group augmentation hypothesis; Kokko et al. 2001), we can expect philopatric helpers to match feeding effort to offspring demand more strongly than the dispersing sex. How helpers of different sex and relatedness respond to offspring demand, and specifically to begging behaviour, has rarely been assessed within species (see Table 5.1). Among these studies, even fewer have estimated whether food provisioning responses from the different group members differ statistically (see Table 5.1), which is essential if one wants to study whether and how the feeding rules of the distinct classes of individuals vary. This has resulted in scarce evidence for feeding adjustments among helpers of different sex and relatedness levels to the offspring (Table 5.1).

Since breeders' and helpers' feeding rules can differ, begging behaviour may in turn vary according to the class and contributions of each individual (Bell, 2008b). In biparental care systems, begging is often preferentially directed towards the breeder that provides more food (Dickens et al., 2008; Kölliker et al., 1998; Paquet et al., 2018). In cooperative breeders, a study on bell miners reported that female breeders, which brought the largest food loads, experienced higher levels of brood begging than breeding males and helpers (Wright et al., 2010). Additional indication that the composition of breeding groups might affect begging behaviour was found in sociable weavers, *Philetairus socius*, where nestlings raised with more helpers were seen to beg less (Paquet, Covas, et al., 2015). Whether this effect was due to a larger number of individuals providing food or to lower begging rates towards helpers than towards breeders is unknown. Offspring could be saving energy by begging less towards individuals that bring less food or that respond less to this stimulus (Bell, 2008a; Kölliker et al., 1998; Paquet et al., 2018). Detailed studies on how begging behaviour varies in relation to male and female breeders, and among different types of helpers, are needed for a better understanding of the coevolution between offspring begging and adaptive food provisioning strategies in cooperative breeders.

Here, we investigated (1) how intervisit intervals of breeders and helpers, distinguished by sex and relatedness to the offspring, varied with brood begging. Furthermore, we quantified (2) the levels of acoustic begging experienced by the breeders and each class of helpers. Importantly, in both (1) and (2), we specifically tested for statistically supported differences between distinct classes of provisioners. Our study model is the sociable weaver, a cooperatively breeding passerine. In this species, there is no evidence of extrapair paternity (Paquet, Doutrelant, et al., 2015) and helpers are typically the offspring of one or both breeders (Covas et al., 2006). Other second-order relatives and distantly related/unrelated birds also provide help (Covas et al. 2006). Moreover, helpers are of both sexes, but males and females have different strategies to obtain a breeding position, as most females disperse to breed, whereas males typically remain in their natal colonies (Covas et al., 2006; Doutrelant et al., 2004; van Dijk et al., 2015). These life history traits lead to different predictions on begging–feeding interactions according to sex and kinship.

We expected (1a) breeders and male helpers to reduce the time between feeding events with increasing begging levels, and more strongly than female helpers which disperse to breed. (1b) For intervisit intervals of helpers distinguished by their relatedness levels to the brood, we had different but nonmutually exclusive predictions according to the types of benefits that helpers can gain. If helpers benefit from responding to brood demand mostly through indirect fitness benefits, we expected full siblings (r=0.5) to shorten intervisit intervals when brood demand is higher, and more so than second-order relatives (r=0.25), and that unrelated individuals (or distant relatives, r≤0.125) would not respond. If individuals are feeding chicks exclusively as a ‘payment’ to be part of the group (Zöttl et al., 2013), we expected helpers to feed at rates that are independent of brood begging, as these direct benefits do not depend on maximizing offspring survival. However, if less related individuals provide care because they benefit as well from increasing offspring chances of survival (e.g. increasing group size; group augmentation hypothesis; Kokko et al. 2001), all relatedness classes of helpers are expected to adjust feeding efforts to begging intensity.

Accordingly, nestlings’ begging was expected to be higher towards the individuals that respond the most to this stimulus. Since nest attendants produce calls before entering the nests, sociable weaver’s chicks could use this information to distinguish their different care provisioners (Beer, 1971; Jacot et al., 2010; McDonald & Wright, 2011). Therefore, in line with our predictions on feeding adjustments, (2a) offspring should beg more towards breeders and male helpers than female helpers and (2b) when comparing differently related helpers, lower levels of begging were expected towards less related individuals.

Table 5. 1 Qualitative summary of results from studies on food provisioning adjustments to increasing food demand in cooperatively breeding species (measured as responses to begging behaviour, offspring age or offspring number)

Offspring demand measure	**Breeders responded**	**Helpers responded**	**Helpers of both sexes responded**	**Helpers of different relatedness responded**	**Species**	**Source**
Begging	**Yes**	**Yes**	**Yes**	-	Arabian babbler, *Turdoides squamiceps*	Wright, 1998
Begging	Only males	Yes	-	-	Superb fairy-wren, *Malurus cyaneus*	MacGregor & Cockburn, 2002
Begging	**Yes**	**Yes**	**Yes**	-	Meerkat, *Suricata suricatta*	English et al., 2008
Begging	Yes[1]	**Yes**	-	-	Bell miner, *Manorina melanophrys*	McDonald et al., 2009
Begging	Yes	Yes	Yes	Yes	Bell miner, *M. melanophrys*	Wright et al., 2010
Begging	Yes	Yes	**Yes**	-	Red-winged fairy-wren, *Malurus elegans*	MacLeod & Brouwer, 2018
Begging	**Yes**	**B>H**	-	-	Black-throated tit, *Aegithalos concinnus*	Li et al., 2019
Age	Yes	**B>H**	-	**Yes**	Bell miner, *M. melanophrys*	te Marvelde et al., 2009
Age	Yes	Yes	-	-	Chestnut-crowned babbler, *Pomatostomus ruficeps*	Browning et al., 2012
Age	**F>M**	**B>H**	-	-	Long-tailed tit, *Aegithalos caudatus*	MacColl & Hatchwell, 2003
Age	**F>M**	Yes	-	**Only related**[2]	Iberian magpie, *Cyanopica cooki*	Cruz et al., 2019
Number nestlings	Yes	Yes	Yes	-	Acorn woodpecker, *Melanerpes formicivorus*	Koenig & Walters, 2012
Number nestlings	**Yes**	**Yes**	-	-	Long-tailed tit, *Aegithalos caudatus*	MacColl & Hatchwell, 2003
Number nestlings	Yes	Yes	-	**Yes**	Iberian magpie, *Cyanopica cooki*	Cruz et al., 2019

Columns show whether individuals of different classes (breeders B versus helpers H) and, where available, sex (females F versus males M) and relatedness, responded to increasing food demand levels. Dashes represent untested variables. Values are in bold when differences within the class were statistically tested for and, when detected, differences are described (in the 'Helpers responded' column, values are bold if differences between breeders' and helpers' responses were tested for).

[1] Only breeding males were tested.

[2] Relatedness was not explicitly tested. Helpers were divided into 'first-option' or 'failed breeders' and relatedness was extrapolated (first-option usually related, failed breeders usually not).

Methods

Study species and site

The sociable weaver is a colonial, cooperatively breeding passerine endemic to southern Africa (Maclean, 1973a). These weavers build massive communal nests, or 'colonies', with several chambers where they breed and roost throughout the year (Maclean, 1973b). Adults feed on both seeds and arthropods (Maclean, 1973d) but offspring are mainly fed with the latter (e.g. small insect larvae, termites, spiders and grasshoppers; Maclean 1973d). Breeding seasons can last for several months (Mares et al., 2017) and sociable weavers may thus have numerous breeding attempts per season. Clutch size typically ranges between two and four eggs and females usually lay one egg per day (Covas & Du Plessis, 2005; Fortuna et al., 2021). The duration of the incubation period is around 15 days and both sexes incubate (Covas & Du Plessis, 2005; Maclean, 1973c). Nestlings normally hatch asynchronously and the subsequent nestling period lasts for 21–25 days (Covas & Du Plessis, 2005; Maclean, 1973c).

This work was conducted at Benfontein Nature Reserve in Northern Cape Province, South Africa (28°520S, 24°500E). Individuals have been captured once or twice per year at the colonies using mist nests since 1999 (Covas, 2002). Birds were ringed with a uniquely coded aluminium ring and a unique colour ring combination, allowing individual visual identification. Blood samples were collected for genetic sexing and determination of parentage relationships. In this population, most helpers are previous years' offspring of one or both breeders (Covas et al. 2006; this study) and assist with nestling feeding (Covas et al., 2008), nest building and sanitation (Ferreira, 2015). Males usually help until later in life than females, and are the most frequent helping sex (Covas et al. 2006; see below).

Data collection

We sampled 14 different colonies in two breeding seasons, 2014/2015 and 2017/2018, between September and January. Brood begging behaviour was recorded 4 and 9 days after the first nestling hatched (hereafter, day 4 and day 9, respectively), to study whether begging and/or provisioning adjustments changed throughout the nestling period (Leonard and Horn 2006; Schwabl and Lipar 2002).

Before each recording, chicks were weighed, a tie-clip microphone (Olympus ME15, frequency response = 100–12 000 Hz) was set at the nest entrance and a recorder (Olympus WS-750M) was placed outside the nest, attached to the colony structure. Calls were recorded at 44.1 kHz in uncompressed 32-bit PCM format.

To identify the birds entering the nests, and to score individual feeding intervals, a video camera (Sony Handycam HD) was placed on a tripod under the colony pointing to the entry of the target nest. Nests were recorded for 2–5 h.

Nestlings' head feathers were marked at hatching to enable individual recognition until day 9, when they were ringed with a unique numbered ring (Covas et al., 2008).

Daily maximum temperature (°C) was collected at Kimberley Airport Station, 12 km from the centre of the study site.

Data analyses

Number of begging calls

Acoustic begging levels were quantified as the number of begging calls during the first 20 s after a bird's arrival at the nest. This measure was extracted at day 4 for 22 broods in 2014/2015 and for 32 broods in 2017/2018. A 20 s duration was defined for each begging 'event' after visually assessing that acoustic begging tends to decline after this period. Begging was not quantified if another bird arrived during those 20 s, or if the provisioner spent less than 20 s inside the chamber (*N*= 362 excluded events, 17%). Begging was not quantified for nonfeeding visits (see below). The first begging event recorded for each nest was excluded from the analyses since hunger levels, and thus possibly begging behaviour, could have been influenced by the time necessary to set up the recorders. We only quantified begging when there was a sufficient signal-to-noise ratio to allow reliable counts (visually assessed; 12% of the events were not quantified because other birds or cicadas were calling too loudly or repeatedly in the background; *N*=255 from 41 recordings).

Begging calls were counted manually in 2014/2015 and with a semiautomatic method in 2017/2018. The Pearson correlation coefficient of the counted number of begging calls between two people scoring manually was 0.98 (95% confidence interval, CI=[0.92,0.99]; *N*=12 randomly chosen events from four different nests) and the correlation coefficient between manual scoring and semiautomatic scoring was 0.94 (95% CI=[0.81,0.98]; *N*=12). The manual counting method consisted of visually marking and counting each begging call on spectrograms of the recordings (sampling frequency=44.1 kHz, FFT length= 512 points, window= Hamming), using Avisoft-SASLab PRO v. 5.2.09 (Avisoft Bioacoustics, Berlin, Germany). A final sample of 688 begging events was quantified manually.

The semiautomatic counting method was performed in three steps. First, we removed background noise from the recordings, applying a high-pass filter that filtered frequencies below 2000 Hz, with a roll-off of 36 dB (see Fig. S5.1a, b) in Audacity v.2.3.2 (available at https://www.audacityteam.org/; Audacity Team (2019). Moreover, on events with high background cicada noise, we band-pass filtered the recording, excluding frequencies between ca. 5000–6000 Hz (precise range defined after visual inspection;

see Fig. S5.1c, d). Second, we cut recordings into short wave files, by only retaining sounds above a manually set amplitude threshold constant for all wave files (using a custom-made software; Maat et al. 2014). This allowed us to separate each over-threshold sound (i.e. begging or other calls) and extract its onset time from the recording's start, enabling its posterior attribution to each bird visit. Third, each begging call contained in the short wave files was automatically identified in Sound Explorer (available at https://github.com/ornith; Maat et al. 2014). Since over-threshold sounds can include adult bird calls, and because begging calls that overlap can sometimes be cut together, all automatically selected sounds were visually assessed and excluded when needed. Finally, we counted the calls relative to each begging event, crossing the timing information of the video recording and the sound files. A final sample of 845 events were analysed with the semiautomatic method, making a total sample of 1533 begging events analysed with the two methods. All begging measurements were done blindly from the identity of the provisioning bird.

At day 9, the sample of recordings for which we could extract acoustic begging information was substantially smaller than at day 4. The acoustic features of older broods' begging did not allow us to distinguish single calls (see Fig. S5.1e) and thus to count them manually or automatically. We therefore used an alternative acoustic measure that was correlated with number of begging calls, the proportion of time spent begging (see Appendix). As this measure depended on amplitude envelopes, it could only be reliably quantified for 45% of the day 9 begging events (see Appendix). Consequently, we consider any findings for older broods only preliminary, owing to high uncertainty levels for the effect sizes, but all methods and results can be found in the Appendix.

Intervisit intervals and proxy of brood hunger

Intervisit intervals were used to measure birds' feeding responses and were defined as the time (s) each bird took to come back to the nest to feed again. This measure was scored from videos, for 1380 of the 1533 events for which number of begging calls was quantified (i.e. for the last recorded visit of each bird, begging was quantified but time to return after that event is unknown). To have a proxy of broods' hunger levels, we also estimated the time (s) between two feeding events ('interval last fed'), regardless of the birds' identity. Feeding visits were distinguished from visits for other purposes (such as building or sanitation) whenever possible. For each nest, group size was calculated as the number of different birds seen feeding the nestlings during each recording. Unringed birds were also included in group size estimates (found in two nests and counted as one more bird). Intervisit intervals and begging experienced by unringed birds were not analysed.

Sex, role and relatedness category attribution

Sex was genetically determined from blood samples (Paquet, Doutrelant, et al., 2015). After group identification, we attributed breeder or helper roles to each individual. Breeding pairs were determined by a combination of genetic analyses from blood samples (Paquet, Doutrelant, et al., 2015) and field data (Silva et al. 2018; there is no evidence of extrapair paternity in this species; Covas et al. 2006; Paquet, Doutrelant, et al. 2015). Individual genotypes were used to genetically identify the parents of nestlings and nest attendants using full-likelihood parentage inference (Fortuna et al., 2021; Paquet, Doutrelant, et al., 2015). When no genetic data were available, we defined rules to determine parentage based on the birds' biology (e.g. the only birds in the group old enough to breed, etc.; for all details on parentage attribution see supporting information in Fortuna et al., 2021). All individuals seen feeding that were not the breeders were considered helpers. In nests where one of the breeders was unknown, remaining birds could still be considered helpers if they were of the same sex as the known breeder.

We further categorized helpers by their level of relatedness to the brood: 0.5 (full siblings), 0.25 (half siblings/uncles/grandparents) or 0.125 or less (cousins, half uncles or more distantly/unrelated individuals). These kinship categories were attributed based on the parentage analyses described above, by identifying the helpers' and breeders' parents using an extensive database of individual genotypes and video recordings that allowed parentage inferences. Helpers with the same parents as the current brood (full siblings) were included in the r=0.5 category and helpers with only one parent in common with the current brood (half siblings) were included in the r=0.25 category. Helpers with the same parents as one of the target nest's breeders (i.e. uncles of the brood) and helpers that were parents of one of the target nest's breeders (grandparents) were also included in the r=0.25 category. Helpers that shared only one parent with one of the target nest's breeders (half uncles) and helpers that were the offspring of siblings of one of the target nest's breeders (cousins of the chicks) were included in the r≤0.125 category. One helper with no known (close) relationship to the chicks was attributed to the r≤0.125 category after ruling out all possible relationships with r≥0.25, except being uncle from the mother's side since this type of helper has never been recorded in our population (N=474 kin relationships; A.C. Ferreira, personal communication, 7 August

2021) as a result of female breeders being mostly immigrants and helpers mostly resident birds (Doutrelant et al., 2004).

Among the sample of helpers, there were previously cross-fostered birds that were placed as eggs into a new nest under experimental conditions (Paquet, Doutrelant, et al., 2015) during previous seasons and hatched in the presence of their foster parents. Some of them were found among our data as helpers of the breeding pairs (*N*=8) and we attributed these to their social relatedness category. However, statistical analyses were also performed in a subset excluding these individuals, and estimates yield qualitatively similar results but with higher uncertainty for helper classes due to sample size reduction.

From the 54 nests sampled, 13% (seven nests) had no helpers. Cooperative groups included more male helpers than female helpers (71% males, 46 of 65 helpers). Around 59% of the helpers were attributed to the *r*=0.5 category (38 of 64 helpers with known relatedness), 37.5% to the *r*=0.25 category and only 3–5% of the helpers included in the analyses (depending on the data set) were attributed to the relatedness category of *r*≤0.125. The low sample of *r*≤0.125 helpers did not allow us to reliably compare the feeding response of these birds in relation to other bird classes, but all estimates are presented in the results.

Statistical analysis

All statistical analyses were performed in a Bayesian framework using JAGS through the 'rjags' package v.4.10 (Plummer, 2019) in R v.4.0.4 (R Core Team, 2021).

To test whether some classes of birds came back faster than others after being exposed to more begging, we built linear mixed models with intervisit intervals (log scaled) as a response variable and estimated the slope between intervisit intervals and number of begging calls for each bird class. Comparisons between classes were calculated by computing the difference between their estimated slopes (see below). To define the classes, we included the interaction between social role (breeder/helper) and sex (female/male) of each bird. For helpers only, we further tested the effect of their relatedness towards the brood (as categories: *r*=0.5, *r*=0.25 or *r*≤0.125). We expected sex to have a similar effect for all helpers independently of their relatedness, and we thus did not test for this interaction. Number of nestlings and mean brood mass were included to account for increased provisioning in larger broods and to control for nestlings' condition. To avoid excluding 26 data points (one nest) because of unknown values for mean brood mass, we estimated the missing information (with high uncertainty) within the model using brood mass as response variable following a normal distribution and the observed mean brood mass as mean prior (5.670 g) and a prior variance of 1000 (see Chapter 15 in McElreath 2020 for more details). This was done for all models that included this variable. A similar step was done for all data sets with individuals with unknown role (*N*=7) and/or unknown relatedness to the offspring (*N*=8). We estimated the missing information on individual roles (breeder versus helper) using a Bernoulli distribution and a uniform prior bounded between 0 and 1. Relatedness class was estimated with a categorical distribution and the prior probabilities of belonging to each relatedness category were defined using a Dirichlet distribution, the joint distribution of independent gamma variables divided by their sum, to keep the probabilities bounded between 0 and 1 and summing to 1 (Kéry & Schaub, 2012). Here, we used the information on whether birds were known not to be full siblings of the brood, in which case their probability of being *r*=0.5 was set to zero and the prior probability of belonging to the *r*=0.25 class was set as a uniform distribution bounded between 0 and 1 and defined as 1 minus the probability of belonging to the *r*≤0.125 class. Daily maximum temperature (°C) and time since sunrise were also included in the models to account for weather effects on food availability and birds' foraging efficiency (du Plessis et al., 2012). We additionally included group size, as individuals' feeding effort may be reduced when breeding with more helpers (i.e. 'load lightening'; Johnstone 2011; Brouwer et al. 2014; MacLeod and Brouwer 2018). However, additive care may instead be expected when the chances of nestling starvation are higher (Hatchwell 1999; but see MacLeod and Brouwer 2018) and we thus predicted load lightening to occur at lower begging levels. Therefore, we included group size in interaction with number of begging calls. To control for repeated visits of the same birds and different feeding visits to the same nest, we added bird and nest identity, as well as colony identity, as crossed random effects. We treated breeding season as a fixed effect of two levels (2014/2015 and 2017/2018; results with season as random effect were nearly identical).

Similarly, to test whether birds of different classes experienced distinct begging levels, we built linear mixed models with number of begging calls as response variable and the interaction between social role and sex as a fixed effect. As before, for helpers, we tested the effect of their relatedness category towards the brood (*r*=0.5, *r*=0.25 or *r*≤0.125). We added number of chicks as covariate, because we expected more begging calls in nests with larger broods, and mean brood mass (g) as a proxy for offspring condition. We additionally accounted for group size effects on begging, which have been previously found in this species (Paquet, Covas, et al., 2015). Colony, nest and bird identity were added as random terms.

To further infer whether begging differences in relation to different classes of birds could be explained by nonrandom visits of birds when nestlings were hungrier, we built a second begging model adding the time interval since last fed (i.e. proxy of hunger) and time since sunrise for each feeding event. In this model, to avoid excluding eight data points (from seven nests) due to unknown intervals between two feeding visits, we estimated the missing information (with high uncertainty) within the model using the observed mean (396.92 s) and a variance of 10 000 as priors. The estimates of both begging models are presented in the results.

Collinearity among predictors was assessed by calculating Spearman rank correlation coefficients (categorical variables were converted to numerical; all correlations below 0.45 except season and daily maximum temperature (r=0.63) but both were kept in the models to account for remaining seasonal variation). All numerical variables were divided by their standard deviation (scaling), and numerical explanatory variables were additionally centred by subtracting their mean (Schielzeth, 2010). Intervisit intervals were first log transformed, then scaled.

