Contrasting effects of cooperative group size and number of helpers on maternal investment in eggs and nestlings

Van de Loock, Dries 1,2,3 †

Cousseau, Laurence 1†

Apfelbeck, Beate 3, 5

Githiru, Mwangi 3,4

Lens, Luc 1,\*

Matthysen, Erik 2,\*

1 Terrestrial Ecology Unit, Ghent University, K. L. Ledeganckstraat 35, 9000 Ghent, Belgium

2 Evolutionary Ecology Group, University of Antwerp, Campus Drie Eiken, Universiteitsplein 1, 2610 Wilrijk, Belgium

3 Department of Zoology, National Museums of Kenya, P.O. Box 40658-00100, Nairobi, Kenya

4 Wildlife Works, P.O. Box 310-80300, Voi, Kenya

5 Evolutionary Zoology Group, Biosciences, University of Salzburg, Hellbrunnerstr. 34, 5020 Salzburg, Austria

† Shared first authorship

\* Shared last authorship

Corresponding author:

L. Cousseau. E-mail: laurence.cousseau@ugent.be

**Keywords** : Placid Greenbul, egg size, feeding rates, social factors, tropical forest, cooperative breeding, load-lightening strategy, additive strategy

# ABSTRACT

Females are predicted to adjust their reproductive investment to optimize the trade-off between current and future reproduction. In many cooperatively breeding birds, females have been shown to reduce their investment both pre- and post-hatching in response to the presence of food-provisioning helpers. However, in species where not all group members help during the post-hatching phase, it is currently unclear to which social cues (i.e. group size vs. number of helpers) females should tune their investment. Here, we use the cooperatively breeding placid greenbul (*Phyllastrephus placidus*) as a model species to examine whether and how group size and number of helpers affect female investment in eggs and food provisioning. We found that females used a contrasting strategy pre- and post-hatching in response to different social cues: they laid larger eggs in larger groups while reducing their feeding ratewhen assisted by more helpers. We also found that fledging success increased with group size and that nestlings raised in groups with helpers fledged with longer wings but found no relation between condition of the young and number of helpers. Since the perceived contrasting investment strategies may have several underlying causes, we conclude that predicting the influence of social conditions on maternal investment may be more challenging than previously believed.

# INTRODUCTION

Life-history theory predicts that animals optimize their life-time reproductive success by trading off their investment in current reproduction against the expected survival and reproduction in the future (Roff 2002; Roff and Fairbairn 2007). Female birds can balance this trade-off by tuning their investment both pre-hatching (e.g. egg size; Christians 2002) and post-hatching (e.g. feeding rate; Mutzel et al. 2013) to environmental or social drivers, such as the predicted or perceived levels of food availability or predation pressure, or the presence of helpers (Crick 1992; Lima 2009; Grüebler et al. 2018; Fortuna et al. 2021). Social drivers are particularly relevant in cooperatively breeding species where breeders may receive help in raising offspring from a variable number of non-breeders. Non-breeder contributions may take the form of food provisioning to nestlings, taking part in territory or anti-predator defence, or performing other nest-related duties (Koenig and Dickinson 2016; Cusick et al. 2018). However, understanding how maternal investment strategies are shaped by the presence of helpers remains challenging due to the various breeding stages involved, the modulating role of environmental conditions, and uncertainties on the exact amount of help to be expected (Langmore et al. 2016; Lejeune et al. 2016; Valencia et al. 2017; Savage and Hinde 2019).

Females may respond to the presence of food provisioning helpers (henceforth called ‘helpers’) by lowering their own investment. Thereby they can improve their survival and future reproductive success (‘load-lightening strategy’; Crick 1992) without jeopardizing the current investment, as helpers can compensate for the reduction in maternal investment (Russell et al. 2007; Canestrari et al. 2011). Accordingly, many studies on cooperative birds have shown that females reduce their nest feeding rates in the presence of helpers (Hatchwell 1999; MacColl and Hatchwell 2003; Koenig and Walters 2012; van Boheemen et al. 2019). Even when females reduce their food provisioning, offspring often receive more food when helpers are present (Hatchwell 1999; Russell et al. 2008). Hence, if pre-hatching and post-hatching investment are substitutable (i.e. change in investment at one stage can be compensated during another stage without affecting offspring fitness, (Savage et al. 2015)), females can also reduce their investment by laying smaller eggs when help during subsequent chick rearing can be expected (Russell et al. 2007; Dixit et al. 2017). When studying maternal investment in cooperatively breeding species, it is thus important to consider how the presence of helpers affects female investment during different stages of reproduction and how different investment decisions affect offspring fitness.

A load-lightening strategy in response to food provisioning by helpers, either pre- or post-hatching, is particularly expected in tropical environments where birds lay small clutches and experience low nest success due to predation, but can breed multiple times per year and in multiple seasons, given their high survival rates (Ghalambor and Martin 2001; Russell and Lummaa 2009). However, load-lightening in response to the presence of helpers is not expected in all contexts. Under adverse environmental breeding conditions, such as low food availability or harsh climatic conditions (Luck 2002; Langmore et al. 2016), the effect of helpers on offspring fitness increases (Magrath 2001) and, in this case, females are predicted to take advantage of the presence of helpers to raise the value of offspring by maintaining or increasing their own investment (‘additive strategy’, Hatchwell 1999). Such increased total investment may improve the offspring’s ability to cope with initial adverse conditions (Ratikainen and Kokko 2010), which can have a long-term positive effect on their fitness (Van De Pol et al. 2006).

In the post-hatching stage (i.e. nestling provisioning), females may be able to modulate their investment in direct response to current socio-environmental rearing conditions. In contrast, this is much more challenging for pre-hatching investment, when resource availability or helper contributions during nestling provisioning may not yet be known (Valencia et al. 2017). While in some species, group size during the onset of egg laying may accurately reflect the amount of help a female will receive during the post-hatching stage (Russell et al. 2007), in many cooperative breeding systems, non-breeding group members may include both helpers and non-helpers and may show individual variation in helping contribution (e.g. Baglione et al. 2010; Kingma et al. 2010; Fortuna et al. 2021). Even though a non-breeding member’s contribution to food provisioning may be predictable to some degree by its sex, age or kinship (Koenig and Walters 2011; Green et al. 2016; Barati et al. 2018), some uncertainty may still be present at the time of egg laying. However, it remains unclear to what extent females tailor their level of pre-hatching maternal investment to the total number of group members present (as a proxy for the number of helpers), or whether they use additional social cues. Moreover, group size can also affect maternal investment strategies directly, irrespective of the fact that it represents a pool of potential helpers. This is for instance the case when larger groups increase competition for resources, with inverse effects on maternal condition and consequently on her reproductive allocation (Christians 2002), or when group size positively affects breeding conditions through reduced predation risk or increased foraging efficiency (Majolo and Huang 2017), which can also affect maternal investment strategies (Valencia et al. 2017; Fortuna et al. 2021). Teasing apart effects of group size and of number of food provisioning helpers on maternal investment strategies is thus crucial when studying maternal investment strategies.

