

# The influence of extreme temperature on incubation and provisioning behaviour in Eswatini birds and in an Australian bird

\*Lian Grabijn (951212276040)

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\*Supervisors Kat Bebbington, Sjouke Kingma and Abigail Robinson

\*Behavioural Ecology Group, Wageningen University & Research

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## Abstract

A consequence of the current changing climate are the increasing events of extreme temperatures. A crucial question is whether bird species are able to adjust their behaviour to this fast-changing environment. Important parental behaviour for survival of offspring are incubation of eggs and food provisioning of the offspring. During incubation, eggs need to remain at a constant optimal temperature for development of the embryo and suboptimal temperatures may hamper this development. Suboptimal temperatures, and especially high temperatures, may influence the food availability and also increase the energetic cost of food provisioning by parents to offspring. These consequences of extreme temperatures may especially visible in altricial species, where offspring require an extensive amount of care when born. In cooperative breeding species, however, a breeding pair may gain an advantage in adverse circumstances during incubation of eggs and provisioning of offspring due to additional helpers when compared to species with no helpers. However, in the current literature little is known about the ability of birds with different breeding systems to adjust their parental behaviour in response to extreme temperatures. Therefore, this study was designed to get a better understanding of the influence of extreme temperature on incubation and provisioning behaviour in three cooperatively breeding bird species and one species with a biparental care system. Three different bird species from Eswatini with a sub-tropical climate, arrow-marked babbler (*Turdoides jardineii*), white-crested helmetshrike (*Prionops plumatus*) and dark-capped bulbul (*Pyconotus tricolor*) and one species from Australia with a temperate climate, superb fairy-wrens (*Malurus cyaneus*) were used. Incubation and provisioning observations were conducted during 3 different breeding seasons in Eswatini and Australia and video analysis on the collected data was performed. It was found that the influence of temperature and group size on incubation and provisioning behaviour differed between the different species. For incubation behaviour it was shown in babblers that off-bout duration was positively influenced by group size. Helmetshrike nests were occupied for longer periods with increasing temperature and group size. For provisioning behaviour, there was a negative relationship found between provisioning rate and group size in babblers. Bulbuls provisioned less when temperature increased whereas provisioning rates of helmetshrikes and fairy-wrens were not affected by temperature and different group size. This study shows that different species vary in their response to temperature and group size which may ultimately have fitness consequences for both offspring and parents.

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## Introduction

The world's climate is currently changing at an unprecedented rate (IPCC 2013) and this may have profound ecological consequences (DuRant 2019; Huntley et al. 2012; Skagen et al. 2012; Thompson 2015). An important question is whether species are able to adapt at a rate fast enough to keep up with this changing environment (Visser 2008). The increasing frequency of extreme heat events, one major component of climate change (Easterling et al. 2000), may have many consequences for bird species throughout the world (Thompson et al. 2015; Conradie et al. 2019). Empirical and theoretical studies

indicate that extreme and fluctuating temperatures have an impact on the cost of care of the parents for their offspring, and this in turn, can influence the fitness of the parents and their offspring (McKechnie & Wolf 2010; Vincze et al. 2017; DuRant et al. 2019). Providing parental care at high temperatures increases the cost of care for parents, which may result in a stronger trade-off between self-maintenance and care for their offspring or brood. Consequently, this trade-off may result in a mismatch between the care that offspring demand and care that the parents are willing to supply and thereby decreasing the fitness of parents and offspring and even their survival chance (DuRant et al. 2019; Vincze et al. 2017). However, in the current literature little is known about the influence of temperature on parental behaviour of avian species to compensate for the increasing costs which may come with high temperatures.

Parental care consists of several energetically costly behaviors, such as incubating of eggs and food provisioning to the offspring. By incubating, birds influence the very early development and hatching circumstances of the eggs and aim to create an optimal development environment (Hanssen et al. 2005; DuRant et al. 2013). The optimal incubation temperature ranges from 36 to 40.5 °C (Huggins 1941; Webb 1987; White and Kinney 1974). When temperature drops below 24 to 26 °C (physiological zero), development of the embryo is stopped and a temperature higher than 40.5 °C is often lethal (Huggins 1941; Webb 1987; White and Kinney 1974). Thus, extremely high temperatures may increase offspring mortality rate (Caroll et al. 2018; Guthery & Hall 2001). Therefore, when the environmental temperature is suboptimal for incubation, parents might adjust their incubation behavior to keep their brood at a temperature that is optimal for the development of the embryo (DuRant et al. 2013).