We estimated parameters using vague priors (see scripts in https://osf.io/ds8vz/ for more details). Posterior samples (3000) from three Markov chain Monte Carlo (MCMC) chains were based on 150 000 iterations after an adaptation period of 5000, burn-in of 30 000 and thinning interval of 150 for each model. To assess models' goodness of fit, we performed postpredictive checks using the χ^2 discrepancy metric (Gelman et al., 1996). Bayesian P values were between 0.484 and 0.496, showing no evidence for lack of fit (values close to 0 or 1 indicate lack of fit). Model convergence was confirmed visually and through the 'R hat' Gelman–Rubin statistic (all parameters under 1.1; Gelman and Rubin 1992). For each estimate, we present mean and 95% credible interval (95% CrI) of the posterior samples. We report effects as credible when 95% CrIs do not overlap zero. When relevant, we also present 'P (>0)', the proportion of the posterior samples that was higher than zero. Mean differences between bird classes (and 95% CrI of the differences) were calculated from the posteriors. No model simplification was performed. We computed mean marginal and conditional R^2 and their 95% CrIs, which reflect variance explained only by fixed effects and by both fixed and random effects, respectively (Gelman & Pardoe, 2006).

Ethical note

This study was conducted under research permits from the Northern Cape Department of Environment and Nature Conservation (permits FAUNA 650/2014 and FAUNA 1338/2017) and the approval of the Ethics Committee of the University of Cape Town (2014/V1/RC) and it follows the ASAB/ABS Guidelines for the use of animals in research. Any disturbance caused by the installation and removal of microphones, sound recorders and video cameras was comparable to that of routine monitoring procedures. Equipment was installed when no adult bird was at the nest by a team of two to three people to minimize time of disturbance. No nest was abandoned following installation of the recording devices. Nestlings were handled at their nest location and no chick suffered adverse effects after handling and routine blood sampling.

Adult birds were annually captured outside the breeding season. Blood samples were collected only when necessary for sex and/or genotyping purposes. While queuing to be processed, birds rested in individual bird bags placed in a quiet, ventilated and shaded area. The blood volume collected (ca. 75 ml) was well below the threshold recommended for this passerine. Birds were given some recovering time after handling and were then released in small groups. Any bird that showed signs of fatigue or injury (1% of the birds captured) was taken to an indoor aviary and released once recovered. To minimize handling times, a team of 8–12 experienced ringers were allocated to specific tasks to streamline the procedures conducted during the captures.

Results

Intervisit intervals

Individuals' intervisit intervals ranged between 28 s and over 3 h and 30 min (mean=1190 s, SD=1374 s, *N*=1371 feeding visits to 54 broods; Fig. 5.1).

Breeding males returned faster to feed after experiencing a higher number of begging calls (Table 5.2, Fig. 5.1). This represents a decrease of over 1.5 min between feeding visits for each unit increase in begging (mean=84 calls, SD=43 calls). In contrast, breeding females did not return credibly faster after experiencing more calls (Table 5.2, Fig. 5.1) and clearly differed from male breeders (estimated difference= 0.142, 95% CrI=[0.009,0.273], *P*(>0)=0.98; Table S5.1, Fig. 5.1). Among helpers, we found no evidence that males or females came back faster after experiencing a higher number of begging calls (Table 5.2, Fig. 5.1). Moreover, our results suggest that the response to begging of full-sibling male helpers (*r*=0.5) was weaker than the response of breeding males, as indicated by the very low proportion of the posterior distribution that was higher than zero, even though credible intervals overlapped zero (estimated difference=-0.185, 95% CrI=[-0.383,0.01], *P*(>0)=0.03; Table S5.1, Fig. 5.1). On the other hand, female helpers' responses did not seem to differ from those of the other classes of birds (Table S5.1). Lastly, we found no evidence that helpers more related to the brood returned faster than less related helpers after experiencing more begging (Tables 5.2, S5.1, Fig. 5.1).

Breeding males were also the class of birds with the shortest intervisit intervals on average. They returned faster than helpers of any sex or relatedness (Table S5.2, Fig. S5.2), and tended to return faster than breeding females, although this difference was not statistically credible (estimated difference=0.12, 95% CrI=[-0.026,0.262], *P*(>0)=0.95; Table S5.2, Fig. S5.2). These differences represented a mean difference of 3–7 min between breeding males and helpers, and around 1 min difference between the two breeders (see Fig. S5.2). Breeding females took less time between feeding visits than male helpers *r*=0.5 and *r*=0.25 and female helpers *r*=0.25 (Table S5.2).

Individual birds in larger cooperative groups showed on average longer intervisit intervals than individuals in smaller groups, but only at high levels of begging (Table 5.2, Fig. S5.3). Intervisit intervals were longer in 2017/2018 than in 2014/2015 (Table 5.2), and birds returned faster to the nest later in the day (Table 5.2, Fig. S5.4). Mean brood mass and number of chicks were not credibly correlated with intervisit intervals (Table 5.2). Nest identity explained on average more random variation in intervisit intervals than colony or bird identity (Table 5.2). Additionally, there was a high proportion of unexplained variation in intervisit intervals, indicated by a high residual standard deviance (Table 5.2) and a conditional R^2 of 0.19 [0.128,0.267] (marginal R^2=0.11; 95% CrI=[0.078,0.156]).

Table 5. 2 Mean estimates and 95% credible intervals (CrI) from model with intervisit intervals as response variable in relation to number of begging calls

Response	Explanatory variable	Level	Mean	95% CrI	*P*(>0)
Intervisit	(Intercept)	(Breeder female)	6.409	[6.199,6.609]	
interval	**Role*Sex**				
		Breeder male	-0.12	[-0.262,0.026]	0.05
		Helper female (*r*=0.5)	0.196	[-0.026,0.422]	0.96
		Helper male (*r*=0.5)	**0.332**	**[0.132,0.533]**	**1**
	Relatedness				
		Helper *r*=0.25	0.13	[-0.142,0.398]	0.83
		Helper *r*≤0.125	-0.099	[-0.709,0.505]	0.38
	Season				
		2017/2018	**0.394**	**[0.155,0.658]**	**1**
	Role*Sex*No. of begging calls				
		Breeder female	0	[-0.106,0.106]	0.5
		Breeder male	**-0.142**	**[-0.232,-0.056]**	**0**
		Helper female (*r*=0.5)	-0.08	[-0.263,0.11]	0.2
		Helper male (*r*=0.5)	0.043	[-0.141,0.221]	0.68
	Relatedness*No. of begging calls				
		Helper *r*=0.25	-0.073	[-0.308,0.167]	0.27
		Helper *r*≤0.125	-0.096	[-0.817,0.633]	0.39
	No. of chicks		0.005	[-0.104,0.108]	0.54
	Mean mass of chicks		0.043	[-0.065,0.157]	0.78
	Group size*No. of begging calls		**0.083**	**[0.007,0.16]**	**0.98**
	Group size		-0.053	[-0.163,0.055]	0.17
	Maximum temperature day		-0.086	[-0.196,0.025]	0.06
	Time since sunrise		**-0.177**	**[-0.249,-0.107]**	**0**
	Random terms	Standard deviance			
	Residuals	0.936		[0.902,0.973]	
	Nest ID	0.224		[0.122,0.328]	
	Bird ID	0.079		[0.002,0.199]	
	Colony ID	0.101		[0.004,0.298]	

Reference for 'Role*Sex' is Breeder female (intercept), reference for 'Relatedness' is Helper *r*=0.5 (for each sex) and reference for 'Season' is 2014/2015. The '*r*' values show helper relatedness to the brood. Credible effects are in bold. '*P* (>0)' shows the proportion of the posterior samples that was higher than zero. Marginal R^2 of 0.114 [0.078;0.156] and conditional R^2 of 0.187 [0.128; 0.267].

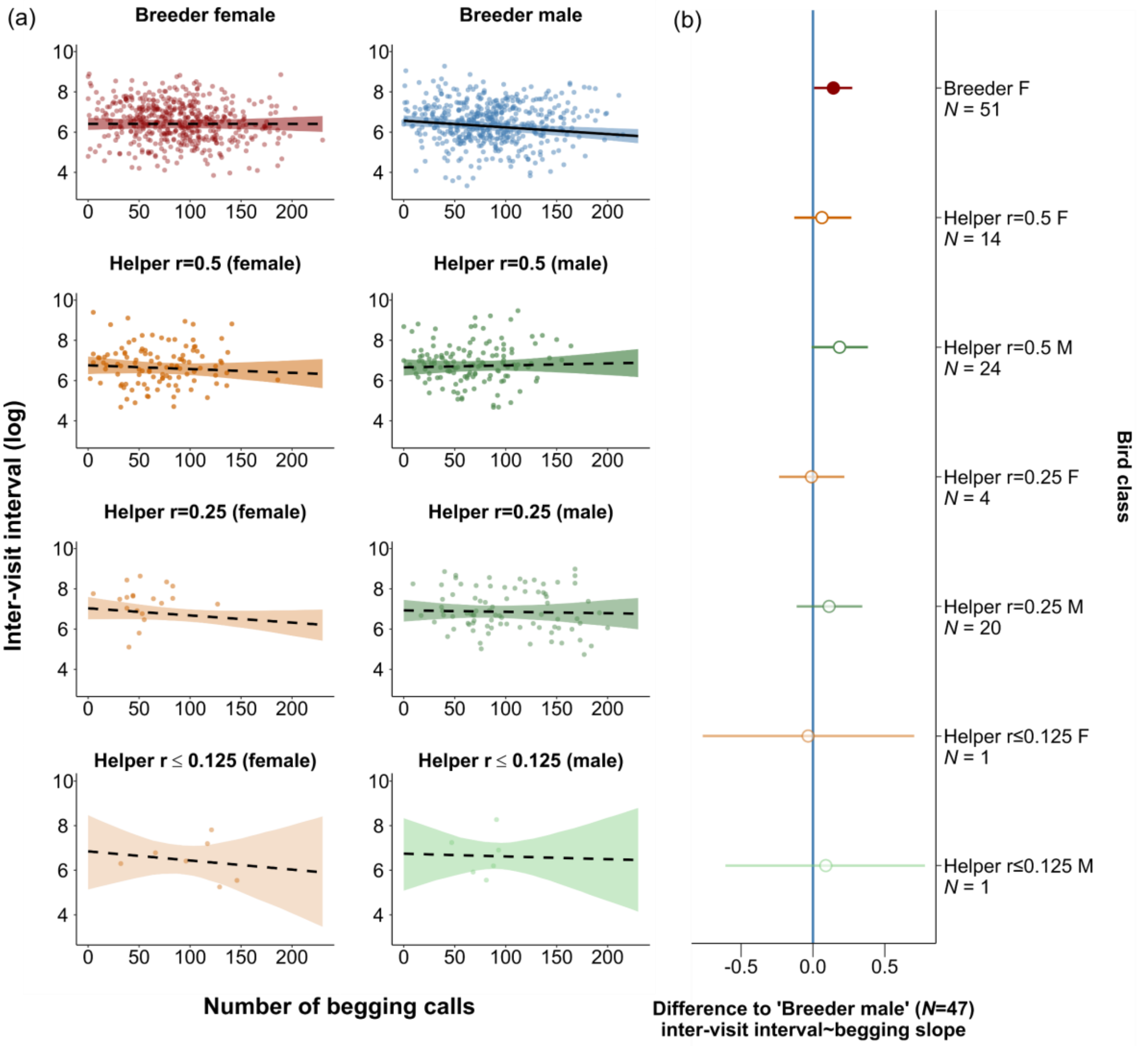

Figure 5. 1 (a) Estimated slopes of intervisit intervals (s; log scale) of birds of different classes in relation to number of begging calls.

Points show observed data and lines represent predicted slopes for each bird class. Bands show predicted credible intervals. Solid lines show intervisit intervals credibly correlated with number of begging calls. (b) Comparison between the breeding males' slope with the other bird classes. Circles represent mean differences and bars are the 95% credible intervals of the difference. Filled circles represent credible differences (see Table S5.1). Next to each class is the number of birds sampled for that category (N; total=162 birds). F: females; M: males. The 'r' values show helper relatedness to the brood.

Number of begging calls

Broods produced an average of 85 begging calls per 20 s event (SD= 43.5, range 0–230 calls, *N*=1519 begging events from 54 broods; Fig. 5.2).

Among breeders, there were no credible differences between the number of begging calls experienced by males and females (Table 5.3, Table S5.3). For helpers, there was a trend for female helpers to experience on average 6% fewer begging calls than male helpers (estimated difference= -0.125, 95% CrI=[-0.289,0.041], *P*(>0)=0.07; Table S5.3) and breeding females (estimated difference between female helpers *r*=0.5 and breeding females=0.124, 95% CrI=[-0.037,0.282], *P*(>0)=0.93; Table S5.3).

Helpers with relatedness levels equal to 0.25 (especially males) experienced the highest mean number of begging calls (mean=100.7 calls, 95% CrI=[84.3,116.9]; Fig. 5.2, Table 5.3). These individuals experienced more begging calls than helpers with the highest relatedness (Fig. 5.2, Table S5.3), representing an average of 10–15 more calls per event (12–18% more calls). They also experienced more calls than breeding females, breeding males and more related female helpers (Fig. 5.2, Table S5.3). These differences were still clear when controlling for a brood hunger proxy (‘interval last fed’) and time since sunrise in the model (model 2; see Tables 5.3, S.4), suggesting that helpers *r*=0.25 did not experience more begging calls due to nonrandom visits to the nests when broods were hungrier, or when groups were feeding less. The number of begging calls produced when female helpers *r*=0.25 visited the nests tended to be higher than in breeding males’ visits (8% more calls on average; estimated difference=-0.164, 95% CrI=[-0.366,0.039], *P*(>0)=0.05; Table S5.3), but differences with breeding females and more related male helpers were less clear (Table S5.3).

Broods with more nestlings produced more begging calls (Table 5.3, Fig. S5.5), showing an average increase to the mean number of begging calls of 20 calls for each extra chick (or 1 more call/s). There was an indication, but noncredible, that broods being fed by larger groups (with more helpers) begged less (Table 5.3), with an average decrease of four begging calls (5% fewer calls) per additional helper. Mean brood mass was not credibly correlated with the number of begging calls produced (Table 5.3). Results from the model including our proxy of brood hunger (model 2) showed that broods produced more begging calls when intervals between feeding visits were longer (Table 5.3, Fig. S5.6) and that begging increased later in the day (Table 5.3, Fig. S5.7). All estimates from model 2 were consistent with model 1 results (Table 5.3, Tables S5.3, S5.4) and both models explained a large proportion of variation in the number of begging calls produced (model 1: marginal R^2=0.201, 95% CrI=[0.097;0.315]; conditional

R^2=0.547, 95% CrI= [0.452; 0.649]; model 2: marginal R^2=0.257, 95% CrI=[0.161;0.361]; conditional R^2=0.589, 95% CrI=[0.504; 0.678]). Still, the residual random variation was high (Table 5.3) and nest identity explained on average over five times more variation in number of begging calls than the identity of the feeding bird or the breeding colony (Table 5.3).

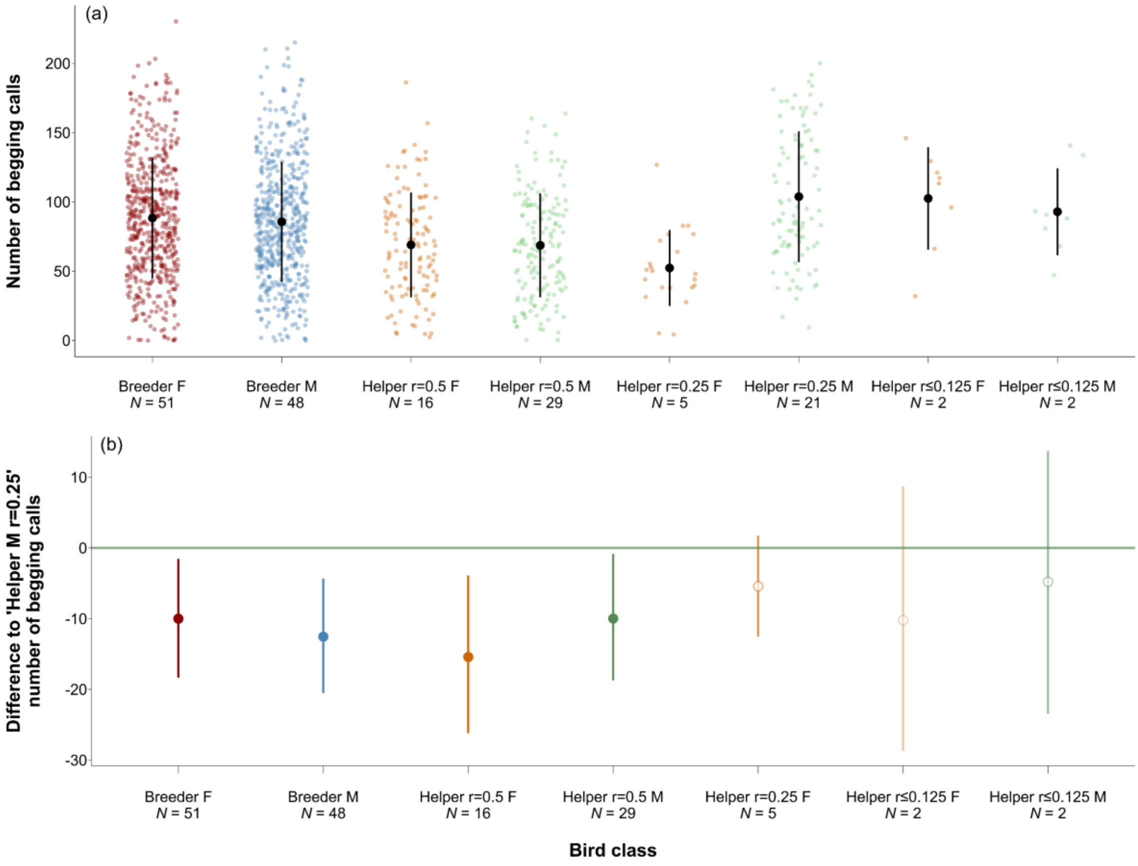

Figure 5. 2 (a) Observed data, mean and SD of number of begging calls experienced by birds of each class, at each feeding event.

Points show observations (N=1519), circles show mean number of begging calls and bars show SD. (b) Predicted estimated differences in number of begging calls experienced by different bird classes in relation to 'Helper male r=0.25' (N=21 birds; estimated from model 1; model 2 showed nearly identical results). Circles show posterior means and bars show 95% credible intervals. Filled circles show differences credibly different from zero (Table S5.3). Below each class is the number of birds sampled in each category (N; total=174 birds). The 'r' values show helper relatedness to the brood.

Table 5. 3 Mean estimates and 95% credible intervals (CrI) from models with number of begging calls as response variable

Response	Explanatory variable	Level	Mean	95% CrI	*P*(>0)
No. of begging calls (model 1)	(Intercept)	(Breeder female)	2.083	[1.738,2.428]	
	Role*Sex				
		Breeder male	-0.058	[-0.178,0.061]	0.18
		Helper female (*r*=0.5)	-0.124	[-0.282,0.037]	0.07
		Helper male (*r*=0.5)	0	[-0.15,0.152]	0.5
	Relatedness				
		Helper *r*=0.25	**0.23**	**[0.019,0.43]**	**0.99**
		Helper *r*≤0.125	0.119	[-0.274,0.53]	0.72
	Season				
		2017/2018	-0.148	[-0.623,0.342]	0.26
	No. of chicks		**0.301**	**[0.114,0.492]**	**1**
	Mean mass of chicks		-0.09	[-0.279,0.099]	0.17
	Group size		-0.174	[-0.364,0.02]	0.04
	Maximum temperature day		0.166	[-0.067,0.387]	0.93
	Random terms	Standard deviance			
	Residuals	0.728		[0.702,0.756]	
	Nest ID	0.61		[0.489,0.767]	
	Bird ID	0.056		[0.002,0.137]	
	Colony ID	0.14		[0.006,0.39]	
No. of begging calls (model 2)	(Intercept)	(Breeder female)	2.13	[1.772,2.47]	
	Role*Sex				
		Breeder male	-0.068	[-0.183,0.049]	0.12
		Helper female (*r*=0.5)	-0.111	[-0.272,0.05]	0.08
		Helper male (*r*=0.5)	0.006	[-0.139,0.155]	0.53
	Relatedness				
		Helper *r*=0.25	**0.214**	**[0.006,0.409]**	**0.98**
		Helper *r*≤0.125	0.035	[-0.353,0.443]	0.56
	Season				
		2017/2018	-0.197	[-0.664,0.292]	0.21
	No. of chicks		**0.295**	**[0.107,0.479]**	**1**
	Mean mass of chicks		-0.128	[-0.323,0.062]	0.1
	Group size		-0.137	[-0.325,0.038]	0.07
	Maximum temperature day		0.165	[-0.056,0.387]	0.93
	Interval last fed		**0.096**	**[0.059,0.134]**	**1**
	Time since sunrise		**0.264**	**[0.212,0.317]**	**1**
	Random terms	Standard deviance			
	Residuals	0.701		[0.675,0.727]	
	Nest ID	0.589		[0.468,0.74]	
	Bird ID	0.065		[0.003,0.148]	
	Colony ID	0.179		[0.011,0.451]	

Reference for 'Role*Sex' is Breeder female (intercept), reference for 'Relatedness' is Helper *r*=0.5 (for each sex) and reference for 'Season' is 2014/2015. The '*r*' values show helper relatedness to the nestlings. Models are similar but second model includes hunger proxies. Credible effects are in bold. '*P* (>0)' shows the proportion of the posterior samples that was higher than zero. Model 1: marginal R^2 = 0.201 [0.097;0.315] and conditional R^2 of 0.547 [0.452; 0.649]. Model 2: marginal R^2 = 0.257 [0.161;0.361] and conditional R^2 of 0.589 [0.504; 0.678].