In this study, we investigate how females of a tropical facultative cooperative bird species, the placid greenbul (*Phyllastrephus placidus)* tune their reproductive investment to group size and the number of food provisioning helpers during different breeding stages (i.e. pre- and post-hatching). While in our study population both pairs (group size = 2) and social groups (group size ≥ 3) can successfully raise young, 72% of the pairs breed with at least one, and up to a maximum of 5 subordinates. In up to 64% of these social groups, one to four of the subordinates help with nestling provisioning and these subordinates are hence referred to as ‘helpers’ (Van de Loock 2019). While first-order kinship to the dominant female seems to be a prerequisite for helping, it is not a strong predictor of helping since only 54% of these individuals take part in provisioning (Cousseau et al. 2022). Subordinate sex, age or relatedness to the dominant male do not explain additional variation in helping propensity (Cousseau et al. 2022). Thus, during the pre-hatching phase, females may not be able to predict helper contribution post-hatching with high certainty. While in this study population nestling starvation very rarely occurs, high predation pressure can result in up to 70% nest failure (Spanhove et al. 2014). Yet, placid greenbuls are relatively long-lived (oldest individual re-trap: 19 year-old) and breeding pairs have multiple reproductive opportunities during their lifetime. We thus expect females to invest in future reproductive opportunities rather than in the current attempt when help is expected, and thus adopt a load-lightening rather than an additive investment strategy during both pre-hatching (egg size) and post-hatching (food provisioning). Given the uncertainty about the expected amount of post-hatching help and resource availability during the pre-hatching stage, we further predict that load-lightening will be less clearly expressed at this stage compared to post-hatching. We also predict that pre-hatching investment is tuned to group size as a proxy for the expected help, rather than to the actual number of helpers. Finally, as a corollary of the load-lightening hypothesis, we predict that neither nestling size, nor condition or fledging success are related to the number of helpers (i.e. helpers fully compensate for the reduction in maternal investment).

# MATERIALS & METHODS

## Study system

We conducted our study in the indigenous cloud forest archipelago of the Taita Hills, South-East Kenya (3°25′S, 38°20′E), where the medium-sized, insectivorous placid greenbul inhabits dense cloud forest understory. Such habitat occurs in a highly scattered and fragmented pattern in the study area, where the landscape is dominated by exotic plantations and small-scale subsistence agriculture (Lovett and Wasser 1993; Burgess et al. 2007; Pellikka et al. 2009). Cloud forest remnants vary in patch size (between 120 and 2 ha, Pellikka et al. 2009) and level of habitat degradation as inferred from the current vegetation composition and structure (Wilder et al. 1998; Chege and Bytebier 2005; Aerts et al. 2011). Due to continued ringing and nest monitoring effort since 1996 and 2007, respectively, ca. 75% of the greenbul population is colour-banded at any time (based on the ratio of colour-banded individuals vs. total traps during mist-netting).

The greenbuls’ extended breeding season coincides with the onset of the short rainy season in November and may last up to March. Typically, female greenbuls lay and incubate a clutch of two eggs (mean +- SD: 1.94 +- 0.38; range 1-3; n = 980 clutches) for 15-17 days, and nestlings fledge around 11-12 days after hatching. Breeding pairs and groups frequently re-nest after failure and occasionally after successfully fledging chicks, and they occupy the same territory for multiple consecutive breeding seasons (Lens L. Unpubl. Data). Both the size and the composition of breeding groups remain stable during a given breeding season. Although forests fragments vary in size, degree of degradation and possibly predation pressure, size of breeding groups and number of helpers do not consistently vary between forest fragments (Van de Loock 2019).

## Data collection and handling

We monitored nests and recorded breeding characteristics in two large (120 and 86 ha) and six small (between 16 and 2 ha) indigenous cloud forest fragments during six breeding seasons between 2012 and 2019. Whenever possible, we measured eggs, nestlings and provisioning rates, and assessed the social structure and composition (group size, number of helpers) associated with each of the located nests. We measured egg length and width with a digital calliper (± 0.01mm) upon clutch completion. We used Hoyt’s formula (0.51 × length × width²) to calculate individual egg sizes and averaged these egg size measures per clutch (Hoyt 1979) as a measure of pre-hatching investment. We used egg size rather than mass, as the latter shows a decrease over time (Krist 2011). Nestlings were metal- and colour- banded and their body mass, wing and tarsus length were measured when ca. 9 days old (range 7 – 12 days). Nests were considered successful when offspring were still in the nest 3 days before the predicted fledging age (~ 12 days), and no signs of nest predation were observed during a follow-up visit. Post-fledging analysis revealed that this accurately reflects fledging success (Van de Loock et al. 2017) while nest disturbance around the fledging date is reduced.

We used a combination of mist-netting, visual observation, and nest video recording at each of the located nests to identify the breeding pair and to assess the presence, identity and role of other group members. These group members, or subordinates, are considered ‘helpers’ when they contribute to nestling provisioning or ‘non-helpers’ when they do not. We conducted focal observations during incubation by hiding less than 10m from the nest (2012-15) or when nestlings were ringed (2012-19). In most cases, group members were actively lured to the nest using playback of distress calls for a maximum duration of 10 min. As group members respond to these playbacks by approach and displays, presumably to distract and lead away potential predators, this method proved to be an efficient way to assess group membership and identity focal groups. Known members from neighbouring groups were never lured by the playback and multi-year data on group structure showed consistency in group memberships. Playback was not used when a predator was present. The same approach was used to capture group members when nestlings were ca. 5 days old (range 3 – 8 days) or after nest depredation. The breeding status of each group member (i.e. breeding female, breeding male, non-breeding subordinate) was determined by the presence of brood patches or cloacal swellings. Playback recordings consisted of distress calls from a handheld conspecific bird from a nearby population (recorded in 2011), alternated by silent periods. All pairs or groups were exposed to the same playback recording set for similar lengths and during at least one occasion, i.e. during observations and/or during trapping.

When nestlings were ca. 8 days old (range 6 – 10 days), we video-recorded food provisioning for 5-6 hrs continuously between 7 a.m. and 2 p.m. using a HD camera (Sony Corp.). The camera was installed on a tripod, positioned about 1.5 m from the nest, protected and camouflaged by a waterproof casing and camo-coloured poncho and secured to a nearby tree by a metal wire. From these recordings, we extracted hourly provisioning rates of breeders and helpers, as well as determined the number of helpers. We only extracted provisioning rates when we could identify the visiting individuals in at least 70% of all visits over the total recording period. To account for a potential bias due to unidentified visits, we also tested cut-off values of 80% and 90% and results were qualitatively similar.

We omitted breeding events from the dataset when estimates of group size or number of helper were ambiguous due to the presence of individual(s) without colour- bands or whose combination could not be determined with certainty (and were not retrapped afterwards to confirm their correct identity), or when the identification rates during video recordings were too low (see above). Because the number of helpers could only be determined later in the breeding season, ‘group size’ is known for a larger number of breeding events than ‘number of helpers’. However, in the final datasets, we included those breeding events for which both group size and number of helpers could be determined, and we subsequently only retained the first observed breeding attempt in a territory during any given breeding season.