Discussion

In this study, we investigated how intervisit intervals of breeders and helpers, distinguished by their sex and relatedness, vary in relation to acoustic begging. Our aim was to test whether individuals of different classes showed different feeding responses and experienced distinct levels of begging, to better understand the rules of nestling feeding behaviour in cooperatively breeding systems. The number of begging calls produced by the broods correlated with our proxy of hunger, confirming that acoustic begging is likely to signal hunger levels in this species. While breeding males returned faster to the nest to feed when experiencing more begging calls, there was no evidence that breeding females or helpers (independently of their sex or relatedness) adjusted food provisioning to brood begging levels. Specifically, we found statistically supported differences between the response to begging of male breeders and female breeders, and an indication that the feeding response of full-sibling male helpers differed as well from breeding males. Surprisingly, second-order relatives (half siblings, uncles and grandparents) experienced more begging calls than breeders and more related helpers, while there were no credible differences in the begging experienced by the two latter classes.

Sex differences in parental responses

Breeding males returned faster with food after experiencing more begging calls while breeding females showed, on average, no response to begging. Sex-specific responses to brood demand have been described in several biparental care systems (reviewed in Müller et al. 2007) and in a few cooperative systems, but the direction of these differences seems to vary across studies (Table 5.1; see Müller et al. 2007). Since sociable weavers are both socially and genetically monogamous (Covas et al. 2006), both breeders should have similar fitness returns from brood survival. Thus, a plausible explanation for a male-only response in this species is that female breeders are responding to begging behaviour through other mechanisms that we did not identify here or are responding to other needs of the brood.

First, when nestlings are young (i.e. at day 4 chicks can be between 1 and 4 days old), breeding females could respond to the need of brooding the nestlings, which could thus weaken the correlation between begging and their feeding response. Indeed, in the two cooperative systems where differences between breeders were found (Table 5.1; MacColl and Hatchwell 2003; Cruz et al. 2019), females increased feeding responses more strongly than males as nestlings aged, probably because of the decreased need to brood the chicks. However, our data do not support this explanation, as we looked at the time spent inside the nest and found no difference according to breeders' sex (see Fig. S5.8, Table S5.5; see also Maclean 1973d). Second, females could be adjusting the quality of prey brought to the nest in response to begging (Browning et al., 2012), given that breeding females have been observed to bring larger prey than other birds in this population (Ferreira, 2015). Yet, nestlings 4 days old or younger are not able to consume large prey and thus little prey size variation is expected at this age. Female breeders could still be responding to nestling begging by bringing small prey with higher nutritional quality or by feeding the hungriest chick (Kölliker et al., 1998). Alternatively, although not responding specifically to begging, mothers could still be adjusting provisioning behaviour by paying more attention to cues of long-term need, such as gape coloration or offspring size (Kilner, 2002). Responding to different signals of need could allow breeders to increase the survival chances of more young, by promoting a more balanced food distribution (Kölliker et al., 1998; McRae et al., 1993), which could otherwise be monopolized by the chick that begs more or the heaviest chick (especially when offspring are born asynchronously, as in sociable weavers). Future studies in this system should focus on begging–feeding interactions within broods, to detect which nestling is being fed and better understand whether female breeders are responding to other cues of need or condition.

On the other hand, discrepancies in parental responses are often attributed to trade-offs between parental care and other sex-specific reproductive behaviours (Siefferman and Hill 2008). The lack of evidence for female breeders' adjustments in sociable weavers may indicate that mothers cannot adjust their feeding responses, possibly because they are already feeding close to their maximum, due, for instance, to recent energetic costs with egg laying (Monaghan & Nager, 1997; Visser & Lessells, 2001). These costs may be exacerbated in this species, since female breeders often produce multiple clutches per season, from which 60–70% normally fail (Covas et al., 2008; Fortuna et al., 2021). Breeding females are thus expected to spend considerable amounts of resources in egg laying every season, which could explain why they respond less to begging than males.

Furthermore, since begging behaviour at young ages can be partially regulated by hormones of maternal origin that are deposited in the eggs, mothers could also use this as a mechanism to shift food provisioning efforts towards their partner (Moreno-Rueda, 2007; Paquet & Smiseth, 2016; Smiseth et al., 2011), and therefore not respond themselves. There is evidence that in sociable weavers mothers without helpers produce eggs with a higher concentration of androgens (Paquet et al., 2013). Additionally, we found some indication that offspring with fewer helpers beg more, and a previous cross-fostering experiment on the same system suggests that this pattern is partly mediated by prenatal effects (Paquet, Covas, et al., 2015). Thus, it is possible that mothers influence offspring begging through strategically varying egg hormonal levels according to their number of helpers (Moreno-Rueda, 2007), which, together with our result that only breeding males respond to begging, further suggests that female breeders may be manipulating their partners to feed more when the pair has less help. This hypothesis could be tested by manipulating females' prenatal environmental conditions (e.g. modifying the size of their groups) and measuring behavioural and fitness consequences for the parents and their offspring (Paquet & Smiseth, 2016).

No evidence of response from helpers

In contrast to all the previous studies that investigated provisioners' responses to brood demand in cooperative breeders (Table 5.1), we found no evidence that helpers, of any sex or relatedness, adjusted feeding behaviour to begging levels in sociable weavers. We predicted that female helpers would respond less than breeders and male helpers, as they should not benefit as much from maximizing brood survival and subsequent group augmentation (Kokko et al., 2001), since they disperse to other colonies to breed (Doutrelant et al., 2004). Our results showed instead that neither male nor female helpers seem to adjust feeding intervals to brood begging. This suggests that helping benefits may not depend on how helpers respond to brood demand, and thus on increasing the chances of offspring survival, or that helpers, like breeding females, are under energetic constraints that do not allow them to increase their feeding efforts. The difference between breeding males and full-sibling male helpers is especially interesting, since these individuals share comparable levels of kinship to the brood and are of the same sex. Contrary to expectations, only breeding males seem to respond to begging, and our comparison tests suggested low similarity between their response and that of the full-sibling male helpers. This finding reinforces the idea that, besides sex and genetic relationships, differences in life history stages may regulate feeding rules by affecting the costs of responding to brood demand. Full-sibling helpers may incur higher energetic costs because they are not as dominant as breeders, which restricts their access to food and increases their chances of engaging in aggressive interactions (Rat et al., 2015).

Increasing feeding efforts may also be costlier for these helpers due to poorer foraging skills, as these are typically younger individuals than breeders (Covas et al. 2006).

We also expected the association between feeding effort and begging to be stronger for helpers more closely related to the brood, since closer-relatives have been predicted to gain the highest indirect fitness benefits from brood survival (Emlen and Wrege 1988; Komdeur 1994; Nam et al. 2010; but see Kay et al. 2020). In contrast, sociable weaver helpers' feeding rules did not appear to depend on offspring begging, and no differences were found according to their genetic relationship to the brood. Similarly, a previous study conducted in bell miners found no difference between relatedness classes, although both related and unrelated helpers adjusted provisioning effort to increasing brood needs (McDonald et al., 2009; te Marvelde et al., 2009). In spite of the major role of inclusive fitness in the evolution of cooperative care in family-based systems like sociable weavers (Hamilton, 1964; Kay et al., 2020), our results indicate that indirect benefits from helping relatives may not be maximized via adjusting feeding effort to begging levels.

Finally, note that helpers, as well as breeding females, may still adjust feeding intervals to begging once nestlings are older. At later stages, helpers may learn how to respond to begging stimuli (especially the younger, less experienced, individuals) or start increasing their feeding effort because older broods have a higher reproductive value. Even though our analyses from older broods' begging (day 9) showed no evidence for feeding adjustments from breeders or any class of helpers (see Appendix and Table S5.6), we consider these findings only preliminary as we used a substantially smaller sample and a different begging measure. Further information is necessary to understand how consistent feeding responses to begging are across the nestling dependence period.

Half siblings experience more begging calls

We expected nestlings to adjust begging levels according to the responsiveness of nest attendants to this signal. Sociable weavers produce calls when entering the nest, which could allow chicks to individually identify food provisioners (Beer, 1971; Jacot et al., 2010; McDonald & Wright, 2011). Our results showed that breeding males returned faster to feed after experiencing more begging, but these were not the individuals experiencing the highest mean number of begging calls per visit. Contrary to our predictions, *r*=0.25 helpers (especially males) experienced higher begging levels than breeders and more closely related helpers. This group of helpers mostly included half siblings of the brood (79%; but also, uncles, 17%, and grandparents, 4%), which were estimated to experience an average of 101 begging calls per 20 s event, around 10–15 more begging calls than full-sibling helpers. To our knowledge, this is the first report of begging intensity differences according to helper relatedness in birds. A previous study on banded mongoose, *Mungos mungo*, found that pups begged less towards helpers that were less responsive to begging (Bell, 2008b). Offspring have also been found to beg more towards female breeders, both in biparental care systems when mothers seem to be a more reliable food source (Kölliker et al., 1998; Paquet et al., 2018; Roulin & Bersier, 2007), and in a cooperative system (Wright et al., 2010), probably because mothers are more often present when offspring are hungry. Here, we found no evidence that half siblings are responsive to begging levels, or that they provide food more often. Therefore, it is unlikely that nestlings are begging preferentially towards second-order helpers, and we propose two other explanations for the high begging levels they experienced. First, these helpers could have been visiting the nests more often when offspring are hungrier. However, when we included a proxy of brood hunger and time since sunrise in the models, we still detected the same effect of helper relatedness on begging levels, suggesting that these helpers do not specifically visit the broods when their levels of hunger are the highest or when feeding activity is generally lower.

Alternatively, the food provisioning behaviour of second-order relatives may differ from the other group members. For example, they could elicit more begging by bringing smaller prey or taking longer to deliver it to the brood (Doutrelant & Covas, 2007). Moreover, this class of helpers could exhibit more false-feeds by consuming the food they bring to the nest (Boland et al., 1997; McDonald et al., 2007), which would explain the estimated number of extra begging calls experienced due to no nestling being fed. This finding raises interesting questions about the quality and purpose of feeding visits of different helpers in this cooperatively breeding system, which could be investigated in future studies by recording feeding behaviour from inside the nest cavities.

Conclusion

We observed clear differences in how breeding males and females adjust provisioning effort to offspring demand. Furthermore, we found no evidence of helpers' responses to increasing begging levels. Relatedness did not seem to explain helpers' feeding adjustments, indicating that indirect fitness benefits may not play a role in how helpers regulate their feeding contributions. Interestingly, breeding females and full-sibling male helpers, which are among the classes of individuals that should benefit the most from maximizing brood survival, did not appear to match feeding responses to begging. This suggests that the costs of increasing feeding effort are distinct for the different members of the group, and that sexual (i.e. reproductive) and life history stage constraints may regulate feeding strategies in this system. Experimental manipulations of acoustic begging levels, and further tests of other phenotypic cues that may signal hunger, such as visual signals, would be necessary to confirm causality and assess the nature of these differences. Moreover, we encourage further investigations on the begging–feeding interplay in cooperative breeders, to understand whether in most species all individuals respond to increases in brood demand, or whether different responses to begging should be expected when individuals vary in sex, relatedness and other life history-related traits.

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Data Availability

Analyses and plots in this manuscript can be fully reproduced using the code and data provided in https://osf.io/ds8vz/.

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Appendix

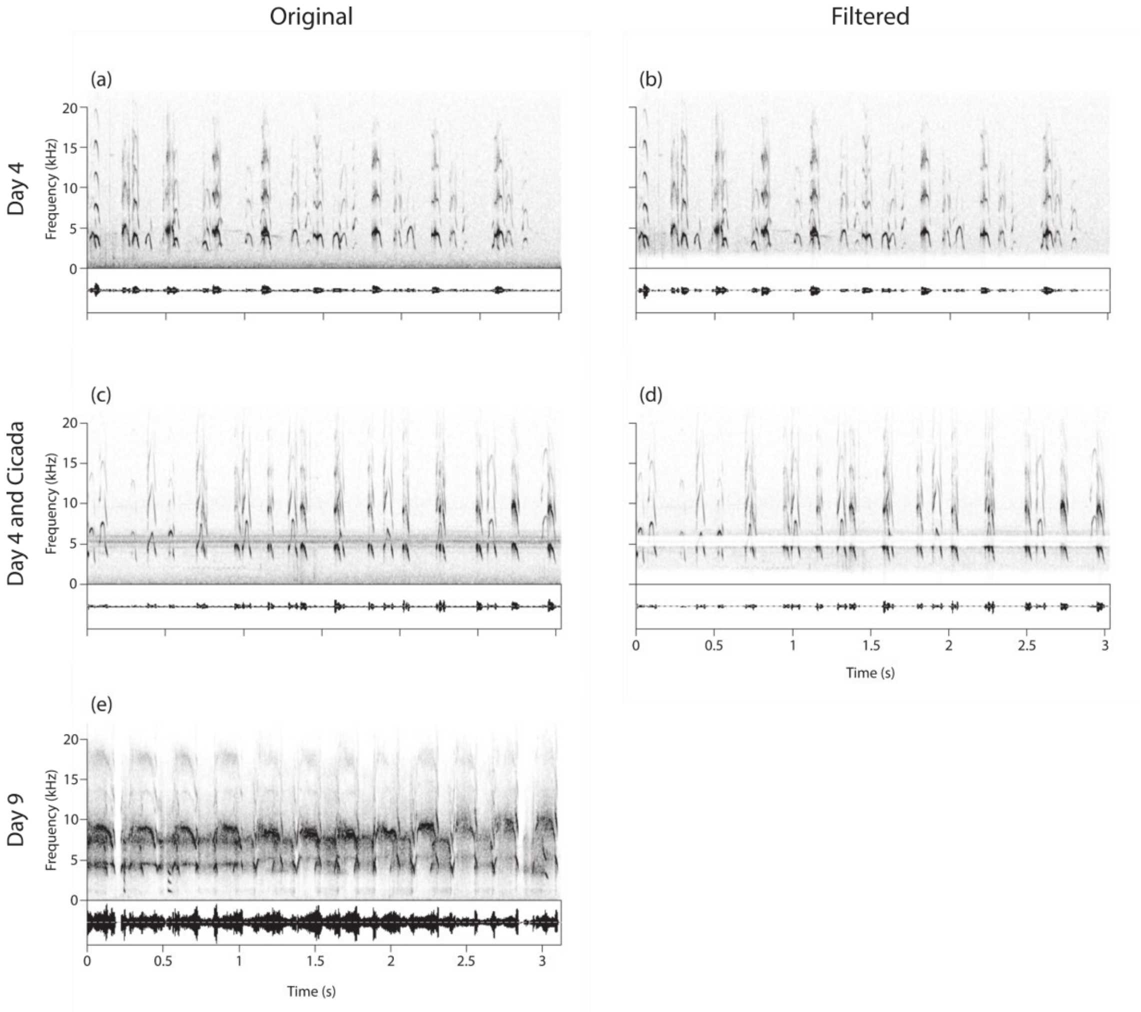

Figure S5. 1 Spectrograms illustrating raw data and the first steps of noise removal (see main text). (a) Typical begging at day 4: it is possible to distinguish each individual call even when they overlap. (b) Same recording as (a) after 2 kHz high-pass filter (36 dB roll-off) to decrease background noise level. (c) Typical begging at day 4 with cicada(s) calling in the background. Cicadas' calls have a stereotyped fixed frequency that can be erased using (d) a band pass excluding frequencies between ca. 5 and 6 kHz, improving substantially the signal-to-noise ratio. (e) Typical begging at day 9: nestlings' vocalizations develop into noisy calls not visually distinguishable from each other. Spectrograms were generated with the 'soundgen' R package (Anikin, 2019), using the original audio files with sampling rate of 44.1 kHz, window type Gaussian, length of (fast Fourier transforms) FFT windows 50 ms, and 70% overlap between successive FFT frames. Oscillograms below each spectrogram represent the non-normalized amplitude envelopes.

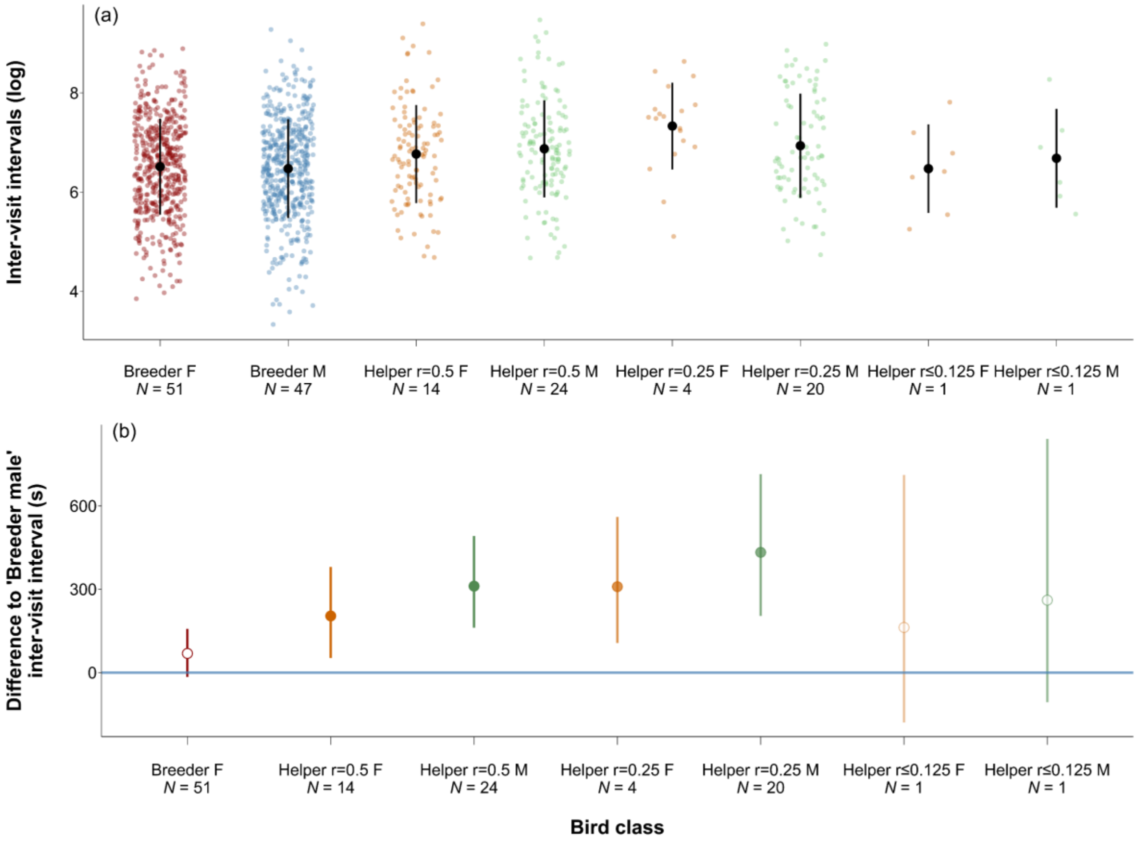

Figure S5. 2 (a) Observed data, mean and SD of intervisit intervals (s; log) of birds of distinct classes. Points show observations (N=1371), filled circles show mean and bars show SD (b) Estimated differences in intervisit intervals (s) of different bird classes in relation to 'Breeder male' (N=47). Below each class is the number of birds sampled in each category (total=162 birds). Circles show posterior means and bars show 95% credible intervals. Filled circles show differences credibly different from zero (Table S5.2). F: females; M: males. The 'r' values show helper class' relatedness to the brood.

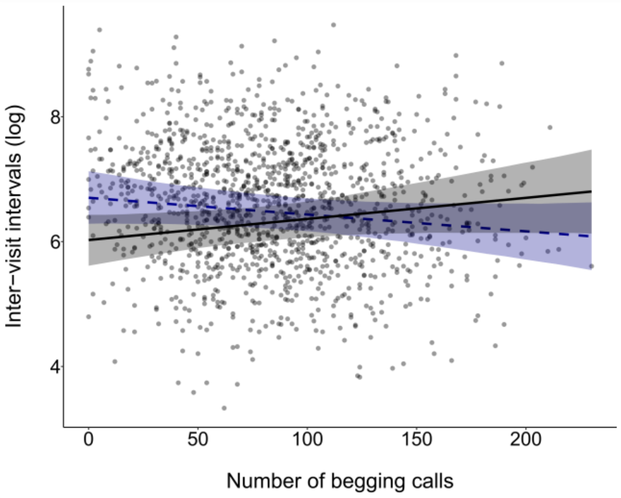

Figure S5. 3 Effect of the interaction between number of begging calls and group size on intervisit intervals (s; log). The solid line represents predicted values for pairs with four helpers (above average) and the dashed line represents predicted values for pairs without helpers (below average). Bands show the predicted 95% credible intervals. Breeder females were used as reference level.