## Statistical analysis

*General statistical procedure*

We modelled variation in maternal investment (egg size and feeding rates) and reproductive success (fledging success and nestling body mass and size) in relation to group size (range: 2 – 7 individuals) and number of helpers (range: 0 – 4 individuals). Since number of helpers is constrained by group size, the two variables are correlated (Pearson’s r between number of subordinates and number of helpers among group-living females: 0.59, n = 105), and we ran separate models with either one or the other as explanatory variable. Next, we assessed the relative importance of each variable in explaining variation in maternal investment and reproductive success by ranking models based on the lowest Akaike’s information criterion corrected for small sample sizes (AICc) (Burnham and Anderson 2002), as computed with the R package MuMIn (Bartoń 2018). When the difference in AICc values between the models including either group size or number of helpers was ≥ 2, we considered that the variable in the model with the lower AIC was more strongly supported than the other one. The model selection procedure was as follows: we first retained all models with ΔAICc ≤ 2 from the most parsimonious model and then discarded models that were more complex versions of simpler (nested) ones with lower AICc values (Richards et al. 2011). All variables other than group size and number of helpers were included in all candidate models, except for mean egg size when modelling variation in nestling body mass and wing length. Continuous predictor variables were centred and divided by two standard deviations to facilitate interpretation and comparison of model coefficients (Gelman 2008). Breeding season (six levels), and female ID nested within forest fragment (eight levels: two large fragments and six small fragments) were added in all analyses as random effects to control for random variation between years and fragments (e.g. variation in rainfall) that may have affected variation in maternal investment and reproductive success among years and fragments, and for non-independence of repeated observations of the same female over years. We checked for multicollinearity by investigating variance-inflation factors (VIFs) and confirmed this to be of no concern in all our models (all VIFs ≤ 1.3; Johnston et al. 2018). Sample sizes vary between analyses due to variation in the stage at which nests were detected, or loss of nests due to predation. (Generalized) linear mixed models ((G)LMMs) were fitted with package ‘lme4’ (Bates et al. 2015), using Maximum Likelihood to allow model selection. Visual inspection of plots of fitted values against residuals did not reveal violation of normality and homoscedasticity assumptions. Based on a comparison between the sum of squared Pearson residuals and the residual degrees of freedom, we found no evidence for overdispersion for GLMMs. All models were run in R 3.6.2 (R Core Team 2019).

*Pre- and post-hatching maternal investment*

We modelled variation in mean egg size per clutch and hourly maternal and total feeding rates (log(feeds/h)) using Linear Mixed Models (LMM). For all response variables, we included either group size or number of helpers (87, 103 and 107 nests, respectively). We included female tarsus length in all models on egg size to account for variation in female body size. To reduce model complexity of the egg models, we removed rare cases of one- and three-egg clutches (2 and 2 out of 93 clutches, respectively), and removed two clutches from one breeding female where egg sizes were identified as outliers (mean egg size per clutch > Q3 + 1.5 \* IQR, Zuur et al. 2007; did not influence model outcome), which resulted in a final sample size of 87 nests. As the number of helpers can only be determined when nestlings are approximately 8 days old and many nests were predated before this date, variation in egg size on the subset of nests for which the number of helpers was known was reduced. Therefore, we also tested the possible effect of group size on egg size by using a larger dataset (n = 122) for which group size was determined from observations during the entire nestling period, (i.e. not just at the time videos were taken to determine the number of helpers). In all models on provisioning rates, we included nestling age (days since hatching (day 1), broods hatch synchronously) and number of nestlings to account for age and brood size effects.

*Fledging success, nestling body size and condition*

We modelled variation in fledging success of hatched young (≥ 1 fledgling (1) *vs*. 0 fledglings) using Generalized Linear Mixed Models (GLMM) with binomial distribution (n = 133 broods). Group size or number of helpers were included as explanatory variables. Most of the nest failures occurred before the number of helpers could be determined, leading to reduced variation in fledging success (16 out of 133 nests failed; 14 of which were due to predation and 2 due to abandonment) and likely limiting statistical power. We therefore also tested the effect of group size on fledging success on a larger dataset covering the entire nestling period, including nests that were predated before the number of helpers could be determined (n = 64 cases of nest failure out of 205 nests; 48 due to predation, 14 were abandoned, and 2 were either predated or abandoned).

We modelled variation in nestling wing length and body mass (147 nestlings from 86 nests) using LMM’s with group size or number of helpers as explanatory variables. In addition, to test whether laying larger eggs results in heavier or larger nestlings, mean egg size per clutch was also included in the models. Finally, to statistically control for other factors that may affect nestling size and mass, we included number of nestlings and nestling age in all models. In addition, we included nestling tarsus length in the model on nestling mass to account for variation in mass due to variation in structural body size. Nest ID was added as a random factor to control for non-independence of siblings. Because some females bred during multiple breeding seasons, nest ID was nested within breeding female ID.

## Ethical note

Animals were treated according to the ethical standards outlined by the National Commission for Science, Technology and Innovation (NACOSTI), the Kenya Wildlife Service (KWS) and the Ghent University ethical committee under approved permits: NACOSTI/P/14/9325/3932, NACOSTI/P/16/61881/14065, NACOSTI/P/18/61881/18658, NACOSTI/P/19/61881/27686, KWS/BRM/5001 and EC2012-052. All animals in this study were free-ranging. They were caught using conventional mist-nets and immediately upon capture they were measured and tagged around the leg with 3 colour bands (size XCL, ecotone) and one numbered aluminium ring (ring prefix AA, Nature Kenya). Every individual was released directly after handling. If several animals were caught simultaneously, they were kept in suspended cotton bags before handling. Mist-nets were erected around nest sites just before capture, monitored continuously, and removed immediately thereafter. Eggs and nestlings were taken directly from the nest and returned immediately after measuring. Care was taken to minimize the time spent close to nests. No animals were killed or harmed during this study. There was no evidence of nest abandonment due to any of our sampling methods. Throughout the study, a total of 787 individuals were manipulated one to seven times (342 full grown, 445 nestlings).

# RESULTS

*Pre-hatching maternal investment*

When examining variation in egg size using the reduced dataset for which the number of helpers could be determined (Table 1.1a), the model with group size was better supported than the model including number of helpers (ΔAICc = 2.42). However, since the null model was as well supported as the model with group size (AIC weight: 0.43 and 0.44 respectively), evidence for group size as a predictor of egg size variation was inconclusive for this dataset. Yet, when including all nests that reached the nestling stage (see Methods), a positive effect of group size on egg size was strongly supported (ΔAICc with the null model: 2.37; Table 1.1b and Fig. 1).

*Post-hatching maternal investment and overall feeding rates*

Maternal feeding rates were inversely related to the number of helpers, and this effect was better supported than the relationship with group size (ΔAICc = 2.56; Table 1.2, Fig. 2). When overall feeding rates were examined (all group members), a model with number of helpers as explanatory variable was also better supported than a model with group size (ΔAICc = 2.44; Table 1.3, Fig. S1) and total feeding rates increased with increasing number of helpers.

Table 1. Model parameters (with their Wald 95% Confidence Intervals) and model selection for (1) female egg investment (mean egg size per clutch, cm³), (2) female feeding rates (log(feeds/h); n = 103) and (3) total feeding rates (n = 107). When modelling egg size, two different datasets were used: (1a) a dataset restricted to nests which survived late into the nestling stage (n = 87) allowing to test both effects of group size and number of helpers and (1b) a dataset including all nests that reach the nestling stage (n = 122) allowing to test the effect of group size only.

|  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| *1a: egg size (reduced dataset)* | *Intercept* | | *Group size* | *Number of helpers* | *Female tarsus length1* |  | *K* | *AICc* | *ΔAICc* | *Weight* |
|  | | **3.08**  **[3.00; 3.16]** | **0.08**  **[-0.01; 0.17]** |  | **0.14**  **[0.03; 0.24]** |  | **3** | **-7.2** | **0.00** | **0.44** |
|  | | **3.08**  **[3.01; 3.15]** |  |  | **0.16**  **[0.06; 0.26]** |  | **2** | **-7.2** | **0.05** | **0.43** |
|  | | 3.08  [3.00; 3.15] |  | 0.00  [-0.09; 0.10] | 0.16  [0.05; 0.26] |  | 3 | -4.8 | 2.42 | 0.13 |
| *1b: egg size (full dataset)* | | *Intercept* | *Group size* |  | *Female tarsus length1* |  | *K* | *AICc* | *ΔAICc* | *Weight* |
|  | | **3.07**  **[2.99; 3.15]** | **0.08**  **[0.01; 0.16]** |  | **0.11**  **[0.02; 0.20]** |  | **3** | **-22.8** | **0.00** | **0.77** |
|  | | 3.07  [3.00; 3.14] |  |  | 0.13  [0.04; 0.22] |  | 2 | -20.4 | 2.37 | 0.23 |
| *2: female feeding rates* | | *Intercept* | *Group size* | *Number of helpers* | *Nestling age1* | *Brood size1* | *K* | *AICc* | *ΔAICc* | *Weight* |
|  | | **0.71**  **[0.58; 0.83]** |  | **-0.35**  **[-0.58; -0.12]** | **0.01**  **[-0.22; 0.24]** | **0.56**  **[0.34; 0.78]** | **4** | **198.1** | **0.00** | **0.75** |
|  | | 0.71  [0.59; 0.83] | -0.30  [-0.54; -0.06] |  | -0.01  [-0.24; 0.22] | 0.50  [0.27; 0.73] | 4 | 200.6 | 2.56 | 0.21 |
|  | | 0.72  [0.59; 0.84] |  |  | -0.05  [-0.29; 0.18] | 0.55  [0.32; 0.78] | 3 | 203.9 | 5.88 | 0.04 |
| *3: total feeding rates* | | *Intercept* | *Group size* | *Number of helpers* | *Nestling age1* | *Brood size1* | *K* | *AICc* | *ΔAICc* | *Weight* |
|  | | **1.53**  **[1.41; 1.64]** |  | **0.17**  **[0.02; 0.33]** | **0.17**  **[0.02; 0.32]** | **0.54**  **[0.39; 0.68]** | **4** | **117.2** | **0.00** | **0.69** |
|  | | 1.53  [1.40; 1.65] |  |  | 0.19  [0.04; 0.35] | 0.54  [0.39; 0.69] | 3 | 119.7 | 2.44 | 0.21 |
|  | | 1.52  [1.41; 1.63] | 0.08  [-0.07; 0.23] |  | 0.17  [0.02; 0.33] | 0.55  [0.40; 0.70] | 4 | 121.0 | 3.81 | 0.10 |

For each response variable, all explanatory variables that were included in the respective models are given as column headings. Model rank is based on Akaike’s information criterion corrected for small sample sizes (AICc). K is the number of parameters estimated for fixed effects (including the intercept), ΔAICc denotes the change in AICc relative to the best model, and weight is the AICc weight of the model. Retained models are in bold. 1Nestling age and brood size (model 2 and 3 only) were included in all candidate models.

Chart, scatter chart

Description automatically generated

*Figure 1. Raw data (dots) and ML model predictions (line) showing mean egg size in relation to group size (including all nests from which group size was determined during the whole nestling period; n = 122). Estimates (± SE) were controlled for female tarsus length and error structure included both fixed and random error terms.*

Chart, scatter chart

Description automatically generated

*Figure 2. Raw data (dots) and ML model predictions (line) showing the number of feeds/hr by breeding females in relation to the number of helpers in their breeding group (n = 103). Estimates (± SE) were controlled for nestling age and number of nestlings and error structure included both fixed and random error terms.*

*Fledging success, nestling body size and condition*

When examining variation in fledging success using the reduced dataset for which the number of helpers could be determined (Table 2.1), the model with groups size and the null model were equally supported (ΔAICc = 0.00). In addition, the model with number of helpers showed a ΔAICc ≤ 2 with the null model and the model with group size. Therefore, evidence for group size or number of helpers as a predictor of fledging success variation was inconclusive for this dataset. Yet, when including all nests that reached the nestling stage, a positive effect of group size on fledging success was strongly supported (ΔAICc with the null model: 9.08) (Table 2.2; Fig. S2). Overall, this suggests a positive effect of the presence group members on fledging success but we cannot assess at this stage whether this is mostly driven by group size or number of helpers.

Table 2. Model parameters (with their Wald 95% Confidence Intervals) and model selection for fledging success (at least one nestling successfully fledged (≥ 1 fledgling (1) *vs*. 0 fledglings). Two different datasets were used: (1) a dataset restricted to nests which survived late into the nestling stage (n = 133) allowing to test both effects of group size and number of helpers; (2) a dataset including all nests that reach the nestling stage (n = 205) allowing to test the effect of group size only.

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
| *1: fledging success (reduced dataset)* | *Intercept* | *Group size* | *Number of helpers* | *K* | *AICc* | *ΔAICc* | *Weight* |
|  | **23.55**  **[11.37; 35.74]** | **11.86**  **[1.51; 22.22]** |  | **2** | **56.1** | **0.00** | **0.41** |
|  | **19.43**  **[7.70; 31.17]** |  |  | **1** | **56.1** | **0.00** | **0.41** |
|  | 23.76  [6.71; 40.82] |  | 4.48  [-2.54; 11.50] | 2 | 57.7 | 1.53 | 0.19 |
| *2: fledging success (full dataset)* | *Intercept* | *Group size* |  | *K* | *AICc* | *ΔAICc* | *Weight* |
|  | **1.03**  **[0.47; 1.60]** | **1.31**  **[0.45; 2.18]** |  | **2** | **247.8** | **0.00** | **0.99** |
|  | 0.94  [0.40; 1.47] |  |  | 1 | 256.9 | 9.08 | 0.01 |

For each response variable, all explanatory variables that were included in the respective models are given as column headings. Model rank is based on Akaike’s information criterion corrected for small sample sizes (AICc). K is the number of parameters estimated for fixed effects (including the intercept), ΔAICc denotes the change in AICc relative to the best model, and weight is the AICc weight of the model. Retained models are in bold.

Nestling wing length increased with the number of helpers (Table 3.1, Fig. S3) (ΔAICc with model containing group size: 2.31). Egg size did not explain variation in nestling wing length (ΔAICc with best model without egg size: 2.30). To investigate whether the effect of helpers on nestling wing length was mediated by increased food provisioning, we tested an alternative model with total feeding rates instead of number of helpers. However, we did not find support for an effect of total feeding rates on nestling wing length (Table S1). For nestling mass, the model with group size was better supported than the null model but the ΔAICc was ≤ 2 (Table 3.2), suggesting that group size was not a strong predictor of the data. Models including the number of helpers and egg size were not supported by the data (ΔAICc ≥ 2 with the best model; Table 3.2).

Table 3. Model parameters (with their Wald 95% Confidence Intervals) and model selection for (1) nestling wing length and (2) nestling mass (147 nestlings from 86 nests).