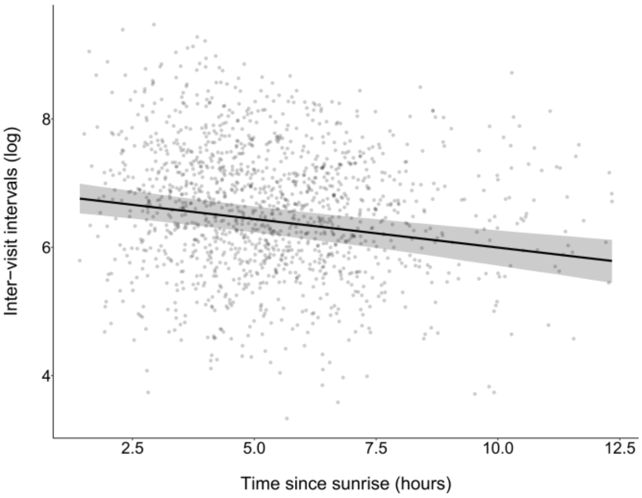

Figure S5. 4 Effect of time since sunrise (h) on intervisit intervals (s; log). Points show observed data and the line represents the predicted slope. Bands show the predicted 95% credible intervals.

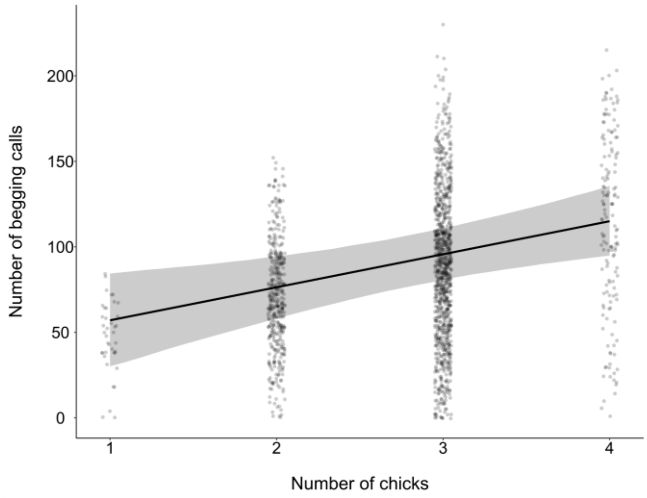

Figure S5. 5 Effect of number of chicks on number of begging calls produced over a 20 s event. Points show observed data and the line represents the predicted slope from model 1. Bands show the predicted 95% credible intervals.

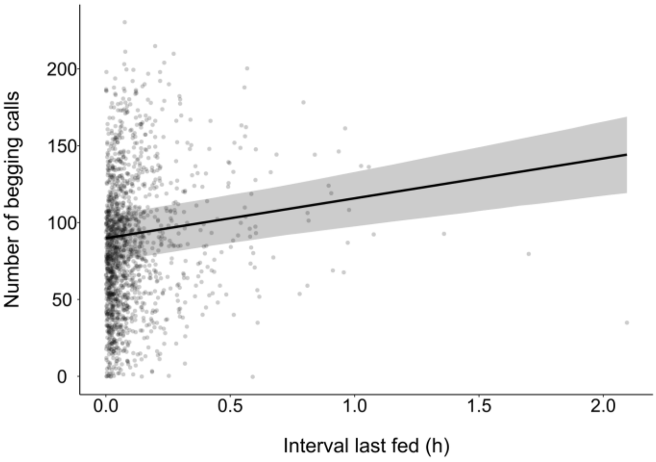

Figure S5. 6 Effect of interval since last time fed (h; i.e. proxy of hunger) on the number of begging calls produced over a 20 s event. Points show observed data and the line represents the predicted slope from model 2. Bands show the predicted 95% credible intervals.

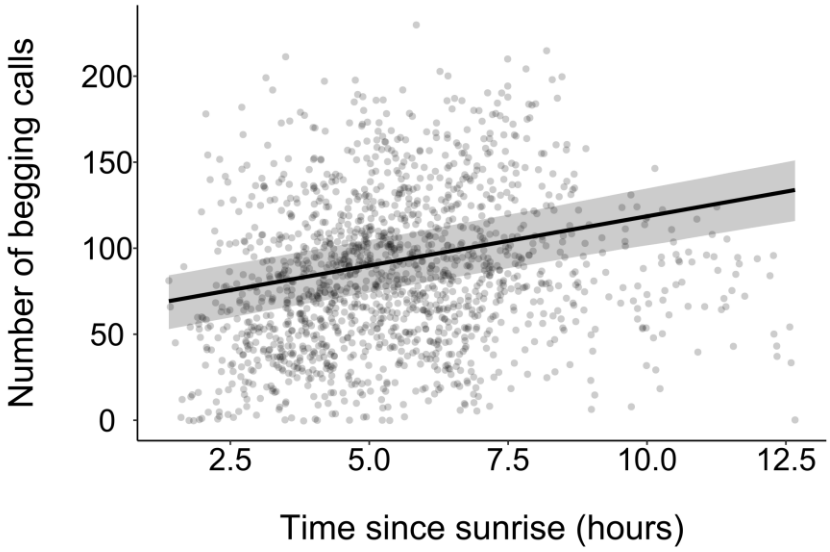

Figure S5. 7 Effect of time since sunrise (h) on the number of begging calls produced over a 20 s event. Points show observed data and the line represents the predicted slope from model 2. Bands show the predicted 95% credible intervals.

Table S5. 1 Comparison of intervisit intervals of different bird classes in relation to number of begging calls

	Breeder female	Breeder male	Helper female *r*=0.5	Helper male *r*=0.5	Helper female *r*=0.25	Helper male *r*=0.25	Helper female *r*≤0.125
Breeder male	**0.142** **[0.009,0.273]** ***P*=0.98**						
Helper female *r*=0.5	0.08 [-0.127,0.286] *P*=0.78	-0.062 [-0.267,0.13] *P*=0.28					
Helper male *r*=0.5	-0.043 [-0.242,0.163] *P*=0.33	-0.185 [-0.383,0.01] *P*=0.03	-0.123 [-0.339,0.094] *P*=0.13				
Helper female *r*=0.25	0.153 [-0.087,0.385] *P*=0.9	0.01 [-0.219,0.235] *P*=0.54	0.073 [-0.167,0.308] *P*=0.73	0.196 [-0.132,0.51] *P*=0.89			
Helper male *r*=0.25	0.03 [-0.213,0.263] *P*=0.6	-0.112 [-0.343,0.113] *P*=0.17	-0.05 [-0.375,0.273] *P*=0.38	0.073 [-0.167,0.308] *P*=0.73	-0.123 [-0.339,0.094] *P*=0.13		
Helper female *r*≤0.125	0.176 [-0.572,0.918] *P*=0.68	0.033 [-0.705,0.767] *P*=0.54	0.096 [-0.633,0.817] *P*=0.61	0.219 [-0.568,0.966] *P*=0.71	0.023 [-0.716,0.743] *P*=0.53	0.146 [-0.668,0.922] *P*=0.64	
Helper male *r*≤0.125	0.053 [-0.664,0.766] *P*=0.57	-0.089 [-0.779,0.609] *P*=0.41	-0.027 [-0.744,0.719] *P*=0.48	0.096 [-0.633,0.817] *P*=0.61	-0.1 [-0.82,0.622] *P*=0.4	0.023 [-0.716,0.743] *P*=0.53	-0.123 [-0.339,0.094] *P*=0.13

For each comparison, we estimated mean difference, 95% credible intervals and *P* (proportion of the posterior samples that was higher than zero). Differences were calculated by subtracting the posteriors of classes on top of the matrix by those of classes on the left (e.g. top left= Breeder female – Breeder male). Credible differences are in bold.

Table S5. 2 Comparison of mean intervisit intervals of different bird classes

	Breeder female	Breeder male	Helper female r=0.5	Helper male r=0.5	Helper female r=0.25	Helper male r=0.25	Helper female r≤0.125
Breeder male	0.12 [-0.026,0.262] *P*=0.95						
Helper female r=0.5	-0.196 [-0.422,0.026] *P*=0.04	**-0.315** **[-0.537,-0.091]** ***P*=0**					
Helper male r=0.5	**-0.332** **[-0.533,-0.132]** ***P*=0**	**-0.452** **[-0.643,-0.255]** ***P*=0**	-0.136 [-0.361,0.098] *P*=0.13				
Helper female r=0.25	**-0.326** **[-0.605,-0.045]** ***P*=0.01**	**-0.446** **[-0.72,-0.18]** ***P*=0**	-0.13 [-0.398,0.142] *P*=0.17	0.006 [-0.34,0.361] *P*=0.52			
Helper male r=0.25	**-0.462** **[-0.737,-0.184]** ***P*=0**	**-0.582** **[-0.842,-0.311]** ***P*=0**	-0.266 [-0.628,0.104] *P*=0.08	-0.13 [-0.398,0.142] *P*=0.17	-0.136 [-0.361,0.098] *P*=0.13		
Helper female r≤0.125	-0.097 [-0.718,0.523] *P*=0.38	-0.216 [-0.835,0.406] *P*=0.24	0.099 [-0.505,0.709] *P*=0.62	0.235 [-0.448,0.917] *P*=0.75	0.229 [-0.391,0.848] *P*=0.76	0.365 [-0.322,1.051] *P*=0.84	
Helper male r≤0.125	-0.233 [-0.813,0.338] *P*=0.21	-0.352 [-0.938,0.213] *P*=0.12	-0.037 [-0.659,0.588] *P*=0.45	0.099 [-0.505,0.709] *P*=0.62	0.093 [-0.521,0.722] *P*=0.6	0.229 [-0.391,0.848] *P*=0.76	-0.136 [-0.361,0.098] *P*=0.13

For each comparison, we estimated mean difference, 95% credible intervals and *P* (proportion of the posterior samples that was higher than zero). Differences were calculated by subtracting the estimates of class on top of the matrix by those of classes on the left (e.g. Breeder female – Breeder male). Credible differences are in bold.

Table S5. 3 Comparison of number of begging calls experienced by different bird classes (estimated from model 1)

	Breeder female	Breeder male	Helper female *r*=0.5	Helper male *r*=0.5	Helper female *r*=0.25	Helper male *r*=0.25	Helper female *r*≤0.125
Breeder male	0.058 [-0.061,0.178] *P*=0.82						
Helper female *r*=0.5	0.124 [-0.037,0.282] *P*=0.93	0.066 [-0.087,0.219] *P*=0.8					
Helper male *r*=0.5	0 [-0.152,0.15] *P*=0.5	-0.059 [-0.197,0.086] *P*=0.22	-0.125 [-0.288,0.041] *P*=0.07				
Helper female *r*=0.25	-0.105 [-0.321,0.105] *P*=0.17	-0.164 [-0.366,0.039] *P*=0.05	**-0.23** **[-0.43,-0.019]** ***P*=0.01**	-0.105 [-0.373,0.163] *P*=0.21			
Helper male *r*=0.25	**-0.23** **[-0.421,-0.036]** ***P*=0.01**	**-0.288** **[-0.471,-0.1]** ***P*=0**	**-0.354** **[-0.602,-0.089]** ***P*=0**	**-0.23** **[-0.43,-0.019]** ***P*=0.01**	-0.125 [-0.288,0.041] *P*=0.07		
Helper female *r*≤0.125	0.005 [-0.393,0.403] *P*=0.51	-0.053 [-0.448,0.337] *P*=0.39	-0.119 [-0.53,0.274] *P*=0.28	0.005 [-0.417,0.416] *P*=0.51	0.11 [-0.315,0.539] *P*=0.7	0.235 [-0.2,0.659] *P*=0.86	
Helper male *r*≤0.125	-0.12 [-0.539,0.296] *P*=0.28	-0.178 [-0.598,0.243] *P*=0.2	-0.244 [-0.703,0.226] *P*=0.14	-0.119 [-0.53,0.274] *P*=0.28	-0.015 [-0.498,0.463] *P*=0.48	0.11 [-0.315,0.539] *P*=0.7	-0.125 [-0.288,0.041] *P*=0.07

For each comparison, we estimated mean difference, 95% credible intervals and *P* (proportion of the posterior samples that was higher than zero). Differences were calculated by subtracting the estimates of classes on top of the matrix by the estimates of classes on the left (e.g. Breeder female – Breeder male). Credible differences are in bold.

Table S5. 4 Comparison of number of begging calls experienced by different bird classes (estimated from model 2)

	Breeder female	Breeder male	Helper female *r*=0.5	Helper male *r*=0.5	Helper female *r*=0.25	Helper male *r*=0.25	Helper female *r*≤0.125
Breeder male	0.067 [-0.051,0.186] *P*=0.86						
Helper female *r*=0.5	0.109 [-0.05,0.262] *P*=0.92	0.042 [-0.106,0.191] *P*=0.7					
Helper male *r*=0.5	-0.006 [-0.151,0.137] *P*=0.47	-0.073 [-0.216,0.069] *P*=0.16	-0.115 [-0.274,0.037] *P*=0.08				
Helper female *r*=0.25	-0.105 [-0.314,0.104] *P*=0.17	-0.172 [-0.361,0.022] *P*=0.04	**-0.214 [-0.406,-0.024] *P*=0.01**	-0.099 [-0.356,0.154] *P*=0.22			
Helper male *r*=0.25	**-0.22 [-0.414,-0.023] *P*=0.01**	**-0.287 [-0.473,-0.104] *P*=0**	**-0.329 [-0.577,-0.089] *P*=0**	**-0.214 [-0.406,-0.024] *P*=0.01**	-0.115 [-0.274,0.037] *P*=0.08		
Helper female *r*≤0.125	0.056 [-0.323,0.446] *P*=0.61	-0.011 [-0.393,0.389] *P*=0.47	-0.053 [-0.449,0.352] *P*=0.4	0.063 [-0.337,0.475] *P*=0.61	0.161 [-0.278,0.59] *P*=0.77	0.277 [-0.145,0.703] *P*=0.9	
Helper male *r*≤0.125	-0.059 [-0.461,0.351] *P*=0.39	-0.126 [-0.542,0.285] *P*=0.28	-0.168 [-0.607,0.292] *P*=0.24	-0.053 [-0.449,0.352] *P*=0.4	0.046 [-0.441,0.523] *P*=0.57	0.161 [-0.278,0.59] *P*=0.77	-0.115 [-0.274,0.037] *P*=0.08

For each comparison, we estimated mean difference, 95% credible intervals and *P* (proportion of the posterior samples that was higher than zero). Differences were calculated by subtracting the estimates of classes on top of the matrix by the estimates of classes on the left (e.g. Breeder female – Breeder male). Credible differences are in bold.

Time spent brooding

To test whether differences in male and female breeders' intervisit intervals could be due to females responding instead to the need of brooding the nestlings, we fitted a linear mixed model using the 'lme4' R package (Bates et al., 2014). Time inside the nest was fitted as response variable (log) assuming a normal distribution and sex (female/male) was included as a predictor. Only breeders were included in the data set. We also added bird and nest identity as crossed random effects.

Table S5. 5 Estimates from a linear mixed model on the differences in time spent inside the nest between breeding females and breeding males (*N*= 950)

Fixed effect	Estimate	SE	2.5%	97.5%	*df*	*t*	*P*
(Intercept)	5.115	0.079	4.961	5.271	94.880	64.892	<0.001
Sex (breeding males)	-0.118	0.106	-0.326	0.091	52.693	-1.120	0.268

Reference level (intercept) for 'sex' is breeding female.

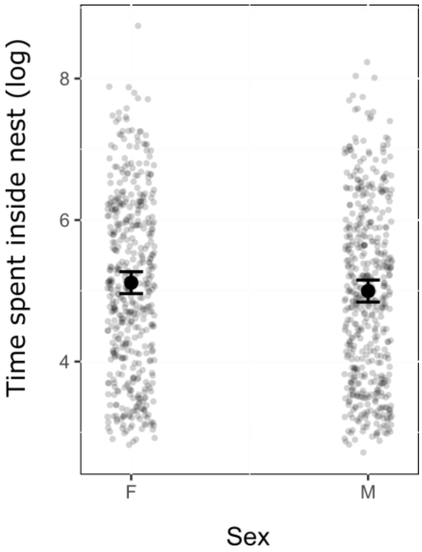

Figure S5. 8 Effect of sex (F: female; M: male) on time spent inside the nest (s; log) at each feeding visit. Points show observed data. Full black circles represent the predicted mean for each sex and bars show 95% confidence intervals (see Table S5.5).

Begging of older broods

Methods

Data analysis. Begging and feeding behaviour were recorded at two different ages (day 4 and day 9). Calls of older chicks are considerably louder, longer and have a broad frequency spectrum noisy component (see Fig. S5.1e); thus, single calls are mostly indistinguishable, which does not allow us to reliably count them either manually or automatically. Therefore, we tried an alternative acoustic measurement on both the day 4 and day 9 data collected in 2017/2018, by quantifying the time spent begging over the 15 s period just after a bird arrived at the nest. We chose a shorter, 15 s duration to reduce the chances of excluding events due to external noise (see below). Time spent begging was estimated by summing the duration of all the over-threshold sounds during this period, using the timer function from the 'seewave' package v. 2.1.4 (Sueur et al., 2008). We used as amplitude threshold 5% of the maximum amplitude recorded for each event, with a time window smooth of 101 points and no overlap. All recordings were initially high-pass filtered at 2000 Hz to attenuate background noise. As for number of begging calls, begging was not quantified if another bird arrived during the event, or for the first begging event recorded for each nest.

Time spent begging was quantified on 398 events (*N*=127 from 21 nests at day 4 and *N*=288 from 29 nests at day 9). As intended, this acoustic variable was highly correlated with the number of begging calls that were estimated at day 4 (Pearson correlation: *r*=0.79, 95% CI=[0.71,0.84], *N*=126). Therefore, besides testing our predictions on day 9 data using time spent begging, we also included day 4 data in the models to confirm that we observed similar results using the two begging measures. However, the estimation of time spent begging was performed using amplitude envelopes, and thus all begging events that included any external noise (e.g. other birds' vocalizations, cicadas, etc.) had to be systematically excluded. This severely decreased the sample of analysable events by 85% at day 4 (when comparing the number of events where number of begging calls could be estimated) and by 55% at day 9 (when comparing the total number of events available). This decrease in available sample led to high uncertainty levels for the effect sizes (see below), and we thus consider these results only preliminary. We therefore recommend this alternative measure for future studies only if it is possible to record begging excluding all external noise.

Statistical analysis. We expected different feeding rules as nestlings get older, since at later stages helpers may learn how to respond to begging stimuli (especially the younger individuals) or start increasing their feeding effort because older broods have a higher reproductive value. To study the correlation between intervisit intervals and time spent begging across bird classes at different brood ages, we used similar models to those described in the main text, but now estimating a different nest age intercept and slope for each level of the interaction between social role and sex, and for each relatedness level of the helpers to the brood (see main text). Similarly, to study the differences in time spent begging experienced by different bird classes at different brood ages, we used the begging models described in the main text, but again estimating a nest age effect for each level of the interaction between social role and sex, and for each relatedness level. To assess whether time spent begging was predicted by hunger and birds' feeding activity, we built a second model adding the time interval since last fed (i.e. proxy of hunger) and time passed since sunrise for each feeding event (see main text). The estimates of both models are presented in the results' tables.

Results

Intervisit intervals. We found no evidence that birds responded to the time spent begging by returning faster to the nest at day 4 or at day 9, independently of their role and sex or relatedness (Table S5.6). At day 9, the mean slopes of male and female breeders seem to be more similar than at day 4 (Tables S5.6, S5.7). The lack of evidence for a response of breeding males at day 4 differs from the result obtained in relation to number of begging calls (see main text), even though both begging measures were highly correlated (see above). However, the 95% CrI found here at day 4 is large (Table S5.6) and contains the effect size obtained when using number of begging calls as response variable (Table 5.2). This suggests that the available sample of breeding males' feeding response to time spent begging (*N*=15 breeding males; 38 events) is not large enough to detect this effect. At day 9, where the sample was bigger (*N*=22 males; 82 events), the breeding males' slope was more similar to that estimated in relation to number of begging calls (Tables 5.2, S5.6), even though the effect was not statistically credible. The credible differences in intervisit intervals detected between bird classes at day 9 (Table S5.8) should be interpreted with caution as the sample for some bird classes was very reduced (see Fig. S5.9).

Time spent begging. We found no credible differences in the time spent begging towards different bird classes at day 4 or at day 9 (Tables S5.9-S5.11). In contrast with the models including number of begging calls (see main text), we did not detect a difference between begging experienced by helpers *r*=0.25 and more related individuals at day 4, or at day 9 (Tables S5.10, S5.11). As expected, older broods begged for longer than younger broods (Table S5.9, Fig. S5.9). Time spent begging, as number of begging calls (see main text, Table 5.3), increased with time since sunrise (Table S5.9), while the correlation between time spent begging and our proxy of hunger (interval since last fed) was in the expected direction but not as clear (Table S5.9).