|  |  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| *1: wing length* | *Intercept* | *Group size* | *Number of helpers* | *Mean egg size* | *Nestling age1* | *Number of nestlings1* |  | *K* | *AICc* | *ΔAICc* | *Weight* |
|  | **40.03**  **[39.04; 41.02]** |  | **2.52**  **[0.94; 4.10]** |  | **5.39**  **[3.84; 6.95]** | **-0.89**  **[-2.18; 0.41]** |  | **4** | **815.2** | **0.00** | **0.56** |
|  | 40.03  [39.04; 41.02] |  | 2.52  [0.94; 4.10] | -0.01  [-1.69; 1.67] | 5.39  [3.84; 6.95] | -0.89  [-2.19; 0.41] |  | 5 | 817.5 | 2.30 | 0.18 |
|  | 40.00  [39.10; 40.90] | 2.15  [0.67; 3.63] |  |  | 5.79  [4.28; 7.30] | -0.60  [-1.87; 0.67] |  | 4 | 817.6 | 2.31 | 0.18 |
|  | 40.00  [39.10; 40.90] | 2.15  [0.67; 3.62] |  | -0.16  [-1.87; 1.55] | 5.78  [4.27; 7.29] | -0.59  [-1.87; 0.68] |  | 5 | 819.8 | 4.57 | 0.06 |
|  | 39.98  [38.92; 41.03] |  |  |  | 5.78  [4.16; 7.39] | -0.71  [-2.06; 0.65] |  | 3 | 822.2 | 6.98 | 0.02 |
|  | 39.97  [38.92; 41.03] |  |  | -0.19  [-1.95; 1.59] | 5.77  [4.15; 7.39] | -0.70  [-2.05; 0.66] |  | 4 | 824.5 | 9.21 | 0.01 |
| *2: nestling mass* | *Intercept* | *Group size* | *Number of helpers* | *Mean egg size* | *Nestling age1* | *Number of nestlings1* | *Nestling tarsus length1* | *K* | *AICc* | *ΔAICc* | *Weight* |
|  | **18.40**  **[17.59; 19.20]** | **-0.52**  **[-1.10, 0.05]** |  |  | **-0.01**  **[-0.61; 0.59]** | **-0.36**  **[-0.83: 0.11]** | **4.07**  **[3.52; 4.61]** | **5** | **528.4** | **0.00** | **0.33** |
|  | 18.42  [17.57; 19.28] |  |  |  | **0.01**  **[-0.59; 0.63]** | **-0.32**  **[-0.78; 0.15]** | **3.99**  **[3.45; 4.52]** | 4 | **528.8** | **0.40** | **0.27** |
|  | 18.42  [17.62; 19.22] | -0.56  [-1.14, 0.02] |  | 0.28  [-0.31; 0.87] | -0.01  [-0.61; 0.58] | -0.38  [-0.85; 0.09] | 4.07  [3.53; 4.61] | 6 | 529.9 | 1.49 | 0.15 |
|  | 18.44  [17.59; 19.30] |  |  | 0.22  [-0.39; 0.82] | 0.02  [-0.58; 0.62] | -0.32  [-0.79; 0.15] | 3.99  [3.45; 4.52] | 5 | 530.6 | 2.21 | 0.11 |
|  | 18.41  [17.57; 19.25] |  | -0.20  [-0.80; 0.39] |  | 0.02  [-0.58; 0.63] | -0.30  [-0.77; 0.17] | 4.03  [3.48; 4.58] | 5 | 530.7 | 2.27 | 0.10 |
|  | 18.43  [17.59; 19.27] |  | -0.21  [-0.80; 0.39] | 0.22  [-0.39; 0.83] | 0.02  [-0.58; 0.63] | -0.31  [-0.78; 0.16] | 4.03  [3.48; 4.58] | 6 | 532.5 | 4.09 | 0.04 |

For each response variable, all explanatory variables that were included in the respective models are given as column headings. Model rank is based on Akaike’s information criterion corrected for small sample sizes (AICc). K is the number of parameters estimated for fixed effects (including the intercept), ΔAICc denotes the change in AICc relative to the best model, and weight is the AICc weight of the model. Retained models are in bold. 1Nestling age, number of nestlings and nestling tarsus length (second model only) were included in all candidate models.

# DISCUSSION

We show that females of a tropical cooperative breeder modulate both their pre- and post-hatching reproductive investment in relation to social conditions. Contrary to our predictions, females with more potential helpers in the group did not systematically reduce their investment during the breeding event. Rather, they employed an additive strategy during the pre-hatching stage by producing larger eggs in larger groups, while they practiced load-lightening in the post-hatching stage by reducing their own feeding ratewhen assisted by a larger number of helpers. As predicted, pre-hatching investment was tuned to group size rather than to the actual number of helpers. Furthermore, we found that fledging success increased with group size and that nestlings were on average larger in groups with more helpers. In contrast, the condition of these young was not related to number of helpers, despite the fact that nestlings received more food when helpers were present.

**Additive strategy during pre-hatching investment**

Post-hatching load-lightening has been shown in many cooperatively breeding species, but there is less evidence for similar effects in pre-hatching investments (Russell and Lummaa 2009; Dixit et al. 2017; Valencia et al. 2017; Cusick et al. 2018; Zhao et al. 2019; Fortuna et al. 2021). Contrary to our predictions, we found that females used an additive strategy during pre-hatching investment, with egg size increasing with group size, even though food provisioning by helpers could theoretically compensate for the reduced maternal investment in eggs (illustrated in this study by increased total provisioning rates with helpers; see also Russell et al. 2007). Two different hypotheses have been proposed in the literature that may explain investment in current instead of future reproduction in species with a slow pace of life (Dixit et al. 2017).

First, the effect of the presence of helpers on maternal investment strategies has been shown to vary with food availability and climatic conditions during breeding, where, under adverse environmental conditions, females take advantage of the presence of helpers to raise the value of offspring by maintaining or increasing their own investment (Luck 2002; Langmore et al. 2016). For instance, in rufous treecreepers (*Climacteris rufa*) (Luck 2002), females showed compensatory provisioning rates when breeding in a continuous landscape but additive provisioning rates when breeding in fragmented one. An additive strategy during the pre-hatching phase in placid greenbuls may thus suggest that environmental conditions for breeding in the study area are poor. The Taita Hills represent the most fragmented and disturbed region within the Eastern Arc Mountains biodiversity hotspot (Newmark 1998). The two larger forest patches in the current study suffered 30% indigenous forest loss between 1955 and 2004 (Pellikka et al. 2009) and some sections are heavily degraded, with similar vegetation characteristics as in small fragments (Thijs 2015). How habitat fragmentation and degradation affect food availability and costs of reproduction in placid greenbuls, remains unclear. Under this hypothesis, the fact that egg size was not associated to the number of helpers suggests that females do not know how many non-breeders in the group will take part in food provisioning, but instead use group size as a proxy for the presence of helpers.

Alternatively, under conditions of high predation risk, females are expected to invest less in current reproduction, in order to save energy for future breeding attempts (Lima 2009). Along this line, when nest predation risk is reduced (Fontaine and Martin 2006; Fortuna et al. 2021), females have been shown to increase their reproductive investment. In placid greenbuls, subordinates, regardless of whether they help with nest feeding or not, have been observed to participate in anti-predator behaviour such as predator mobbing and distracting predators from the nest (DVL and BA personal observations). In addition, we have shown that the probability that at least one young fledged increased with group size, which is consistent with higher survival after fledging in larger groups (Van de Loock et al. 2017). This suggests that larger groups are more efficient in protecting nestlings against predators, thereby reducing predation pressure. Thus, females may increase egg investment in the presence of subordinates because of the increased prospect of having fledged offspring. A similar explanation was proposed to explain increased egg investment in cooperative groups in Iberian magpie (*Cyanopica cooki*) (Valencia et al. 2017). While we originally hypothesized group size to be used by females as a proxy for expected help with food provisioning, this explanation in fact implies a different role for non-breeding subordinates, with females adjusting their pre-hatching investment to the total group size in response to the reduced predation risk, regardless of the number of subordinates helping with food provisioning.

Owing to the correlative nature of our study, it is not possible at this stage to assess whether plasticity in egg investment is a response to nutritional conditions during breeding, or to predation pressure, and both may play a role in modulating maternal investment strategy in our species. Alternatively, the positive relationship between egg size and group size may result from a confounding effect of territory quality or climatic conditions affecting both variables (Legge 2000; Christians 2002; Langmore et al. 2016; Bourne et al. 2020).

**Load-lightening strategy during post-hatching investment**

Maternal feeding rates decreased with the number of helpers, implying that females adjust their feeding rate to the actual contributions made by group members (Russell et al. 2008; Canestrari et al. 2011). In addition, we showed that a reduction in maternal feeding rates was fully compensated (and even over-compensated, as overall feeding rates increased in groups with more helpers present) when assisted by helpers, suggesting that maternal load-lightening does not impose costs on offspring (see below). Placid greenbuls are relatively long-lived passerines (oldest individual re-trap: 19 year-old) with an extended breeding season (up to 5 months), multiple reproductive opportunities (up to 4 nest attempts recorded within one breeding season, of which up to 2 successful) and low rates of nestling starvation (rarely recorded, unpublished data DVL & BA). Such life-history characteristics are expected to favour a maternal load-lightening strategy (Ghalambor and Martin 2001; Russell and Lummaa 2009). A comparative study on a taxonomically diverse set of 27 cooperative breeding species identified load-lightening during post-hatching as the prime strategy in 63% of these species (Hatchwell 1999). Therefore, a load-lightening strategy during nestling feeding in placid greenbuls seems in accordance with the current theory on post-hatching maternal decision-making in cooperative breeders.

Yet, load-lightening post-hatching seems to contradict the apparent additive strategy pre-hatching. If the additive strategy pre-hatching reflects a response to nutritional condition during the nestling stage, the contrasting strategies adopted by females appear incongruous since females would be expected to adopt a similar strategy during both stages. One possible explanation is that an increase in female investment would have a small effect on offspring fitness when the number of helpers increases (e.g. when nestlings receive enough food), which would not favour an additive strategy post-hatching (Savage et al. 2015). In this context, females are expected to maintain their investment, or even load-lighten if nestlings receive more food, when the number of helpers increases (such as in our study population) (Savage et al. 2015).

However, if pre-hatching investment is a response to reduced predation risk in larger groups, this means that investments pre- and post-hatching reflect separate responses to different environmental conditions (predation risk pre-hatching vs. quantity of food provisioned post-hatching). Unlike compensatory effects of food provisioning helpers, anti-predator benefits of subordinates are not predicted to induce load-lightening, since reduced predation pressure increases reproductive success independently of the amount of maternal investment provided to offspring (Carranza et al. 2008). Females can thus adopt opposite strategies depending on the type of contribution provided by subordinates (Carranza et al. 2008). Since load-lightening strategy has been found to benefit females through higher female survival probabilities and higher lifetime reproductive success in many species (Khan and Walters 2002; MacColl and Hatchwell 2004; Russell et al. 2007; Cockburn et al. 2008; Covas et al. 2008; Kingma et al. 2010; Li et al. 2015), this would suggests that females are able to invest more in both current and future reproduction when breeding cooperatively.

Finally, the reduction in maternal food provisioning may also be the consequence of a trade-off on resource allocation between reproductive phases (Reid et al. 2000) since we showed that females in larger groups laid larger eggs. How much load-lightening may allow to compensate for increased pre-hatching investment and/or save energy for future reproduction, remains to be studied.

**Effects of social context on breeding outcomes**

We showed that females with helpers fledged offspring with longer wings whereas offspring did not differ in body condition. While body condition may represent an important component of fitness as it is associated with higher post-fledging survival in placid greenbuls (Van de Loock et al. 2017), growing longer wings may allow nestlings to fledge earlier and increase their ability to escape predators (Martin 2015). While females in larger groups laid larger eggs, this cannot explain the presence of larger nestlings, since egg size was not associated with nestling size (nor with condition) at fledging. While it thus remains unclear how females benefit from laying larger eggs, we here propose two possible explanations: (i) larger eggs have other fitness benefits (e.g. increased hatching rate; Krist 2011), or (ii) pre- and post-hatching investments have an synergistic effect where higher pre-hatching investment must be complemented by a higher post-hatching investment for potential benefits of larger eggs to be realized (‘silver-spoon’ hypothesis, Savage et al. 2015). The latter can occur when larger hatchlings require more food during their development. Under such a scenario, producing larger eggs is a valuable strategy only when extra care can be expected during food provisioning. The lack of a relationship between egg size and offspring size or condition may reflect a confounding effect of such interdependence, i.e. where the benefit of a high egg investment by group-living females is (partially) lost when no helpers are available to deliver additional food to the nestlings. How pre- and post-hatching investments interact in contributing to offspring fitness therefore deserves further study, especially because such ‘silver spoon’ effects between egg size and food provisioning, while described conceptually (Savage et al. 2015), have never been reported in cooperatively breeding species.

While we found a clear positive effect of the social context on fledging success, we failed to disentangle whether this effect was mostly driven by group size or by the number of helpers. Both may actually contribute to reproductive success. First, in our study population, nestling starvation is very rare and predation is the main cause of nest failure. The higher fledging success in larger group may likely be attributed to the collective anti-predator behaviour of all subordinates (both helpers and non-helpers), independent of the specific food supply by helpers. Second, we found that nestlings from groups with more helpers fledged with longer wings. This may contribute to fledging success if, as suggested above, this allows nestlings to fledge earlier (Martin 2015).

**Conclusion**

By differentiating between total number of subordinates (group size) and number of food-provisioning subordinates (helpers), we were able to reveal unexpected contrasting maternal investment strategies during the pre- and post-hatching phase, in response to different social conditions. Our study highlights the importance of examining multiple reproductive investments during different breeding stages, as well as different social contexts, when aiming to predict how cooperative breeding affects maternal investment strategies.

# Acknowledgements.

We thank the Kenyan government, the Kenya Wildlife service and the Kenya Forest Service for permitting research in the Taita Hills and L. Chovu, P. Kafusi, J. Kiiru, A. Mwakulombe, O. Mwakesi, M. Makomba and V. Otieno Onyango for fieldwork. Kenya Forest Service kindly facilitated access to the forest fragments. We also thank Peter Njoroge and the National Museums of Kenya for support.

This work was funded by the Fonds Wetenschappelijk Onderzoek (FWO) grant G.0308.13N, by the Alexander von Humboldt Foundation, The National Geographic Foundation (NGS) grant GEF191-16, the German Research Foundation (FDG) grant AP296/1-1, the Gesellschaft für Tropenornithologie and the Linean Society of London.

All authors gave final approval for publication and declare no competing interests.

# REFERENCES

Aerts R, Thijs KW, Lehouck V, Beentje H, Bytebier B, Matthysen E, Gulinck H, Lens L, Muys B. 2011. Woody plant communities of isolated Afromontane cloud forests in Taita Hills, Kenya. Plant Ecol. 212(4):639–649. doi:10.1007/s11258-010-9853-3.

Baglione V, Canestrari D, Chiarati E, Vera R, Marcos JM. 2010. Lazy group members are substitute helpers in carrion crows. Proc R Soc B Biol Sci. 277(1698):3275–3282. doi:10.1098/rspb.2010.0745. http://rspb.royalsocietypublishing.org/cgi/doi/10.1098/rspb.2010.0745.

Barati A, Andrew RL, Gorrell JC, Etezadifar F. 2018. Genetic relatedness and sex predict helper provisioning effort in the cooperatively breeding noisy miner. Behav Ecol. 29(6):1380–1389. doi:10.1093/beheco/ary109.

Bartoń K. 2018. Multi-model inference. R package version 1.42.1. http://cran.r-project org/web/packages/MuMIn/inde.