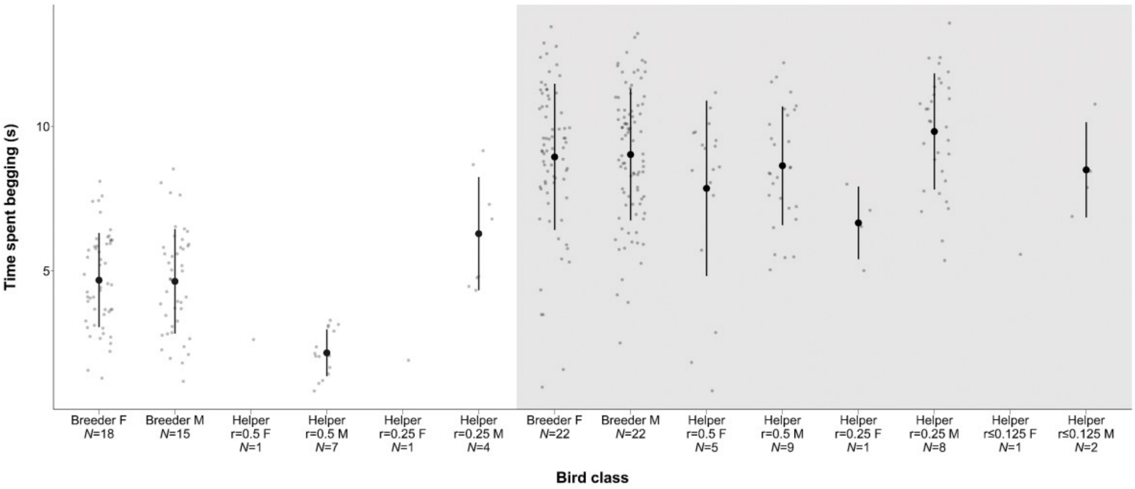

Figure S5. 9 Observed data and means ± SD of time spent begging (s; out of 15 s) towards birds of each class, at day 4 (white) and at day 9 (grey). Points show observations (N=363), circles show mean time spent begging and bars show SD. F: female; M: male Below each class is the number of birds sampled in each category (N; total=46 birds at day 4 and 70 birds at day 9). The 'r' values show helper relatedness to the brood.

Table S5. 6 Estimates from model with intervisit intervals as response variable in relation to time spent begging and across different brood ages

Explanatory variable	Level	Mean	95% CrI	*P*(>0)
(Intercept)	(Breeder female day 4)	6.248	[5.595,6.874]	
Age of brood*role*sex				
4 days old	Breeder male	0.522	[-0.339,1.362]	0.88
	Helper female (*r*=0.5)	1.3	[-1.78,4.551]	0.81
	Helper male (*r*=0.5)	1.177	[-2.084,4.46]	0.77
9 days old	Breeder female	0.125	[-0.637,0.878]	0.64
	Breeder male	0.143	[-0.53,0.83]	0.66
	Helper female (*r*=0.5)	-0.516	[-1.25,0.229]	0.08
	Helper male (*r*=0.5)	0.163	[-0.575,0.922]	0.66
Age of brood*relatedness				
4 days old	Helper *r*=0.25	-1.459	[-4.699,1.584]	0.17
	Helper *r*<0.125	0.736	[-60.995,62.997]	0.5
9 days old	Helper *r*=0.25	0.534	[-0.056,1.157]	0.96
	Helper *r*<0.125	1.054	[-0.097,2.199]	0.97
Age of brood*role*sex*time begging				
4 days old	Breeder female	-0.22	[-0.854,0.433]	0.25
	Breeder male	0.144	[-0.412,0.687]	0.7
	Helper female (*r*=0.5)	0.545	[-1.055,2.261]	0.74
	Helper male (*r*=0.5)	0.362	[-1.425,2.178]	0.65
9 days old	Breeder female	-0.11	[-0.491,0.291]	0.29
	Breeder male	-0.112	[-0.384,0.161]	0.2
	Helper female (*r*=0.5)	0.036	[-0.412,0.482]	0.56
	Helper male (*r*=0.5)	-0.052	[-0.533,0.43]	0.42
Age of brood*relatedness*time begging				
4 days old	Helper *r*=0.25	-1.061	[-3.005,0.837]	0.14
	Helper *r*<0.125	0.177	[-61.111,60.203]	0.5
9 days old	Helper *r*=0.25	-0.281	[-0.9,0.299]	0.18
	Helper *r*<0.125	0.491	[-1.273,2.356]	0.7
Number of chicks		-0.1	[-0.271,0.059]	0.12
Mean mass of chicks		-0.1	[-0.272,0.072]	0.12
Group size*time begging		-0.094	[-0.257,0.069]	0.13
Group size		0.003	[-0.187,0.197]	0.51
Maximum temperature day		-0.106	[-0.304,0.091]	0.13
Time since sunrise		**-0.191**	**[-0.343,-0.049]**	**0**
Random terms	Standard deviance			
Residuals	0.957		[0.883,1.04]	
Nest ID	0.181		[0.009,0.432]	
Bird ID	0.128		[0.005,0.34]	
Colony ID	0.134		[0.005,0.382]	

Reference for 'Age of brood*role*sex' is Breeder female at day 4 (intercept) and reference for 'Age of brood*relatedness' is Helper *r*=0.5 (for each sex at day 4). The 'r' values show helper relatedness to the brood. Credible effects are in bold. '*P*(>0)' shows the proportion of the posterior samples that was higher than zero. Marginal R^2 = 0.185 [0.116;0.256] and conditional R^2 of 0.262 [0.159; 0.394].

Table S5. 7 Comparison of intervisit intervals in relation to time spent begging of different bird classes at day 9

	Breeder female	Breeder male	Helper female *r*=0.5	Helper male *r*=0.5	Helper female *r*=0.25	Helper male *r*=0.25	Helper female *r*≤0.125
Breeder male	0.002 [-0.472,0.479] *P*=0.49						
Helper female *r*=0.5	-0.146 [-0.729,0.446] *P*=0.31	-0.148 [-0.664,0.363] *P*=0.29					
Helper male *r*=0.5	-0.058 [-0.675,0.543] *P*=0.43	-0.061 [-0.605,0.484] *P*=0.41	0.087 [-0.488,0.685] *P*=0.61				
Helper female *r*=0.25	0.135 [-0.521,0.798] *P*=0.65	0.133 [-0.441,0.732] *P*=0.67	0.281 [-0.299,0.9] *P*=0.82	0.193 [-0.645,0.996] *P*=0.67			
Helper male *r*=0.25	0.222 [-0.501,0.934] *P*=0.72	0.22 [-0.429,0.857] *P*=0.74	0.368 [-0.478,1.246] *P*=0.79	0.281 [-0.299,0.9] *P*=0.82	0.087 [-0.488,0.685] *P*=0.61		
Helper female *r*≤0.125	-0.636 [-2.621,1.222] *P*=0.26	-0.639 [-2.599,1.167] *P*=0.25	-0.491 [-2.356,1.273] *P*=0.3	-0.578 [-2.619,1.378] *P*=0.29	-0.772 [-2.745,1.036] *P*=0.21	-0.859 [-3.01,1.147] *P*=0.21	
Helper male *r*≤0.125	-0.549 [-2.424,1.213] *P*=0.28	-0.551 [-2.388,1.15] *P*=0.28	-0.403 [-2.325,1.335] *P*=0.34	-0.491 [-2.356,1.273] *P*=0.3	-0.684 [-2.622,1.09] *P*=0.24	-0.772 [-2.745,1.036] *P*=0.21	0.087 [-0.488,0.685] *P*=0.61

For each comparison, we estimated mean difference, 95% credible intervals and *P* (proportion of the posterior samples that was higher than zero). Differences were calculated by subtracting the estimates of classes on top of the matrix by the estimates of classes on the left (e.g. Breeder female – Breeder male).

Table S5. 8 Comparison of intervisit intervals of different bird classes at day 9

	Breeder female	Breeder male	Helper female *r*=0.5	Helper male *r*=0.5	Helper female *r*=0.25	Helper male *r*=0.25	Helper female *r*≤0.125
Breeder male	-0.018 [-0.508,0.475] *P*=0.48						
Helper female *r*=0.5	0.641 [-0.034,1.246] *P*=0.97	**0.66** **[0.143,1.162]** ***P*=0.99**					
Helper male *r*=0.5	-0.038 [-0.642,0.584] *P*=0.45	-0.019 [-0.505,0.5] *P*=0.46	**-0.679** **[-1.201,-0.126]** ***P*=0.01**				
Helper female *r*=0.25	0.107 [-0.628,0.858] *P*=0.61	0.125 [-0.483,0.718] *P*=0.65	-0.534 [-1.157,0.056] *P*=0.04	0.145 [-0.74,0.984] *P*=0.64			
Helper male *r*=0.25	-0.572 [-1.211,0.088] *P*=0.04	**-0.554** **[-1.113,-0.034]** ***P*=0.02**	**-1.213** **[-1.952,-0.465]** ***P*=0**	-0.534 [-1.157,0.056] *P*=0.04	**-0.679** **[-1.201,-0.126]** ***P*=0.01**		
Helper female *r*≤0.125	-0.413 [-1.592,0.781] *P*=0.25	-0.395 [-1.513,0.783] *P*=0.25	-1.054 [-2.199,0.097] *P*=0.03	-0.375 [-1.619,0.906] *P*=0.28	-0.52 [-1.675,0.653] *P*=0.19	0.159 [-1.097,1.421] *P*=0.6	
Helper male *r*≤0.125	-1.092 [-2.278,0.063] *P*=0.03	-1.074 [-2.184,0.083] *P*=0.03	**-1.733** **[-2.982,-0.428]** ***P*=0.01**	-1.054 [-2.199,0.097] *P*=0.03	-1.199 [-2.47,0.168] *P*=0.04	-0.52 [-1.675,0.653] *P*=0.19	**-0.679** **[-1.201,-0.126]** ***P*=0.01**

For each comparison, we estimated mean difference, 95% credible intervals and *P* (proportion of the posterior samples that was higher than zero). Differences were calculated by subtracting the estimates of classes on top of the matrix by the estimates of classes on the left (e.g. Breeder female – Breeder male). Credible differences are in bold.

Table S5. 9 Estimates from models with time spent begging as response variable

Response	Explanatory variable	Level	Mean	95% CrI	*P*(>0)
Time spent begging	(Intercept)	(Breeder female day 4)	1.413	[1.019,1.792]	
	Age of brood*role*sex				
(model 1)	4 days old	Breeder male	0.029	[-0.31,0.365]	0.57
		Helper female (*r*=0.5)	-0.399	[-0.904,0.105]	0.06
		Helper male (*r*=0.5)	-0.213	[-0.634,0.2]	0.16
	9 days old	**Breeder female**	**1.343**	**[1.02,1.66]**	**1**
		Breeder male	**1.341**	**[1.017,1.67]**	**1**
		Helper female (*r*=0.5)	**1.455**	**[1.044,1.844]**	**1**
		Helper male (*r*=0.5)	**1.431**	**[1.038,1.806]**	**1**
	Age of brood*relatedness				
	4 days old	Helper *r*=0.25	0.12	[-0.368,0.603]	0.68
		Helper *r*<0.125	0.101	[-60.456,60.261]	0.5
	9 days old	Helper *r*=0.25	-0.201	[-0.553,0.131]	0.13
		Helper *r*<0.125	-0.579	[-1.174,0.036]	0.03
	Number of chicks		0.039	[-0.211,0.295]	0.62
	Mean mass of chicks		0.004	[-0.253,0.274]	0.5
	Group size		-0.083	[-0.345,0.195]	0.27
	Maximum temperature day		0.002	[-0.258,0.251]	0.51
	Random terms	Standard deviance			
	Residuals	0.509		[0.472,0.55]	
	Nest ID	0.66		[0.485,0.878]	
	Bird ID	0.112		[0.008,0.231]	
	Colony ID	0.187		[0.008,0.525]	
Time spent begging	(Intercept)	(Breeder female day 4)	1.442	[1.048,1.826]	
	Age of brood*role*sex				
(model 2)	4 days old	Breeder male	0.028	[-0.309,0.354]	0.57
		Helper female (*r*=0.5)	-0.35	[-0.84,0.135]	0.07
		Helper male (*r*=0.5)	-0.272	[-0.686,0.158]	0.1
	9 days old	**Breeder female**	**1.338**	**[1.028,1.65]**	**1**
		Breeder male	**1.373**	**[1.031,1.699]**	**1**
		Helper female (*r*=0.5)	**1.453**	**[1.062,1.846]**	**1**
		Helper male (*r*=0.5)	**1.468**	**[1.075,1.839]**	**1**
	Age of brood*relatedness				
	4 days old	Helper *r*=0.25	0.049	[-0.475,0.551]	0.58
		Helper *r*<0.125	0.398	[-62.773,62.825]	0.5
	9 days old	Helper *r*=0.25	-0.249	[-0.601,0.08]	0.07
		Helper *r*<0.125	-0.424	[-1.034,0.22]	0.09
	Number of chicks		0.023	[-0.242,0.28]	0.56
	Mean mass of chicks		0.03	[-0.229,0.3]	0.58
	Group size		-0.125	[-0.393,0.14]	0.17
	Maximum temperature day		0.061	[-0.203,0.331]	0.69
	Interval last fed		0.024	[-0.029,0.077]	0.81
	Time since sunrise		**0.237**	**[0.157,0.315]**	**1**
	Random terms	Standard deviance			
	Residuals	0.482		[0.445,0.523]	
	Nest ID	0.693		[0.516,0.92]	
	Bird ID	0.149		[0.024,0.264]	
	Colony ID	0.177		[0.007,0.518]	

Reference for ‘Age of brood*role*sex’ is Breeder female at day 4 (intercept) and reference for ‘Age of brood*relatedness’ is Helper *r*=0.5 (for each sex at day 4). The ‘*r*’ values show helper relatedness to the nestlings. Models are similar but second model includes hunger proxies. Credible effects are in bold. ‘*P*>0’ shows the proportion of the posterior samples that was higher than zero. Model 1: marginal R^2 = 0.403 [0.279;0.516] and conditional R^2 0.795 [0.729; 0.855]. Model 2: marginal R^2 = 0.386 [0.271;0.498] and conditional R^2 0.816 [0.757; 0.874].

Table S5. 10. Comparison of time spent begging in visits of different bird classes at day 4 (estimated from model 1)

	Breeder female	Breeder male	Helper female *r*=0.5	Helper male *r*=0.5	Helper female *r*=0.25	Helper male *r*=0.25	Helper female *r*≤0.125
Breeder male	-0.029 [-0.365,0.31] *P*=0.43						
Helper female *r*=0.5	0.399 [-0.105,0.904] *P*=0.94	0.428 [-0.045,0.887] *P*=0.96					
Helper male *r*=0.5	0.213 [-0.2,0.634] *P*=0.84	0.241 [-0.162,0.629] *P*=0.87	-0.187 [-0.613,0.281] *P*=0.2				
Helper female *r*=0.25	0.28 [-0.263,0.823] *P*=0.84	0.308 [-0.194,0.806] *P*=0.89	-0.12 [-0.603,0.368] *P*=0.32	0.067 [-0.605,0.724] *P*=0.58			
Helper male *r*=0.25	0.093 [-0.378,0.559] *P*=0.66	0.122 [-0.32,0.566] *P*=0.71	-0.306 [-0.975,0.358] *P*=0.18	-0.12 [-0.603,0.368] *P*=0.32	-0.187 [-0.613,0.281] *P*=0.2		
Helper female *r*≤0.125	0.298 [-59.94,60.95] *P*=0.51	0.327 [-60.06,60.96] *P*=0.51	-0.101 [-60.26,60.46] *P*=0.5	0.086 [-60.03,60.75] *P*=0.5	0.019 [-60.37,60.64] *P*=0.5	0.205 [-60.14,60.68] *P*=0.5	
Helper male *r*≤0.125	0.112 [-60.17,60.93] *P*=0.5	0.14 [-60.30,60.82] *P*=0.5	-0.288 [-60.56,60.472] *P*=0.5	-0.101 [-60.26,60.46] *P*=0.5	-0.168 [-60.60,60.37] *P*=0.5	0.019 [-60.37,60.65] *P*=0.5	-0.187 [-0.613,0.281] *P*=0.2

For each comparison, we estimated mean difference, 95% credible intervals and *P* (proportion of the posterior samples that was higher than zero). Differences were calculated by subtracting the estimates of classes on top of the matrix by the estimates of classes on the left (e.g. Breeder female – Breeder male).

Table S5. 11. Comparison of time spent begging in visits of different bird classes at day 9 (estimated from model 1)

	Breeder female	Breeder male	Helper female *r*=0.5	Helper male *r*=0.5	Helper female *r*=0.25	Helper male *r*=0.25	Helper female *r*≤0.125
Breeder male	0.002 [-0.236,0.249] *P*=0.5						
Helper female *r*=0.5	-0.113 [-0.455,0.218] *P*=0.26	-0.114 [-0.411,0.173] *P*=0.22					
Helper male *r*=0.5	-0.089 [-0.405,0.226] *P*=0.29	-0.09 [-0.365,0.185] *P*=0.26	0.024 [-0.259,0.308] *P*=0.57				
Helper female *r*=0.25	0.088 [-0.204,0.378] *P*=0.73	0.087 [-0.209,0.377] *P*=0.73	0.201 [-0.131,0.553] *P*=0.87	0.177 [-0.244,0.58] *P*=0.82			
Helper male *r*=0.25	0.113 [-0.206,0.431] *P*=0.76	0.111 [-0.224,0.444] *P*=0.75	0.225 [-0.251,0.707] *P*=0.83	0.201 [-0.131,0.553] *P*=0.87	0.024 [-0.259,0.308] *P*=0.57		
Helper female *r*≤0.125	0.466 [-0.163,1.066] *P*=0.93	0.465 [-0.148,1.031] *P*=0.94	0.579 [-0.036,1.174] *P*=0.97	0.555 [-0.129,1.206] *P*=0.95	0.378 [-0.292,0.988] *P*=0.88	0.354 [-0.381,1.046] *P*=0.84	
Helper male *r*≤0.125	0.49 [-0.149,1.079] *P*=0.93	0.489 [-0.109,1.054] *P*=0.94	0.603 [-0.08,1.254] *P*=0.96	0.579 [-0.036,1.174] *P*=0.97	0.402 [-0.306,1.07] *P*=0.87	0.378 [-0.292,0.988] *P*=0.88	0.024 [-0.259,0.308] *P*=0.57

For each comparison, we estimated mean difference, 95% credible intervals and *P* (proportion of the posterior samples that was higher than zero). Differences were calculated by subtracting the estimates of classes on top of the matrix by the estimates of classes on the left (e.g. Breeder female – Breeder male).

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Chapter 6

Interactive effects of breeding group size and climate on offspring first-year survival

Interactive effects of breeding group size and climate on offspring first-year survival

Rita Fortuna[a,b,c,d], Matthieu Paquet[e], André C. Ferreira[a,c,d], Liliana R. Silva[a,c], Franck Theron[d], Claire Doutrelant[d,f] and Rita Covas[a,c,f]

[a] CIBIO, Centro de Investigação em Biodiversidade e Recursos Genéticos, InBIO Laboratório Associado, Campus de Vairão, Universidade do Porto, Vairão, Portugal
[b] Departamento de Biologia, Faculdade de Ciências, Universidade do Porto, Porto, Portugal
[c] BIOPOLIS Program in Genomics, Biodiversity and Land Planning, CIBIO, Campus de Vairão, Vairão, Portugal
[d] CEFE, CNRS, Univ Montpellier, EPHE, IRD, Montpellier, France
[e] Institute of Mathematics, University of Bordeaux, Talence, France
[f] Percy FitzPatrick Institute, DST-NRF Centre of Excellence, University of Cape Town, Cape Town, South Africa

Abstract

In cooperatively breeding species, helpers are thought to gain indirect and/or direct fitness benefits from improving offspring survival. Yet, evidence that helpers increase breeders' reproductive output is not consistently found and helper effects have mostly been investigated under short periods. Long-term helper effects on offspring survival can be expected because offspring may reach independence in better condition, receive more post-fledging care, and associate with the helpers after nutritional independence. In addition, climatic conditions as rainfall and temperature can directly or indirectly affect survival, and helpers may modulate climatic effects on offspring early-life survival. Here we tested whether helper number and climatic conditions during the breeding season and winter associated with offspring first-year survival. We found limited evidence for interactive effects of group size and climatic conditions. Female offspring first-year survival was higher when raised in larger groups under low rainfall conditions. However, females born in wet conditions that were raised with more helpers appeared to be at a disadvantage comparing to females in small groups. In general, rainfall was negatively associated with females first-year survival, with no evident effects for males, whereas maximum and minimum temperature effects on first-year survival were not evident. Group size was not found to interact with maximum temperatures during breeding, but offspring raised by large groups showed a tendency for higher survival over cold winters and lower survival over warm winters. Lastly, we found no evidence of general breeding group size effects on offspring interannual survival. These results indicate that, in sociable weavers, optimal breeding group size for first-year offspring survival may vary according to climatic conditions. Future studies on how breeding group sizes and climatic context influence post-fledging survival in other cooperatively breeding systems would improve our understanding of the long-term reproductive benefits of helping-at-the-nest.

Keywords: climate, cooperative breeding, helpers, post-fledging survival, rainfall, reproductive success, temperature, winter

Introduction

Cooperative breeders are social systems where breeding pairs and 'helpers' cooperate to raise the young (Brown, 1978). Studying the fitness benefits and costs of this life history strategy is needed to understand how this form of cooperation has evolved (Brown, 1978; Skutch, 1935). Key among these benefits/costs is the production and survival of the offspring. In many cooperative breeders, most helpers are close relatives of the breeding pair (Hatchwell, 2009) and one of the central explanations for the evolutionary stability of these systems is that helpers propagate their genes by helping relatives to produce more offspring (i.e.: indirect fitness benefits or inclusive fitness; Hamilton, 1964; West et al., 2007). In addition, helpers can directly benefit from improving offspring survival through group augmentation benefits i.e., when increases in group size lead to reproductive or survival advantages for helpers, for instance through reduced predation risk or thermoregulation costs (du Plessis & Williams, 1994; Kokko et al., 2001; Sorato et al., 2012). Therefore, across cooperatively breeding systems, breeders with more helpers are expected to have greater reproductive success.