Bates D, Mächler M, Bolker BM, Walker SC. 2015. Fitting linear mixed-effects models using lme4. J Stat Softw. 67(1). doi:10.18637/jss.v067.i01.

van Boheemen LA, Hammers M, Kingma SA, Richardson DS, Burke T, Komdeur J, Dugdale HL. 2019. Compensatory and additive helper effects in the cooperatively breeding Seychelles warbler (Acrocephalus sechellensis). Ecol Evol. 9(5):2986–2995. doi:10.1002/ece3.4982.

Bourne AR, Cunningham SJ, Spottiswoode CN, Ridley AR. 2020. High temperatures drive offspring mortality in a cooperatively breeding bird: Temperature drives offspring mortality. Proc R Soc B Biol Sci. 287(1931). doi:10.1098/rspb.2020.1140rspb20201140.

Burgess ND, Butynski TM, Cordeiro NJ, Doggart NH, Fjeldså J, Howell KM, Kilahama FB, Loader SP, Lovett JC, Mbilinyi B, et al. 2007. The biological importance of the Eastern Arc Mountains of Tanzania and Kenya. Biol Conserv. 134(2):209–231. doi:10.1016/j.biocon.2006.08.015. https://linkinghub.elsevier.com/retrieve/pii/S0006320706003314.

Burnham K, Anderson D. 2002. Model selection and multimodel inference: a practical information-theoretic approach. 2nd ed. New York (NY): Springer-Verlag.

Canestrari D, Marcos JM, Baglione V. 2011. Helpers at the nest compensate for reduced maternal investment in egg size in carrion crows. J Evol Biol. 24(9):1870–1878. doi:10.1111/j.1420-9101.2011.02313.x.

Carranza J, Polo V, Valencia J, Mateos C, de la Cruz C. 2008. How should breeders react when aided by helpers? Anim Behav. 75(4):1535–1542. doi:10.1016/j.anbehav.2007.10.006.

Chege J, Bytebier B. 2005. Vegetation Structure of Four Small Forest Fragments in Taita Hills, Kenya. J East African Nat Hist. 94(1):231–234. doi:10.2982/0012-8317(2005)94[231:vsofsf]2.0.co;2.

Christians JK. 2002. Avian egg size: Variation within species and inflexibility within individuals. Biol Rev Camb Philos Soc. 77(1):1–26. doi:10.1017/S1464793101005784.

Cockburn A, Sims RA, Osmond HL, Green DJ, Double MC, Mulder RA. 2008. Can we measure the benefits of help in cooperatively breeding birds: the case of superb fairy-wrens Malurus cyaneus ? J Anim Ecol. 77:430–438. doi:10.1111/j.1365-2656.2007.0.

Cousseau L. 2020. Kin structure and behavioral strategies in a cooperatively breeding bird. PhD thesis. Ghent University.

Cousseau L, Van de Loock D, Apfelbeck B, Githiru M, Matthysen E, Lens L. 2022. Kin do not always help: testing multiple hypotheses on nest feeding in a cooperatively breeding bird. Behav Ecol.:1–13. doi:10.1093/beheco/arac073.

Covas R, Du Plessis MA, Doutrelant C. 2008. Helpers in colonial cooperatively breeding sociable weavers Philetairus socius contribute to buffer the effects of adverse breeding conditions. Behav Ecol Sociobiol. 63(1):103–112. doi:10.1007/s00265-008-0640-2.

Crick H. 1992. Load‐lightening in cooperatively breeding birds and the cost of reproduction. Ibis (Lond 1859). 134(1):56–61. doi:10.1111/j.1474-919X.1992.tb07230.x.

Cusick JA, de Villa M, DuVal EH, Cox JA. 2018. How do helpers help? Helper contributions throughout the nesting cycle in the cooperatively breeding brown-headed nuthatch. Behav Ecol Sociobiol. 72(3). doi:10.1007/s00265-018-2470-1.

Dixit T, English S, Lukas D. 2017. The relationship between egg size and helper number in cooperative breeders: A meta-analysis across species. PeerJ. 2017(11):1–16. doi:10.7717/peerj.4028.

Fontaine JJ, Martin TE. 2006. Parent birds assess nest predation risk and adjust their reproductive strategies. Ecol Lett. 9(4):428–434. doi:10.1111/j.1461-0248.2006.00892.x.

Fortuna R, Paquet M, Ferreira AC, Silva LR, Theron F, Doutrelant C, Covas R. 2021. Maternal allocation in relation to weather, predation and social factors in a colonial cooperative bird. J Anim Ecol. 90(5):1122–1133. doi:10.1111/1365-2656.13438.

Gelman A. 2008. Scaling regression inputs by dividing by two standard deviations. Stat Med. 27(15):2865–2873. doi:10.1002/sim.3107.

Ghalambor CK, Martin TE. 2001. Fecundity-survival trade-offs and parental risk-taking in birds. Science (80- ). 292(5516):494–497. doi:10.1126/science.1059379.

Green JP, Freckleton RP, Hatchwell BJ. 2016. Variation in helper effort among cooperatively breeding bird species is consistent with Hamilton’s Rule. Nat Commun. 7. doi:10.1038/ncomms12663.

Grüebler MU, Müller M, Michel VT, Perrig M, Keil H, Naef-Daenzer B, Korner-Nievergelt F. 2018. Brood provisioning and reproductive benefits in relation to habitat quality: a food supplementation experiment. Anim Behav. 141:45–55. doi:10.1016/j.anbehav.2018.05.009.

Hatchwell BJ. 1999. Investment strategies of breeders in avian cooperative breeding systems. Am Nat. 154(2):205–219. doi:10.1086/303227.

Hoyt D. 1979. Practical methods of estimating volume and fresh weight of bird eggs. Auk.

Johnston R, Jones K, Manley D. 2018. Confounding and collinearity in regression analysis: a cautionary tale and an alternative procedure, illustrated by studies of British voting behaviour. Qual Quant. 52(4):1957–1976. doi:10.1007/s11135-017-0584-6.

Khan MZ, Walters JR. 2002. Effects of helpers on breeder survival in the red-cockaded woodpecker (*Picoides borealis*). Behav Ecol Sociobiol. 51(4):336–344. doi:10.1007/s00265-001-0441-3.

Kingma SA, Hall ML, Arriero E, Peters A. 2010. Multiple benefits of cooperative breeding in purplecrowned fairy-wrens: A consequence of fidelity? J Anim Ecol. 79(4):757–768. doi:10.1111/j.1365-2656.2010.01697.x.

Koenig WD, Dickinson JL, editors. 2016. Cooperative Breeding in Vertebrates : studies of ecology, evolution and behavior. Cambridge: Cambridge University Press.

Koenig WD, Walters EL. 2011. Age-related provisioning behaviour in the cooperatively breeding acorn woodpecker: Testing the skills and the pay-to-stay hypotheses. Anim Behav. 82(3):437–444. doi:10.1016/j.anbehav.2011.05.028. http://dx.doi.org/10.1016/j.anbehav.2011.05.028.

Koenig WD, Walters EL. 2012. Brooding, provisioning, and compensatory care in the cooperatively breeding acorn woodpecker. Behav Ecol. 23(1):181–190. doi:10.1093/beheco/arr172.

Krist M. 2011. Egg size and offspring quality: A meta-analysis in birds. Biol Rev. 86(3):692–716. doi:10.1111/j.1469-185X.2010.00166.x.

Langmore NE, Bailey LD, Heinsohn RG, Russell AF, Kilner RM. 2016. Egg size investment in superb fairy-wrens: Helper effects are modulated by climate. Proc R Soc B Biol Sci. 283(1843):10–12. doi:10.1098/rspb.2016.1875.

Legge S. 2000. The effect of helpers on reproductive success the laughing kookaburra. J Anim Ecol. 69(4):714–724. doi:10.1046/j.1365-2656.2000.00429.x.

Lejeune L, van de Pol M, Cockburn A, Louter M, Brouwer L. 2016. Male and female helper effects on maternal investment and adult survival in red-winged fairy-wrens. Behav Ecol. 27:arw121. doi:10.1093/beheco/arw121.

Li Y, Li S, Guo C, Zhang G, Zhou Y, Lu X. 2015. Nest helpers improve parental survival but not offspring production in a high-elevation passerine, the Ground Tit Pseudopodoces humilis. Ibis (Lond 1859). 157(3):567–574. doi:10.1111/ibi.12266.

Lima SL. 2009. Predators and the breeding bird: Behavioral and reproductive flexibility under the risk of predation. Biol Rev. 84(3):485–513. doi:10.1111/j.1469-185X.2009.00085.x. http://doi.wiley.com/10.1111/j.1469-185X.2009.00085.x.

Van de Loock D. 2019. Life-history strategies of a facultative cooperative breeder in a fragmented Afrotropical cloud forest. PhD thesis. Ghent University.

Van de Loock D, Strubbe D, De Neve L, Githiru M, Matthysen E, Lens L. 2017. Cooperative breeding shapes post-fledging survival in an Afrotropical forest bird. Ecol Evol. 7(10):3489–3493. doi:10.1002/ece3.2744.

Lovett JC, Wasser SK, editors. 1993. Biogeography and Ecology of the Rain forests of Eastern Africa. Cambridge: Cambridge University Press.

Luck GW. 2002. The parental investment strategy of an avian cooperative breeder differs between a fragmented and an unfragmented landscape. Am Nat. 160(6):809–814. doi:10.1086/343881.

MacColl ADC, Hatchwell BJ. 2003. Sharing of caring: nestling provisioning behaviour of long-tailed tit, Aegithalos caudatus, parents and helpers. Anim Behav. 66(5):955–964. doi:10.1006/anbe.2003.2268.

MacColl ADC, Hatchwell BJ. 2004. Determinants of lifetime fitness in a cooperative breeder, the long-tailed tit Aegithalos caudatus. J Anim Ecol. 73(6):1137–1148. doi:10.1111/j.0021-8790.2004.00887.x.

Magrath RD. 2001. Group breeding dramatically increases reproductive success of yearling but not older female scrubwrens: A model for cooperatively breeding birds? J Anim Ecol. 70(3):370–385. doi:10.1046/j.1365-2656.2001.00498.x.

Majolo B, Huang P. 2017. Group living. In: Jennifer Vonk TS, editor. Encyclopedia of Animal Cognition and Behavior. Springer, Cham.

Martin TE. 2015. Age-related mortality explains life history strategies of tropical and temperate songbirds. Science (80- ). 349(6251):966–970.

Mutzel A, Blom MPK, Spagopoulou F, Wright J, Dingemanse NJ, Kempenaers B. 2013. Temporal trade-offs between nestling provisioning and defence against nest predators in blue tits. Anim Behav. 85(6):1459–1469. doi:10.1016/j.anbehav.2013.03.043.

Newmark WD. 1998. Forest Area, Fragmentation, and Loss in the Eastern Arc Mountains: Implications For the Conservation of Biological Diversity. J East African Nat Hist. 87(1):29–36. doi:10.2982/0012-8317(1998)87[29:fafali]2.0.co;2.

Pellikka PKE, Lötjönen M, Siljander M, Lens L. 2009. Airborne remote sensing of spatiotemporal change (1955-2004) in indigenous and exotic forest cover in the Taita Hills, Kenya. Int J Appl Earth Obs Geoinf. 11(4):221–232. doi:10.1016/j.jag.2009.02.002.

Van De Pol M, Bruinzeel LW, Heg D, Van Der Jeugd HP, Verhulst S. 2006. A silver spoon for a golden future: Long-term effects of natal origin on fitness prospects of oystercatchers (Haematopus ostralegus). J Anim Ecol. 75(2):616–626. doi:10.1111/j.1365-2656.2006.01079.x.

R Core Team. 2019. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/.

Ratikainen II, Kokko H. 2010. Differential allocation and compensation: Who deserves the silver spoon? Behav Ecol. 21(1):195–200. doi:10.1093/beheco/arp168.

Reid JM, Monaghan P, Ruxton GD. 2000. Resource allocation between reproductive phases: The importance of thermal conditions in determining the cost of incubation. Proc R Soc B Biol Sci. 267(1438):37–41. doi:10.1098/rspb.2000.0963.

Richards SA, Whittingham MJ, Stephens PA. 2011. Model selection and model averaging in behavioural ecology: The utility of the IT-AIC framework. Behav Ecol Sociobiol. 65(1):77–89. doi:10.1007/s00265-010-1035-8.

Roff D. 2002. Life History Evolution. Sunderland (Massachusetts, USA): Sinauer Associates.

Roff DA, Fairbairn DJ. 2007. The evolution of trade-offs: Where are we? J Evol Biol. 20(2):433–447. doi:10.1111/j.1420-9101.2006.01255.x.

Russell AF, Langmore NE, Cockburn A, Astheimer LB, Kilner RM. 2007. Reduced egg investment can conceal helper effects in cooperatively breeding birds. Science (80- ). 317(5840):941–944. doi:10.1126/science.1146037.

Russell AF, Langmore NE, Gardner JL, Kilner RM. 2008. Maternal investment tactics in superb fairy-wrens. Proc R Soc B Biol Sci. 275(1630):29–36. doi:10.1098/rspb.2007.0821.

Russell AF, Lummaa V. 2009. Maternal effects in cooperative breeders: From hymenopterans to humans. Philos Trans R Soc B Biol Sci. 364(1520):1143–1167. doi:10.1098/rstb.2008.0298.

Savage JL, Hinde CA. 2019. What Can We Quantify About Carer Behavior? Front Ecol Evol. 7(November):1–7. doi:10.3389/fevo.2019.00418.

Savage JL, Russell AF, Johnstone RA. 2015. Maternal allocation in cooperative breeders: Should mothers match or compensate for expected helper contributions? Anim Behav. 102:189–197. doi:10.1016/j.anbehav.2015.01.015. http://dx.doi.org/10.1016/j.anbehav.2015.01.015.

Spanhove T, Callens T, Hallmann CA, Pellikka P, Lens L. 2014. Nest predation in Afrotropical forest fragments shaped by inverse edge effects, timing of nest initiation and vegetation structure. J Ornithol. 155(2):411–420. doi:10.1007/s10336-013-1021-9.

Thijs K. 2015. Tree community dynamics and ecosystem function in a tropical landscape under deforestation pressure. PhD thesis. KU Leuven.

Valencia J, Mateos C, de la Cruz C, Carranza J. 2017. Maternal allocation in eggs when counting on helpers in a cooperatively breeding bird. J Avian Biol. 48(4):536–543. doi:10.1111/jav.01020.

Wilder C, Brooks T, Lens L. 1998. Vegetation Structure and Composition of the Taita Hills Forests. J East African Nat Hist. 87(1):181–187. doi:10.2982/0012-8317(1998)87[181:vsacot]2.0.co;2.

Zhao Q, Hammers M, Li C, Zeng X, Hao C, Lu X, Komdeur J. 2019. Egg investment in response to helper presence in cooperatively breeding Tibetan ground tits. J Avian Biol. 50(6):1–8. doi:10.1111/jav.02075.

Zuur AF, Leno EN, Smith GM. 2007. Analysing Ecological Data. Berlin: Springer-Verlag.