Evidence that helpers increase breeders' reproductive output is not consistently found (Cockburn, 1998; Kingma et al., 2010; Van de Loock et al., 2017), but recently a general positive effect of helpers on annual reproductive success was detected across cooperative breeders (Downing et al., 2020). However, most studies assess short-term helper effects on productivity i.e., usually the number of fledglings or pups produced, while longer-term helper effects on offspring survival have received less attention.

Interannual offspring survival can be expected to be positively associated to number of helpers for different reasons. In many cooperative breeders, helpers provide extended care to offspring, when young leave the nests or burrows but are still nutritionally dependent (Langen, 2000). Helpers' care during the pre-independence stage was found to positively associate with offspring survival in a few cooperatively breeding species such as Arabian babblers *Turdoides squamiceps* (Ridley, 2007), but most studies find no evidence of helper effects on offspring survival just before independence (see literature review in Van de Loock et al., 2017; Bourne et al., 2020a). It is also possible that offspring raised in larger groups reach independence in better condition (Hatchwell et al., 2004; Ridley, 2007; Solomon, 1991), which is expected to favour survival, recruitment and acquisition of a higher dominance rank (Russell et al., 2007). In addition, being raised with more helpers is likely to mean that offspring have a larger social group after becoming nutritionally independent (A. C. Ferreira et al., 2020;

Mcgowan et al., 2006). This in turn is thought to favour foraging efficiency (Bednarz, 1988), reduce predation risk (through vigilance or dilution effects; Bertram, 1980; Guindre-Parker & Rubenstein, 2020; Rasa, 1989; Sorato et al., 2012), and/ or provide thermoregulatory benefits (e.g. through communal roosting; Allainé et al., 2000; du Plessis & Williams, 1994; Hatchwell et al., 2009; McKechnie & Lovegrove, 2001; Paquet et al., 2016).

In accordance with the idea that large breeding groups confer benefits at independence, offspring interannual survival was positively correlated with number of helpers in long-tailed tits *Aegithalos caudatus* (Hatchwell et al., 2004; McGowan et al., 2003) and rifleman *Acanthisitta chloris* (Preston et al., 2016), among other species (see Van de Loock et al., 2017). In other cooperative breeders however, as southern pied babblers *Turdoides bicolor*, no evidence was found that group size had any positive or negative effect on interannual survival of juveniles (Bourne et al., 2020b). When offspring become independent, they may as well more directly compete with helpers for resources, especially in social systems with marked hierarchies (Rat et al., 2015). In sociable weavers *Philetairus socius*, first-year local recapture probability was lower for offspring raised with helpers and this was suggested to arise from competition with helpers forcing dispersal or leading to higher mortality (Covas et al., 2011; see also Griesser et al., 2008).

Climatic conditions can exert a major influence on survival (Riddell et al., 2019; Román-Palacios & Wiens, 2020) and cooperatively breeding species occurrence is associated to temporally variable environments with low annual rainfall and high mean temperatures (Jetz & Rubenstein, 2011). In these areas, rainfall levels influence food availability (i.e.: plant and invertebrates' abundance; Noy-Meir, 1973), and rain has often lasting effects on breeding activity and reproductive success (Altwegg & Anderson, 2009; Dean & Milton, 2001; Lloyd, 1999; Mares et al., 2017). Temperature, on the other hand, may directly lead to mortality due to the high physiological costs of living in extremely hot or cold conditions (Altwegg et al., 2014; Bourne et al., 2020b; Robinson et al., 2012), but may affect as well food resources and animals' foraging strategies (Cunningham et al., 2015) or predation levels by snakes (D'Amelio et al., 2021).

Recent investigations suggest that helpers may mitigate the effects of adverse weather on offspring survival. For instance, in meerkats *Suricata suricatta*, pup survival was similar across group sizes in high rainfall conditions, but greater for groups with more helpers in low rainfall periods (Groenewoud & Clutton-Brock, 2021). In white-browed sparrow-weavers *Plocepasser mahali*, even though there was no evidence for an effect of helpers on mean reproductive success, helper number was found to mediate rainfall-related variance in nestling survival (Capilla-Lasheras et al., 2021; see also Rubenstein, 2011). On the other hand, helpers do not appear to successfully counteract negative effects of high temperatures during rearing on nestling survival (Bourne et al., 2020a; D'Amelio et al., 2021), or of hot and dry weather on offspring interannual survival, although the latter has, to our knowledge, only been studied in southern pied babblers (Bourne et al., 2020b). We are thus in need of more studies testing whether helpers and breeding climatic conditions have interactive effects on offspring post-fledging survival, and studies investigating if being raised with more helpers confers advantages/disadvantages to offspring during wintertime. Offspring raised in larger groups may fledge in better condition or have access to a larger social group at independence, which may be especially advantageous in cold winters (du Plessis & Williams, 1994) and for young and unexperienced individuals (Robinson et al., 2007), but may also represent higher competition for resources (Brouwer et al., 2006; Dickinson et al., 2016).

Here, we assessed whether breeding group size and climatic conditions during the breeding season and during winter had interactive effects on offspring first-year survival. To do so, we used capture-recapture data collected over 7 years on over 1,000 fledglings in a population of sociable weavers, where cooperative breeding is kin-based and facultative (Covas et al., 2006; Fortuna et al., 2022). We predicted that survival differences between offspring with different group sizes would be more pronounced when nestlings were reared under adverse (hot and dry) climatic conditions and after severe (cold) winters. In addition, in sociable weavers, most helpers are males (Doutrelant et al., 2004) and males are dominant over females (Rat et al., 2015). We therefore expected less positive effects of group size on female offspring first-year survival, if breeding group sizes predict females' social group sizes after fledging.

Methods

Study system

Sociable weavers are a cooperatively breeding passerine endemic to southern Africa. They breed and roost in communal nests with several chambers, hereafter referred to as 'colonies' (Maclean, 1973a). Breeding pairs may be assisted by one or several helpers that contribute to nestling feeding (Covas et al., 2008; Maclean, 1973c), nest building and sanitation (A. Ferreira, 2015). Both sexes help, but there are more male helpers as females disperse more often, typically during their second-third year (Covas et al., 2004; van Dijk et al., 2015).

Sociable weavers breed for several months (Mares et al., 2017) and can have up to 11 breeding attempts per season, with sometimes up to 70% being predated by snakes before fledging (Covas et al., 2008). Clutch size typically ranges between 2-4 eggs and females lay one egg per day (Covas & Du Plessis, 2005; Fortuna et al., 2021). The incubation period lasts around 15 days and nestlings normally hatch asynchronously (Covas & Du Plessis, 2005; Maclean, 1973b). The subsequent nestling period lasts for 21-25 days (Maclean, 1973b).

This work was conducted at Benfontein Nature Reserve, Northern Cape Province, South Africa (28°520 S, 24°500 E), under permission from landowners, provincial authorities and the UCT Ethics committee.

Breeding monitoring

From 2011/2012 to 2017/2018 (7 breeding seasons) we monitored breeding activity in 17 sociable weaver colonies. Breeding usually happens between September and April (Fortuna et al., 2021). Nest contents were inspected every 3 days from mid-September and, after finding the first egg, nests were monitored until hatching. When the first nestling was 9 days old, nestlings were weighed and ringed with a unique numbered aluminium ring and a blood sample was taken for sexing and genotyping (see below). When the first chick was 17 days of age (day 17 of the nest; the last day nests can be visited without increasing the chances of inducing fledging), all nestlings' wing, tarsus, and weigh were measured. The fate and fate date of each chick was registered and when a chick survived until day 17 it was considered as having fledged. Over the 7 seasons included, a total of 2001 nestlings have fledged (840 breeding events). However, in the seasons 2013/2014 and 2015/2016, 92 nestlings hatched and/or fledged during winter months and were therefore excluded from the analyses as we wanted to separate breeding climate from winter climate effects on survival. Hence, the sample size was 1909 nestlings.

Capture-mark-recapture

Individuals have been captured routinely since 1999 at the colonies using mist nests (Covas et al., 2002). From 2011 to 2019 (9 years), birds were captured once a year before the breeding season started, between August and September. The number of individuals caught at each colony was used as colony size measure and, when birds escaped the nets, these were still counted and included. When unringed birds were captured, they were given a uniquely coded aluminium ring and a unique colour-ring combination, allowing individual visual identification. Blood samples were collected for genetic sexing and determination of parentage relationships (see below). When many birds escaped in the first capture, a second capture was done, and we considered these as one single capture event.

Group size and breeders' identification

Individuals visiting the nests were identified by their colour-ring combination using video recording nests for a minimum of 2h (see Silva et al., 2018).

Group size was calculated as the number of birds seen feeding the nestlings over all observations of each breeding attempt. Only birds that fed at least 3 times (in the same day or different days) were considered part of the group. Unringed birds were included in group size estimates (counted as 1 more bird). Average group size was 4 individuals (including breeders), and maximum group size was 11.

To identify the breeders of each nest, we combined information from incubation and feeding videos with genetic analyses from blood samples (Paquet et al., 2015). All individuals were sexed genetically from blood samples (Paquet et al., 2015). The parents of each nestling were genetically determined by full-likelihood parentage inference using microsatellite markers (Fortuna et al., 2021; Paquet et al., 2015). When no genetic data was available, parentage was determined based on the birds' biology (e.g., by combining information on age, breeding history and pedigree; for details on parentage attribution see Supplementary materials in Fortuna et al., 2021).

Group size, mother and father identity, and nestling sex could be reliably determined for 1094 out of 1909 fledglings. Our final sample had 567 male fledglings and 527 female fledglings. We had offspring mass data at day 17 for 1088 of 1094 fledglings (see Appendix).

Climatic variables and windows

Daily rain, maximum and minimum temperatures were collected at Kimberley Airport weather station (10 km from the study site; Mares et al., 2017).

Breeding climatic conditions were defined as 1) mean maximum temperature (°C; hereafter meanTmax) during the nestling period (from hatching to fledging), as high maximum temperatures during the nestling period were found to negatively correlate with full-brood fledging probability in a previous study (D'Amelio et al., 2021); and 2) mean rainfall (mm; hereafter rainfall) from 90 to 53 days before fledging date, following previous findings that rainfall levels during this time window were positively correlated with full-brood fledging probability (D'Amelio et al., 2021).

Winter climatic conditions were defined as the mean minimum temperature (°C; hereafter winterTmin) estimated during winter months - June, July and August - for each year (1 value per year). Rainfall occurs during summer in this region, and we thus did not test for winter rainfall effects on survival (96% of winter days in our dataset had no rain).

Survival model

We estimated climate and breeding group size effects on male and female offspring first-year survival using a capture-recapture model (CMR). We quantified apparent survival (hereafter 'survival') and capture probabilities in the first year (ϕ^{1st} and p^{1st}, respectively), and survival and recapture probabilities in the remaining years (ϕ^{A} and p^{A}, respectively). For this, we assembled a capture history of 9 years (2011-2019) of 1094 fledglings born between 2011 and 2018. There were two possible observation events: 'captured' and 'not captured'. We tested the effect of the following interactions of interest and their single terms on ϕ^{1st}: 1) the interaction between group size and meanTmax; 2) the interaction between group size and rainfall; and 3) the interaction between group size and winterTmin. Different slopes for male and female offspring were estimated for each of these interactions. As intervals between fledging and recapture will be longer for birds that fledged earlier, we controlled for this by including a variable representing the time difference between the nest laying date and the offspring natal colony's capture date in the following year. For 3 females that were recaptured in a different colony, representing less than 0.7% of all nestlings, capture date of their new colony was used instead of capture date of their birth colony. Besides, some colonies have been under a predator-removal experiment (D'Amelio et al., 2021; Fortuna et al., 2021), and we thus accounted for a predation treatment effect on ϕ^{1st}, conditional on group size. Indeed, nestlings in larger groups have been observed to fledge later (A. Ferreira, 2015), thus incurring higher risks of nest predation, which can lead to opposite group size effects on survival in colonies protected/unprotected from nest predation. We accounted for non-independence between nestlings from the same brood, the same mother, the same father, the same colony and born in the same season by adding these as random terms. Lastly, we estimated sex-dependent p^{1st}, as females may be less likely to be recaptured due to dispersing to colonies outside of the study area, even though dispersal during the first year seems quite rare (see above). Both ϕ^{1st} and p^{1st} were fitted in the logit scale.

The analysis was performed in a Bayesian framework using Nimble (de Valpine et al., 2017) in R v. 4.0.4 (R Development Core Team, 2021). Two independent Markov chain Monte Carlo (MCMC) chains of 155,000 iterations were used, with a burn-in period of 5,000. We used vague priors for all parameters, with normal distributions of mean = 0 and standard deviation = 1.5 for fixed effects (intercepts and slopes) and half-cauchy priors for random effects (variances). To improve mixing and MCMC efficiency, parameters estimated in relation to first year survival were block sampled using the Automated Factor Slide sampler (Tibbits et al., 2014). To assess models' goodness of fit, we performed post-predictive checks by simulating the number of times each individual was recaptured and confirming that the mean and coefficient of variation of this estimate were similar to those observed (mean observed = 0.94; mean simulated = 0.92, 95% credible interval or 95CrI = [0.83,1.02]; CV observed = 1.42; CV simulated = 1.38, 95CrI = [1.29,1.48]). Model convergence was satisfactory based on the R hat Gelman Rubin statistic (all parameters <1.001) and trace plots' inspection. Effective sample size was above 2000 for all parameters. Final inferences were derived from 300,000 iterations after merging the posterior samples of the two chains. In the results, we present the means and [95CrI] of the posterior distributions of interest. We report effects as credible when 95CrI do not overlap zero, but still discuss effects when credible intervals slightly overlap zero. We further computed the proportion of posterior samples greater than 0 (P>0) as an indication of evidence for positive or negative effects (values close to 1 or 0, respectively). To explicitly test for differences between years and sexes, we computed the difference between posteriors and its 95CrI (Δ), and its proportion of positive values ($P\Delta>0$). Values of $P\Delta>0$ close to 0 or 1 indicate clear tendencies for positive or negative differences, respectively.

Results

The CMR analyses showed that first-year survival was similar between sexes and lower than survival in the remaining years, while capture probabilities between first and remaining years did not credibly differ. Specifically, the estimated ϕ^{1st} for females was 0.47 [0.31,0.65], not credibly different from the estimated ϕ^{1st} for males of 0.51 [0.35,0.69]

($\Delta\ \phi^{1st}$ = -0.19 [-0.51 0.12], P$\Delta\ \phi^{1st}$ = 0.12). Likewise, p^{1st} was similar for females 0.86 [0.80,0.90] and males 0.83 [0.76,0.88] ($\Delta\ p^{1st}$ = 0.25 [-0.32,0.83]; P$\Delta\ p^{1st}$ = 0.8). Survival probability was higher after the first year (ϕ^{A} = 0.7 [0.67,0.74]; $\Delta\ \phi^{females}$ = -0.24 [-0.4,-0.05], P$\Delta\phi^{females}$ = 0.01; $\Delta\ \phi^{males}$ = -0.19 [-0.36,-0.01], P$\Delta\phi^{males}$ = 0.02). Average recapture probability p^{A} (0.81 [0.77,0.85]) was lower than p^{1st} of both sexes, although this difference was not credible ($\Delta\ p^{females}$ = 0.05 [-0.02,0.11], P$\Delta p^{females}$ = 0.91; $\Delta\ p^{males}$ = 0.01[-0.06,0.08], PΔp^{males} = 0.65).

We found credible rainfall effects on female offspring first-year survival that varied with group size (Fig. 6.1). In dry conditions (rainfall below 1 mm), helpers were positively associated with survival: female offspring raised with four more helpers than average had a predicted first-year survival probability of 58% [32,81], while females raised without helpers in the same rainfall conditions were predicted to have 46% [28,66] chances of surviving (Fig. 6.1). On the other hand, when rainfall was higher, helpers were negatively associated with survival: females born after high rainfall levels (above 2 mm) had a predicted survival probability of 16% [3;42] if raised by an above-average helper number and of 44% [17,75] if raised without helpers. At average group sizes, rainfall was negatively credibly associated with female offspring survival (Table 6.1) and the predicted female survival probability decreased from 50% [34,69] in dry conditions to 32% [14,56] in wet conditions (Fig. 6.1). Instead, for males' first-year survival, we found no credible effects of group size and rainfall alone or in interaction (Table 6.1), although the rainfall effect tended to go in the same negative direction as for females and there was no statistical evidence that rainfall effects differed between the sexes (Δ = -0.13 [-0.46,0.18], PΔ = 0.21).

There was no evidence that group size interacted with maximum temperatures during the nestling period in relation to first-year survival (Table 6.1; Fig.1). MeanTmax tended to negatively correlate with offspring first-year survival in both sexes, with credible intervals slightly overlapping zero (Table 6.1 and Fig. 6.1). At average group sizes, male offspring raised in low meanTmax (<25 °C) had a predicted survival probability of 60% [40,79], while male offspring born in warm conditions (meanTmax>35 °C) had an estimated survival probability of 44% [26,64].

There was a non-credible tendency for an interaction between winter minimum temperature and group size, similar for females and males (Table 6.1 and Fig.1), and the predicted effects of this interaction on survival had as well wide credible intervals (Fig. 6.1). In colder-winter years (winterTmin<1.5 °C), male offspring raised with an above-average helper number were predicted to have a survival probability of 70%

[35,94], while offspring raised with no helpers had 50% [24,77] chances of surviving in the same conditions (Fig. 6.1). By contrast, when winterTmin was high (above 3 °C), offspring raised by groups of 8 individuals were predicted to have a survival probability of 33% [9,69] and offspring raised without helpers were predicted to have 54% [27,79] chances of surviving (Fig. 6.1). Winter minimum temperatures showed on average negative effects on offspring first-year survival but with credible intervals that broadly overlapped zero (Table 6.1).

Table 6. 1 Parameter estimates (mean, SD standard deviation, 95CrI the 95% credible intervals and P>0 the proportion of the posterior that is greater than zero) for CMR model on offspring survival.

Parameter	Mean	SD	95CrI	P>0
ϕ^{1st} intercept (females)	-0.14	0.36	-0.81 – 0.6	0.31
Sex (reference = female)				
Male	0.19	0.16	-0.12 – 0.51	0.88
Group size (females)	0.02	0.17	-0.3 – 0.35	0.56
Group size (males)	-0.02	0.18	-0.39 – 0.33	0.45
Group size:Rain (females)	-0.24	0.12	-0.48 – 0	0.02
Group size:Rain (males)	-0.03	0.12	-0.27 – 0.21	0.39
Group size:MeanTmax (females)	0.02	0.14	-0.24 – 0.29	0.57
Group size:MeanTmax (males)	0.15	0.14	-0.12 – 0.42	0.86
Group size:WinterTmin (females)	-0.18	0.13	-0.44 – 0.07	0.08
Group size:WinterTmin (males)	-0.2	0.13	-0.46 – 0.05	0.06
Rain (females)	-0.35	0.18	-0.71 – -0.01	0.02
Rain (males)	-0.22	0.18	-0.58 – 0.14	0.11
MeanTmax (females)	-0.16	0.12	-0.4 – 0.08	0.1
MeanTmax (males)	-0.18	0.13	-0.44 – 0.07	0.08
WinterTmin (females)	-0.24	0.28	-0.85 – 0.27	0.18
WinterTmin (males)	-0.19	0.28	-0.81 – 0.32	0.24
Time difference (birth-capture)	-0.28	0.19	-0.66 – 0.09	0.07
Predation treatment (reference = natural)				
Protected	0.17	0.23	-0.27 – 0.64	0.78
Predation treatment:Group size				
Protected	0.08	0.2	-0.32 – 0.48	0.65
Colony ID	0.26	0.16	0.02 – 0.62	
Father ID	0.2	0.14	0.01 – 0.51	
Mother ID	0.2	0.14	0.01 – 0.52	
Breeding attempt ID	0.71	0.22	0.2 – 1.11	
Season	0.6	0.34	0.11 – 1.44	
p^{1st} intercept (females)	1.8	0.22	1.38 – 2.25	1
Sex				
Males	-0.25	0.29	-0.83 – 0.32	0.2
ϕ^{A}	0.7	0.02	0.67 – 0.74	
p^{A}	0.81	0.02	0.77 – 0.85	

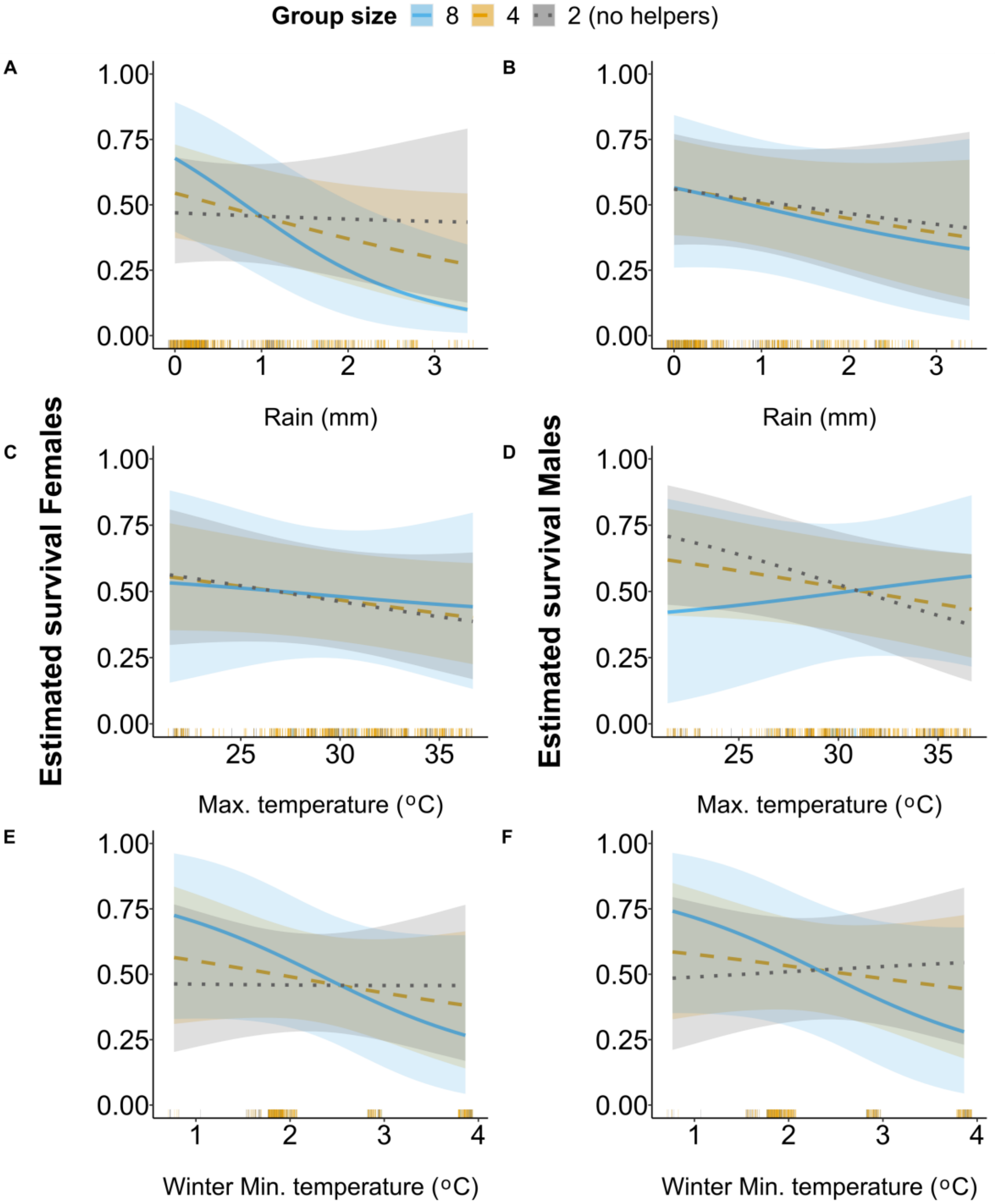

Figure 6. 1 Predicted first-year survival probability for female (A,C,E) and male (B,D,F) fledglings in relation to mean rain (A-B) and mean maximum temperature (C-D) during the breeding season and mean minimum temperature during winter (E-F). Estimated survival is shown for fledglings raised in groups of different sizes: grey dotted line shows groups of 2 individuals (no helpers), orange dashed line shows groups of 4 (the nearest integer of average group size) and blue solid line shows groups of 8 (the nearest integer of mean between average group size and maximum group size). Rugs show the distribution of the x-axis variables for the respective sex and rug colours show raw data of group size values (grey for groups without helpers, orange for groups between 3 and 7 individuals, blue for groups above 7 individuals).

Discussion

In this study we investigated whether helper number and climatic conditions during the breeding season and winter associated with offspring first-year survival. Our aim was to investigate positive or negative effects of breeding group size on offspring long-term survival. We predicted that being raised with more helpers could buffer negative effects of adverse climatic conditions on first-year survival, or instead intensify the effects of adverse climatic conditions if large breeding groups translate into higher post-fledging competition. We also predicted that females, being the subordinate sex, would incur higher costs in larger (male-biased) groups than male offspring. We found that being raised in larger groups appeared beneficial for females' first-year survival when rainfall was low, but potentially disadvantageous for females born in benign rainfall conditions. In general, rainfall was negatively associated with females first-year survival, with no evident effects for males. Maximum temperature during breeding tended to negatively associate with first-year survival but there was no evidence of an interaction with breeding group size or offspring sex. Winter minimum temperature was not found to be associated with survival. Nevertheless, male and female offspring raised by large groups showed a tendency for higher survival over cold winters, and lower survival over warm winters, than offspring raised in smaller groups. We found no evidence of general breeding group size effects on offspring interannual survival.

Interactive effects of helpers and climate on first-year survival

Previous studies in sociable weavers have shown that fledging success is higher when offspring are raised by larger groups (D'Amelio et al., 2021; see Chapter 3). Here we found that breeding group size was not associated with offspring survival in the first year, which suggests that being raised with more helpers does not, in general, confer longer-term survival benefits or costs for offspring. These results update findings from an earlier study in this population, conducted over only two breeding seasons, which had showed that helper presence was associated with lower offspring interannual survival (Covas et al., 2011). The findings presented here suggest instead that being raised with more helpers may translate into either fitness benefits or costs for the offspring, depending on the climatic conditions experienced and their effects.

We detected a negative association between rainfall during the breeding period and female offspring survival in the first year, but the strength of rainfall effects was conditional on group size, appearing stronger when females were raised by larger groups. Specifically, females born after periods of low rainfall had a higher predicted survival probability when raised in larger groups than when raised with few or no helpers. This concurs with the prediction that offspring raised by more helpers in adverse breeding conditions may have a long-term survival advantage. Yet, the negative association between rainfall levels and first-year survival appeared as well stronger for females raised in larger groups. This instead implies that there may be long-term survival costs associated with group size when female offspring are raised in benign breeding conditions. However, as illustrated in Figure 1, fewer data points are available in very wet conditions and those predictions are thus associated to higher uncertainty. Rainfall effects on survival are discussed in detail below.

We found some indication that winter minimum temperature and group size had interactive effects on offspring survival. Offspring with larger group sizes were predicted to have a survival advantage in colder winters but benefits of being in a large group were less evident in warm winters. The results were similar for males and females (Fig. 6.1). On average, in cold winters, male offspring raised by a group with six helpers had 20% more chances to survive than males raised by pairs without helpers. Being true, this difference could be due to offspring reaching winter in better condition, and/or having access to a larger group size during winter. In sociable weavers, most breeding group members are offspring of the breeding pair (Covas et al., 2006; Fortuna et al., 2022) and breeding group sizes appear correlated with group sizes in non-breeding periods (Paquet et al., 2016), but winter groups' composition is yet to be studied. Existing evidence in other social systems indicates that individuals are expected to more strongly associate with their kin during winter and that non-breeding associations can predict helping decisions (Hatchwell et al., 2001; Kraaijeveld & Dickinson, 2001; Mcgowan et al., 2006; Napper & Hatchwell, 2016). This could also explain the tendency observed for negative effects of being part of larger groups in warm winters, as thermoregulation benefits obtained from communal roosting are not as important when it is warmer, and therefore may not mask negative effects caused by competition for resources. Here, since winterTmin was considered as an annual value and only seven winters were sampled, we may not yet have enough variation to clearly understand interactions between winter harshness and group size effects. Even though the effects were statistically unclear, this may be a first indication that social bonds regulate how winter climate affects offspring early-life survival.

In sum, we found limited evidence suggesting that breeding group size buffers adverse climatic effects on offspring interannual survival in sociable weavers. Helper buffering effects were only detected on the survival of female offspring born in low rainfall conditions, but not in relation to maximum temperature during breeding or minimum winter temperature. Here, we show that being raised with more helpers may translate into some benefits later in offspring's life, especially for female offspring raised under dry conditions, through increased survival probability in their first year. On the other hand, our findings also suggest that female offspring in larger groups may lose this advantage in benign climatic conditions. It therefore seems that optimal group sizes in this species vary according to offspring's environment, and these findings stimulate future work aimed at understanding social groups' composition, stability and effects during non-breeding periods.

Rainfall effects on first-year survival

Sociable weavers have been shown to lay larger clutches when pre-laying rainfall was higher (Fortuna et al., 2021) and to more likely fully fledge their broods (D'Amelio et al., 2021). The negative rainfall effect on post-fledging survival found here was unexpected and could be caused by a combination of factors. Specifically, it could arise from higher intra- and/or inter-brood competition after high rains as productivity increases (D'Amelio et al., 2021; Fortuna et al., 2021) and consequently the size of the broods and colonies. This could lead to chicks fledging in poorer condition and showing reduced post-fledging survival, especially females as they are less dominant and therefore have more restricted access to food and other resources (Rat et al., 2015). To test whether rainfall effects on survival were mediated by nestlings' mass at fledging, we fitted the same survival model but accounting for fledging mass and its interaction with group size and offspring sex (see Appendix). Although fledging mass was positively associated with first-year survival (Table S6.1; Fig. S6.1; see also Gimenez et al., 2006), rainfall effects alone and in interaction with group size were still detected with similar strength (Table S6.1). This implies that mass at fledging does not mediate rainfall effects on offspring survival.

Hence, the effect of rainfall found here is more likely to arise from high competition after fledging at the colony level after high rainfall periods (i.e., productive breeding periods), which may lead to higher mortality or push females to permanently disperse more often during their first year (see also Brouwer et al., 2006; Griesser et al., 2008; Leon et al., 2022). In our dataset, from 433 individuals that were captured after their first winter (217 females and 216 males), only 3 females were captured at a colony different from their birth colony, meaning that less than 2% of the females dispersed within our study area in their first year. If this short-range dispersal (i.e.: within study area) is representative of dispersal patterns in this system, it appears unlikely that the decrease in apparent survival observed is caused by higher first-year dispersal. However, long-range dispersal appears to be important for sociable weavers, as several new females arrive each year in our population (all authors, personal observation). Future work on survival would benefit from a more complete description of dispersal patterns in this system, specifically the timing of (full range) dispersal and whether decisions to disperse are influenced by the conditions experienced by the offspring during their first year(s) of life. Furthermore, regular observations of the offspring right after fledging may allow a finer assessment of their survival probability and interactions within and outside the breeding group.

Temperature effects on first-year survival

There was only a tendency for MeanTmax during breeding to negatively associate with offspring first-year survival. Experiencing high maximum temperatures during nestling development could affect offspring early-life survival due to negative effects on nestling growth and body mass, caused by thermoregulation constraints, resource depletion or even reduced feeding activity of provisioners (Bourne et al., 2021). Studies in southern pied babblers, a cooperatively breeding species inhabiting a similar habitat to sociable weavers', have shown that being raised under hot and dry conditions can have negative effects on chicks' survival probability (Bourne et al., 2020a) and on juveniles' interannual survival (Bourne et al., 2020b). In our system, meanTmax has been similarly shown to associate with higher nestling mortality, both through predation and non-predator-related causes (e.g.: starvation, disease, etc.; D'Amelio et al., 2021). Here we only find a trend for negative meanTmax effects later in life, suggesting that harmful effects of being raised under high temperatures are mostly detectable at the nestling stage in this system, and may not have strong and long-lasting survival consequences.

We did not detect general winterTmin effects on first-year survival. In this semi-arid environment, temperature frequently drops below zero in winter (Paquet et al., 2016). Despite this, sociable weavers may be well equipped to deal with this temperature variation, as they live in massive colony structures and roost in groups inside their chambers. These structures have been shown to buffer external temperature variation and communal roosting appears to have important thermoregulation benefits in this species (Paquet et al., 2016; van Dijk et al., 2013; White et al., 1975).

Conclusion

Our study shows some indication that climatic conditions modulate the association between group size and offspring survival, although evidence was limited to the effect of rainfall on female offspring survival. This has important implications for our understanding of helper effects on reproductive output. In sociable weavers, optimal breeding group sizes for long-term offspring survival appear to differ according to the effects of climatic conditions and this is likely to be the case in other cooperative systems. With the increased possibilities offered by long-term data collections and the analytical methods currently available, we believe that more studies of the factors affecting survival in the post-fledging periods will considerably improve our understanding of the reproductive benefits of helping-at-the-nest.

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Appendix

Survival model accouting for fledging mass

A survival model was fitted with the same parameters described in the main text, now adding the interaction between group size and offspring mass at fledging, conditional on offspring sex, and the single effect of offspring mass on survival conditional on offspring sex. Model priors and diagnostics were as described in the main text and posterior estimates were obtained likewise too. Results are summarised in Table S6.1 and Figure S6.1.

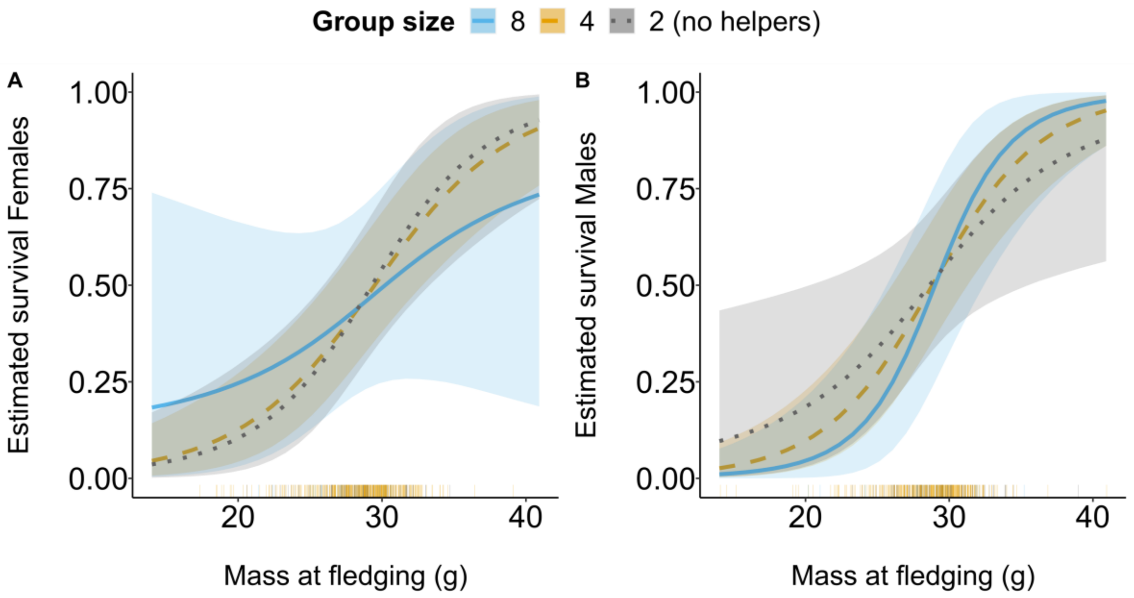

Figure S6. 1 Predicted effect of offspring mass at fledging on first-year survival probability of females (left) and males (right). Estimated survival is shown for fledglings raised in groups of different sizes: grey dotted line shows groups of 2 individuals (no helpers), orange dashed line shows groups of 4 (the nearest integer of average group size) and blue solid line shows groups of 8 (the nearest integer of mean between average group size and maximum group size). Rugs show the distribution of the x-axis variable for the respective sex and rug colours show raw data of group size values (grey for groups without helpers, orange for groups between 3 and 7 individuals, blue for groups above 7 individuals).

Table S6. 1 Parameter estimates (mean, SD standard deviation, 95CrI the 95% credible intervals and P>0 the proportion of the posterior that is greater than zero) for CMR model on offspring survival accounting for offspring mass at fledging.

Parameter	Mean	SD	95CrI	P>0
ϕ^{1st} intercept (females)	-0.22	0.32	-0.81 – 0.46	0.22
Sex (reference = female)				
Male	0.12	0.17	-0.21 – 0.45	0.76
Group size (females)	-0.01	0.17	-0.35 – 0.34	0.49
Group size (males)	-0.05	0.19	-0.43 – 0.32	0.39
Group size:Mass (females)	-0.1	0.13	-0.35 – 0.16	0.22
Group size:Mass (males)	0.17	0.15	-0.11 – 0.47	0.88
Group size:Rain (females)	-0.27	0.13	-0.52 – -0.02	0.02
Group size:Rain (males)	0.02	0.13	-0.24 – 0.29	0.57
Group size:MeanTmax (females)	-0.03	0.14	-0.31 – 0.25	0.41
Group size:MeanTmax (males)	0.23	0.16	-0.08 – 0.55	0.93
Group size:WinterTmin (females)	-0.15	0.13	-0.42 – 0.11	0.12
Group size:WinterTmin (males)	-0.16	0.14	-0.43 – 0.11	0.13
Mass (females)	0.6	0.14	0.34 – 0.89	1
Mass (males)	0.78	0.16	0.48 – 1.11	1
Rain (females)	-0.3	0.18	-0.66 – 0.05	0.05
Rain (males)	-0.17	0.19	-0.55 – 0.2	0.18
MeanTmax (females)	0.03	0.13	-0.23 – 0.29	0.59
MeanTmax (males)	0.13	0.14	-0.15 – 0.42	0.82
WinterTmin (females)	-0.21	0.25	-0.76 – 0.26	0.18
WinterTmin (males)	-0.11	0.25	-0.66 – 0.36	0.33
Time difference (birth-capture)	-0.35	0.19	-0.72 – 0.02	0.03
Predation treatment (reference = natural)				
Protected	0.25	0.23	-0.2 – 0.71	0.86
Predation treatment:Group size				
Protected	0.11	0.21	-0.31 – 0.53	0.69
Colony ID	0.22	0.15	0.01 - 0.57	
Father ID	0.22	0.15	0.01 - 0.57	
Mother ID	0.2	0.15	0.01 - 0.54	
Breeding attempt ID	0.76	0.23	0.23 - 1.19	
Season	0.48	0.3	0.04 - 1.23	
p^{1st} intercept (females)	1.8	0.22	1.38 - 2.26	1
Sex				
Males	-0.28	0.3	-0.86 - 0.3	0.17
ϕ^{A}	0.7	0.02	0.66 - 0.73	
p^{A}	0.81	0.02	0.76 - 0.85	

Chapter 7

General Discussion

The aims of this thesis were to 1) provide a comprehensive understanding of how environmental factors – climate, predation risk, social groups – associate with prenatal maternal allocation, 2) explore the link between offspring begging behaviour and cooperative care rules, and 3) investigate whether helpers modulate the effect of climatic conditions on offspring early-life survival, in cooperatively breeding sociable weavers *Philetairus socius*.

The first three studies of this thesis focused on environmental effects on prenatal maternal allocation. First, a long-term dataset was used to examine how egg mass and clutch size varied in relation to climatic conditions, experimentally reduced nest predation risk and number of helpers (Chapter 2). Then, an exhaustive analysis was conducted to test whether egg nutrients and hormones varied with number of helpers, and if resource distribution with laying order was modulated by number of helpers (Chapter 3). In the last study on maternal allocation, adult predation risk was experimentally manipulated to understand how adults' predation risk affected clutch size, egg size and composition, and if group size buffered negative effects of predation risk on maternal allocation (Chapter 4). Altogether, these studies showed that the number of helpers did not detectably buffer climatic or predation risk effects on maternal allocation. Helpers' presence appeared, however, to mitigate the negative association between laying order and yolk mass and lipids concentration. Overall, sociable weaver females seemed to allocate more resources to reproduction when breeding in better conditions. Females laid larger clutches after higher rainfall and under reduced nest predation risk, and laid eggs with greater nutritional content, specifically lipids and yolk mass of later-laid eggs, when breeding with more helpers. In addition, mothers laid eggs with lighter yolks when breeding under higher perceived adult predation risk. No evidence for egg mass adjustments was detected in relation to environmental variables.

The fourth study investigated how offspring begging behaviour, a trait found to be affected by prenatal maternal effects in this species, was associated with breeders' and helpers' feeding effort. While breeding males returned to the nest to feed faster after broods begged at higher rates, there was no evidence that helpers' feeding behaviour was adjusted to offspring begging, and this was independent of their sex and level of relatedness to the offspring (Chapter 5).

How the number of helpers in a breeding group associated with offspring survival was also assessed, to investigate if group size, either via its influence on maternal allocation and/or via helping-at-the-nest, had effects on offspring short- and long-term survival. Helper number was found to positively correlate with nestling fledging probability independently of egg laying order, suggesting that all hatched nestlings gain similar survival benefits when raised with more helpers (Chapter 3). To estimate possible long-term effects of being raised in larger breeding groups and how this interacts with rainfall and temperature conditions, I used capture-mark-recapture analyses and found some, although limited, indication that number of helpers modulates the association between climatic conditions and offspring first-year survival. Specifically, female offspring showed higher first-year survival when raised with more helpers in low rainfall conditions (Chapter 6).

Environmental effects on prenatal maternal allocation

In cooperatively breeding systems, helper presence and number have been suggested to influence maternal allocation strategies mostly via clutch size or egg size (Dixit et al., 2017; Lejeune et al., 2016; Russell, Langmore, et al., 2007; Taborsky et al., 2007; Woxvold & Magrath, 2005). While the associations reported between helpers' presence and clutch size indicate that females with helpers produce larger clutches (Lejeune et al., 2016; Woxvold & Magrath, 2005), the association with egg mass is often found to be negative (Russell, Langmore, et al., 2007; Taborsky et al., 2007; but see Valencia et al., 2017). A recent meta-analysis across cooperatively breeding species reported that, for egg mass, load-lightening in the presence of helpers received overall greater support than differential allocation (Dixit et al., 2017). Egg components have rarely been studied in relation to helpers' presence, but existing evidence likewise suggests lower allocation to yolk mass and lipids, along with hormones, when females breed with helpers (Paquet et al., 2013; Russell, Langmore, et al., 2007).

In sociable weavers, we predicted that females would lay smaller eggs when breeding with more helpers (i.e., prenatal load-lightening) especially under favourable climatic and nest predation risk conditions. There were several reasons to predict prenatal load-lightening in this species, as opposed to differential allocation (Sheldon, 2000; Valencia et al., 2017), at least in certain environmental conditions. First, parents assisted by helpers were found to feed at lower rates than pairs without helpers (Covas et al., 2008), and prenatal load-lightening has been suggested to be more evident in species where females also show postnatal load-lightening (Dixit et al., 2017). Moreover, sociable weavers are relatively long-lived birds, and can therefore be expected to maximise lifetime reproductive success through favouring own survival over reproduction (Clutton-Brock, 1988), which could be done via reducing allocation to eggs when breeding with more helpers (Paquet, Doutrelant, et al., 2015). And lastly, previous findings from a short-term investigation in sociable weavers showed that females with helpers laid lighter eggs than females without helpers (Paquet et al., 2013).

Contrary to these predictions, the first study of this thesis showed that egg mass and clutch size were not found to vary as sociable weaver females gained and lost helpers over nine breeding seasons (Chapter 2). Egg mass did not detectably vary in relation to number of helpers, nor in relation to variation in climatic conditions and predation risk (Chapters 2 and 4). Moreover, we found a clear effect of females' size (tarsus) on egg mass, and found that female identity traits, independent of size, explained a large proportion of egg mass variation (Chapter 2). This lack of evidence for egg mass plasticity suggests that, in sociable weavers, females' ability to lay eggs of variable size may be limited by individual features (Chapter 2). Likewise, variation in clutch size in response to helper number was not detected (see Lejeune et al., 2016; Woxvold & Magrath, 2005; for helper effects on clutch size). However, clutch size showed low within-female repeatability and varied positively with rainfall and nest predation risk (Chapter 2). This indicates that females might benefit from adjusting clutch size in relation to climate and predation risk, but not in relation to number of helpers, which may be a strategy to maximise reproductive output under favourable conditions (Stearns, 1992).

The findings from Chapter 3 showed that helper effects on maternal allocation were more evident at the level of the eggs' nutritional content (Chapter 3). Specifically, females with more helpers produced later-laid eggs with heavier yolks and richer in lipids, and yolk lipids were generally positively correlated with number of helpers (Chapter 3). This concurs with 'differential allocation' predictions that females should invest more when breeding with more helpers (Savage et al., 2015; Sheldon, 2000) and is the first evidence of a positive association between females' allocation to yolk mass and lipids and number of helpers in cooperative breeders. Theoretical work suggests that maternal investment can be predicted to be reduced in the presence of helpers if prenatal resource allocation is interchangeable with postnatal care (Savage et al., 2015). If instead prenatal resource allocation confers benefits to the offspring that are not interchangeable, for instance, by priming offspring to receive more postnatal care, maternal investment is expected to increase in the presence of helpers (Savage et al., 2015). The latter could be the case in sociable weavers, as there is evidence that prenatal investment may influence offspring begging behaviour (Paquet, Covas, et al., 2015) and thus the rate at which nestlings are fed (Chapter 5). This should be especially important for hatchlings from later-laid eggs, which may be at a disadvantage due to hatching asynchrony (Covas & Du Plessis, 2005; van Dijk et al., 2013). Besides, concentrations of some yolk lipids, as fatty acids, have been found to associate with higher hatching probability in great tits *Parus major* (Mentesana et al., 2021), which could be another example of non-interchangeable pre-birth investment in sociable weavers, as later-laid eggs have been found to have lower hatching success (Chapter 3). Yet, there was no evidence of an association between group size and egg hatching success overall, nor for later-laid eggs (Chapter 3), suggesting that eggs laid by females with more helpers do not appear to have this fitness advantage.

Among the egg components analysed in Chapter 3 – yolk mass, lipids, proteins, carotenoids, vitamins A and E, testosterone, androstenedione and corticosterone concentrations – differences in relation to number of helpers were only found in yolk mass and concentration of lipids. This contrasts with results from a previous investigation in sociable weavers, where females with helpers laid eggs with lower concentration of hormones (only the first laid egg was analysed; Paquet et al., 2013). The discrepancy between the two studies may have been caused by variation in other environmental or social cues that also affect hormones' accumulation in the eggs (Bebbington & Groothuis, 2021; Groothuis et al., 2020), such as social interactions at the colony level (Schwabl, 1997). Colony size appears to have important effects on fitness in this species, as it has been found to negatively associate with the number of fledglings produced per season (Covas et al., 2008), although it may have positive effects on juveniles' and adults' survival (Brown et al., 2003). Whether colony size influences maternal allocation is therefore something that deserves attention in the future and could help understanding whether hormonal allocation to eggs is affected by this additional level of sociality in sociable weavers. Given the importance of social contexts for hormonal transfers from females to eggs (Gil et al., 2007; Pilz & Smith, 2004; Safran et al., 2010), and that sociable weavers are the only study system where egg hormones variation in relation to females' breeding group sizes has been investigated (Chapter 3; Paquet et al., 2013), it would be relevant to extend this assessment to other cooperatively breeding species before discarding the potential for helper effects on egg hormonal changes.

Another environmental factor that was expected to affect maternal allocation strategies was adult predation risk, especially because sociable weavers are a long-lived species and can therefore be expected to invest less in reproduction when their own survival is threatened (Erikstad et al., 1998; Ghalambor & Martin, 2000). The aim of Chapter 4 was to experimentally test how this different type of predation risk affected maternal allocation, and to investigate whether breeding group sizes would buffer potential predation risk effects on maternal allocation. Results showed that yolk mass was the only maternal allocation component that was affected by playbacks of an avian predator of adult sociable weavers, whereas clutch size, egg mass and yolk corticosterone levels were not affected by the predator playback (Chapter 4). Manipulating two types of predation pressure, adult predation risk (Chapter 4) and nest predation risk (Chapter 2), led to different maternal allocation responses. Females laid more eggs per clutch when nest predation risk was reduced and instead laid eggs with lighter yolks when exposed to an adults' predator. In high predation risk environments, allocating less nutrients to eggs when exposed to predators may be a more 'reversible' strategy (i.e.: less permanent) than laying less eggs per clutch, if the conditions improve after laying (Fontaine & Martin, 2006).

These findings indicate once more that yolk mass variation may be an important pathway for flexible maternal allocation in response to the environment. However, the findings in Chapters 3 and 4 may be limited by relatively low sample sizes for yolk mass measurements, 122 and 77 eggs respectively, and by including only between-female comparisons over a short period. One other limitation of these studies is that we cannot conclude on the mechanisms behind the egg content differences detected. Reduced yolk mass when under high predation risk conditions could be a passive or active process. It could be a carry-over effect of females being in lower condition, for instance due to reduced foraging behaviour. Alternatively, it could arise from an active 'selfish' strategy of lower investment in reproduction in adverse conditions, if this energy saving allows females to have higher reproductive success and/or survival in the future. A third possibility is an active 'anticipatory' strategy if offspring from predator-exposed females have higher success in high predation-risk environments, for instance due to being lighter and thus faster at escaping predators (Badyaev, 2005; Coslovsky & Richner, 2011; Marshall & Uller, 2007; Morales et al., 2018; Mousseau & Fox, 1998). In the case of Chapter 4, it would be feasible and relevant to assess hatching/fledging probability of offspring from predator-exposed females, as well as their size and condition, to better understand whether differences in yolk mass, or other maternal allocation measures that we did not account for, could have been an advantage or a disadvantage for offspring.

Even though yolk mass was negatively affected by females' perception of predation risk (measured in the 3rd egg; Chapter 4) and was found to positively vary with number of helpers for later-laid eggs (Chapter 3), interactive group size and predation risk effects on yolk mass were not detected. Similarly, in Chapter 2, we found no evidence that helper effects on maternal allocation were modulated by climatic conditions, which contrasts with results from a long-term investigation in superb fairy-wrens (Langmore et al., 2016). In addition, we assessed whether helper effects were modulated by experimentally manipulated nest predation risk, an environmental factor that is critical for sociable weavers' reproductive success (Covas et al., 2008). Again, no interactive effect between nest predation risk and social environment was detected on maternal allocation. Overall, these findings challenge the idea that helper number may buffer the effects of other ecological and climatic factors on maternal allocation (Chapters 2 and 4). Yet, this has been investigated in few species (Koenig et al., 2009; Langmore et al., 2016; Chapter 2), and we therefore cannot conclude if interactive effects of helper presence and remaining environmental conditions on maternal allocation are frequent in cooperatively breeding systems.

Offspring begging and feeding responses of breeders and helpers

The next study investigated if offspring phenotype, specifically begging behaviour, associated with feeding effort, showing that breeding females' and helpers' feeding intervals did not seem to be influenced by offspring begging behaviour, while breeding males appeared responsive to this cue (Chapter 5). These findings provided a better understanding of feeding rules in this cooperatively breeding species and are interesting both from a maternal effects perspective and from a cooperative breeding one.

It is interesting for the study of maternal effects because offspring begging behaviour has been found to vary with females' prenatal social environment in sociable weavers, with females with less helpers producing offspring that begged at higher rates (Paquet, Covas, et al., 2015). If nest attendants respond to begging behaviour, females might have an influence on the amount of care provided by other individuals via prenatal allocation of resources to offspring, such as egg hormones (Eising & Groothuis, 2003). Our study showed that breeding males, but not females, fed faster after experiencing higher begging rates, thus concurring with the idea that maternal effects on begging behaviour may influence the parental investment of their partners (see Paquet & Smiseth, 2016).

On the other hand, helpers' feeding intervals were not found to vary with offspring begging, and this result was similar for helpers of both sexes and with different levels of relatedness to the offspring. This suggests that helpers' feeding investment does not seem to be conditional on this phenotypic trait that may be under maternal influence.

From a cooperatively breeding benefits/costs perspective, it implies that any direct and/or indirect fitness benefits for helpers are not maximised via adjusting feeding effort to offspring demand. Nevertheless, it is possible that care provisioners respond to other offspring phenotypic and behavioural traits that were not investigated here, like offspring size or condition (Kilner, 2002), which could also be under the influence of prenatal maternal effects (Krist, 2011; Williams, 1994). Additional data on nestlings' gape yellow colouration has been collected and found to vary with nestling mass, age and brood size (author's personal observation), thus suggesting that it may vary with resource availability, and this could be an alternative phenotypic trait used to test whether care provisioners respond to other potential signals of need or quality. In this and other species, experimental manipulations of offspring phenotype, for instance via food-supplements or begging playback experiments, could be used to verify that there is a causal effect of offspring phenotype on the amount of care they receive. Furthermore, manipulating females' environment, via food supplementation or removal of helpers, and then measuring offspring phenotypic traits found to influence care levels, would provide a greater insight on whether females may modify their offspring phenotype via maternal effects and ultimately influence helping-at-the-nest.

Helper responses to begging behaviour, and specifically helpers of different sex and relatedness to the offspring, have rarely been explored within cooperatively breeding species. However, existing studies have shown that helpers, like parents, increase their feeding effort when offspring begging is higher (see Chapter 5), even when helpers of different sex (English et al., 2008; MacLeod & Brouwer, 2018; Wright, 1998; Wright et al., 2010) and relatedness (te Marvelde et al., 2009) are present. This study provided novel insights on cooperative care rules in relation to offspring demand, by suggesting that these can vary with provisioners' sex and life-history stage. A necessary next step would be to test whether sociable weaver helpers use any other offspring phenotypic cue to modulate their feeding effort or are indeed an exception to the general pattern found in cooperative breeders.

Helper number and climatic effects on offspring first-year survival

The last study in this thesis investigates if helper number influences offspring early-life survival, which could happen via helper effects on maternal allocation, postnatal helper effects on offspring condition and survival, or a combination of both. The aim here was to test if there were "concealed" helper effects, after the postnatal rearing period, that could still influence offspring survival and thus breeders' reproductive success. For this, I tested if being raised by more helpers associated with offspring first-year survival, and if helper effects on offspring survival interacted with climatic conditions during the breeding season and during winter (Chapter 6).

A recent multi-year investigation in sociable weavers found a clear general association between group size and full-broods' fledging success (D'Amelio et al., 2021; see also Covas et al., 2008). This finding is in agreement with the results from Chapter 3, showing that nestlings have a higher probability of fledging in larger groups independently of laying order, and thus independently of potential negative effects of biased resource distribution within clutches or of hatching asynchrony (van Dijk et al., 2013; Chapter 3). Generally, this suggests that helpers improve females' environment and confer short-term fitness advantages to the offspring, as shown in other cooperatively breeding birds (Downing et al., 2020).

After fledging, we found interactive effects of group size and climatic conditions on first-year survival, but evidence was limited to female offspring. Females had higher survival if raised with more helpers under low levels of rainfall. Instead, when benign climatic conditions were experienced, associations between helper number and offspring survival tended to be negative. No general helper effects on offspring survival were detected. These findings suggest that, contrary to what happens during the rearing period (D'Amelio et al., 2021), optimal group sizes for long-term offspring survival differ according to climatic effects, especially rainfall and especially for female offspring. The sex-specific effects of rainfall levels found here could be caused by dominance differences, as in sociable weavers females are the subordinate sex (Rat et al., 2015), or by sex-specific dispersal patterns (Leon et al., 2022; van Dijk et al., 2015). Even though dispersal within the study area is uncommon for females in their first year (1-2%; Chapter 6), this may not be the full picture of dispersal patterns in sociable weavers, as females are known to disperse long distances in this system (author's personal observation). In systems where dominance, dispersal and other life-history strategies are sex-specific, it is thus recommended that sex effects are integrated when addressing environmental effects on early-life offspring survival.

This study generated novel insights on lasting helper effects on offspring first-year survival by showing that, different from what was found in relation to hot dry weather in southern pied babblers (Bourne et al., 2020), helpers may buffer negative effects of low rainfall levels on female offspring first-year survival. It was interesting to note that being raised in large groups may also have strengthened negative high rainfall effects on females' survival or dispersal decisions (Chapter 6). This indicates that if longer-term helper effects on offspring post-fledging survival and their interaction with other environmental effects are overlooked, we may be under or overestimating helping-at-the-nest benefits for reproductive success, which is amongst the most central questions in the study of cooperative breeding.

Concluding remarks and future research

The findings obtained here contributed to our current knowledge on helper effects in sociable weavers and across cooperatively breeding species. In sociable weavers, previous findings of load-lightening in relation to egg mass (Paquet et al., 2013) have now been updated with the result that egg mass does not appear to vary with number of helpers (Chapter 2). Moreover, the results from Chapter 2 concur with findings in other long-term investigations showing that when plastic responses to helper number are specifically tested for, no clear variation in egg size is found (Lejeune et al., 2016; see also Langmore et al., 2016). This highlights the importance of individual-based long-term datasets to tackle these type of questions (Cockburn, 2014). Besides this, we found evidence for variation in egg components, for which helper effects are still poorly understood, suggesting that females allocate more resources via yolk mass and lipids when breeding with more helpers (Chapter 3). Even if based on a short-term study, these last findings changed our perspective of helper effects on maternal allocation in sociable weavers, as there is now more support for differential allocation, via egg nutritional composition and specifically towards later-laid eggs, than for prenatal load-lightening (Chapters 2 and 3).

Moreover, the estimate of egg mass variation with group size obtained here was used to recalculate the estimates in the meta-analysis of Dixit et al. (2017; Chapter 2), and results now indicate no general tendency of load-lightening via egg size across cooperative breeders (see Chapter 2). This challenges the generalised idea of 'concealed helper effects', via prenatal load-lightening, in cooperative breeders (Dixit et al., 2017; Russell, Langmore, et al., 2007). Generalised helper effects on prenatal maternal allocation should therefore be reassessed in light of the latest studies suggesting that helper number is not found to associate with egg size in long-term investigations (Chapter 2; Cusick et al., 2018; Lejeune et al., 2016; Zhao et al., 2019; see also non peer-reviewed work in Capilla-Lasheras et al., 2021; Van de Loock, 2019).

The finding that yolk mass and lipids varied with number of helpers, particularly for later-laid eggs, brings back the idea that variation in eggs' nutritional content may be an alternative pathway for flexible maternal allocation, as suggested in Russel et al. (2007). Here, it suggests a plastic prenatal strategy that could benefit females when brood reduction is likely to occur (on average 25-35% of nests suffer brood reduction in sociable weavers; stronger effects without helpers, see D'Amelio et al., 2021), as they could bias investment towards eggs that are more likely to be successful (Chapter 3), instead of decreasing maternal investment in all eggs. These findings therefore suggest an alternative prediction to differential allocation in relation to helpers, focused on later-laid eggs, which should be investigated in other cooperatively breeding birds where brood reduction is frequent. The fitness relevance of eggs with larger yolks and more lipids also needs to be investigated in the future. This could be done by food-supplementing females, after confirming that this leads to the production of larger yolks with more lipids (Morosinotto et al., 2019), and measuring offspring quality and survival of food-supplemented females. Alternatively, non-destructive methods could be developed to directly assess yolk mass (Ardia et al., 2006) and yolk:albumen ratio in eggs, based on techniques frequently used in food quality and poultry studies (Ketelaere et al., 2004; Kuchida et al., 1999). Besides, it would be important to assess the robustness of this finding by testing whether the differences detected represent within-female adjustments to helper number or fixed differences between females, and how these vary across environmental conditions, in a similar way to what has been done for egg mass (Chapter 2). In sum, more detailed data is needed in sociable weavers and in other systems to establish if variation in egg components, specifically yolk size and nutrients, is a pathway for maternal allocation adjustments to number of helpers.

There are also other avenues for helper effects that were not explored in this work but could be interesting to tackle in the future. Since females reduce their postnatal care when breeding in larger groups in this (Covas et al., 2008) and other cooperatively breeding species (Crick, 1992), females in larger groups could be able to invest more in their subsequent reproductive attempts, or take less time to start a new breeding attempt when the previous one fails (Blackmore & Heinsohn, 2007; Woxvold & Magrath, 2005; but see Covas et al., 2008 where a two-year study in sociable weavers has not found the latter; see also De la Cruz et al., 2022 for helper effects on replacement clutches' success). Offspring mortality by predators can be quite high in some of these cooperatively breeding systems (e.g.: sociable weavers, Covas et al. 2008; long-tailed tits, Hatchwell, 2016; superb fairy-wrens, Cockburn et al., 2016; bell miners, Wright &

McDonald; 2016; etc.), and it would be interesting to test these helper effects in species where nest predation is intense and there may be the need to lay (several) replacement clutches within a season.

To conclude, I encourage long-term investigations in other cooperatively breeding species (e.g.: Dickinson & Koenig, 2016) to adopt this multivariate view of the environments when studying helper effects, as they offer a unique opportunity to address within-individual changes across time and environmental conditions. Here, this allowed us to better understand which reproductive traits seem fixed and plastic within females (Chapter 2) and the remaining environmental pressures that females may be exposed to at the time of egg laying (Chapters 2, 3 and 4). At the end of this work, it also becomes clear that it is necessary to study how helpers influence prenatal maternal allocation, along with offspring survival after the rearing period, to have a full picture on the benefits and costs of breeding with helpers in cooperative breeders (see also Russell, Young, et al., 2007; Russell & Lummaa, 2009). Lastly, Chapters 5 and 6 highlight that the study of maternal allocation strategies and helper effects in cooperative breeders continues to offer exciting future research avenues, as we are at the start of understanding whether maternal effects may influence the care provided by other individuals, and how prenatal maternal care and postnatal helper care combine to affect offspring short and long-term survival in multidimensional and dynamic environments.

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Appendix A: List of additional publications

Ferreira AC, Covas R, Silva LR, Esteves SC, Duarte IF, Fortuna R, Theron F, Doutrelant C & Farine, DR (2020). *How to make methodological decisions when inferring social networks*. Ecology and Evolution, 2020;00:1–12. https://doi.org/10.1002/ece3.6568

Author contributions: André C. Ferreira: Conceptualization (equal); data curation (equal); formal analysis (equal); methodology (equal); writing–original draft (equal). Rita Covas: Funding acquisition (equal); resources (equal); supervision (supporting); writing–original draft (equal); writing–review and editing (equal). Liliana R. Silva: Data curation (equal); methodology (equal); writing–review and editing (equal). Sandra C. Esteves: Data curation (equal); methodology (equal); writing–review and editing (equal). Inês F. Duarte: Data curation (equal); writing–review and editing (equal). Rita Fortuna: Data curation (equal); writing–review and editing (equal). Franck Theron: Data curation (equal); writing–review and editing (equal). Claire Doutrelant: Funding acquisition (equal); methodology (equal); resources (equal); supervision (supporting); writing–original draft (equal); writing–review and editing (equal). Damien R. Farine: Conceptualization (equal); methodology (equal); supervision (lead); writing–original draft (equal); writing–review and editing (equal).

D'Amelio PB, Ferreira AC, Fortuna R, Paquet M, Silva LR, Theron F, Doutrelant C & Covas R. (2021). *Disentangling climatic and nest predator impact on reproductive output reveals adverse high-temperature effects regardless of helper number in an arid-region cooperative bird*. Ecology Letters, 25, 151-162, https://doi.org/10.1111/ele.13913

Author contributions:

PD, RC, CD, RF, AF and LS designed the study. MP, RC, CD, RF, FT, AF and LS contributed to collecting the data. RF, AF, FT and LS processed and stored the data. PD analysed and interpreted the data with input from all the authors. PD wrote the first manuscript draft and all authors contributed substantially to every draft since. RC and CD initiated the data collection and supervised the work.