In addition to incubation behaviour, food provisioning by parents to offspring may also be influenced by ambient temperature. It is known that food availability declines during high temperatures (Rauter et al. 2000; Carey 2009), which may result in reduced food provisioning by the parents (Rauter et al. 2000). In addition, research shows that foraging efficiency declines when temperature raises to a critical temperature, which was investigated in the study of du Plessis et al. (2012). Here, the researchers investigated the effect of high temperature on foraging behaviour in pied babblers (*Turdoides bicolor*). The researchers found that at a critical temperature of 35.5 °C the foraging efficiency declined (du Plessis et al. 2012). Moreover, extreme heat events can influence the dependency of the offspring regarding protection and provisioning by the parents. The offspring demands an increase in care of the parent because of the extreme temperature which may result in a decrease of fitness of the parent due to thermic costs. Therefore, parents may invest less energy and time in their offspring, which ultimately leads to a lower survival chance of the offspring (Heist et al. 2016). This mismatch between parental care (for both incubation and provisioning behaviour) that offspring demand and self-maintenance of the parents may especially be visible in altricial species, where the offspring requires an extensive amount of care when born. During suboptimal circumstances, parents may therefore be forced to adjust their parental care patterns (Olson et al. 2008; Vincze et al. 2017).

A system that may buffer against this mismatch in care and food availability during parental care may be a cooperative breeding system (Wiley & Ridley 2016). In cooperative breeding species, so-called ‘helpers’ provide parental care for offspring of another breeding pair and forgo their own reproduction (Gaston 1978; Hatchwell & Komdeur 2000; Cant 2012). An advantage of cooperative breeding is that there may be an increase in incubation constancy, which is the amount of time spent in contact with the eggs (Webb 1987). The constancy may be higher due to the helpers that may also incubate the eggs and this might eventually lead to an increase in hatching success. This effect of additional helpers is especially observed when circumstances are adverse (Blackmore & Heinsohn 2007; Mortensen & Reed 2018).

During suboptimal circumstances, a cooperative breeding group may also gain an advantage via a load lightening effect, where parents reduce the investment in offspring while helpers may buffer against this reduction of investment when also providing care for the offspring (Crick 1992). For example, Wiley & Ridley (2016) investigated the influence of temperature on the provisioning rate in

a cooperative species, pied babblers (*Turdoides bicolor*). They found that the overall provisioning of offspring was significantly less on warmer days. When looking at the social structure in cooperative breeders, they found that dominant birds decreased their provisioning whereas subordinates did not decrease their rate (Wiley & Ridley 2016), which shows that helpers can have a load lightening effect. However, contradicting results were also found. Nomano et al. (2019) investigated the provisioning rates and group coordination in a cooperatively breeding chestnut-crowned babblers (*Pomatostomus ruficeps*). They found that several environmental factors, including high temperatures, influenced the group coordination. This effect of environmental factors was especially pronounced in larger groups and lead to a problem in coordination in provisioning which may have severe impacts on offspring development (Nomano et al. 2019). Thus, previous studies found contradicting results about the effect of temperature on parental behavior in different bird species with different breeding systems. To get a better understanding of temperature effects it is necessary to investigate this in a broad range of different species with different breeding system. An often over-looked factor in the literature is also the exposure of nests to direct sunlight, which might influence the temperature locally and might affect parental behaviour as well.

In this study, both bird species with biparental care and cooperative breeding birds were investigated, whereas in most previous literature, bird species with the same breeding systems were studied. Also, in the current literature little is known about the effect of extreme temperatures in wild bird populations (Vincze et al. 2017), which were studied in this research. To study the effect of extreme temperatures on incubation and provisioning behaviour, a broad range of temperatures are required. These broad ranges of temperatures can be found in Eswatini with a sub-tropical climate, where temperature can vary enormously between days as well as within a day (mean daily temperature ranges from 15 to 28 °C) (Huntley & Barnard 2012; Dodsworth & Sweet 1990). In addition, temperature was measured throughout the entire area in Eswatini which result in a more precise measurement of the ambient temperature locally near the nests. In Australia, temperature fluctuates less extremely which allows a comparison in patterns of provisioning in sub-tropical species and species living in a temperate climate with different breeding systems.

This study is designed to get a better insight in what the consequences of extreme temperatures are on both incubation and provisioning behaviour in birds with biparental care and species with a cooperative breeding system. Firstly, it is expected that incubation behaviour is negatively influenced by fluctuating temperatures and especially by extremely high temperatures. Between the optimal incubation temperature of 36 to 40.5 °C (Huggins 1941), it is expected that temperature will not severely affect incubation behaviour. However, when temperature falls below this optimal range, birds may try to limit their off-bouts from the nest to keep the eggs at an optimal temperature. On the other hand, when temperature is raised above the 40.5 °C, it is predicted that birds might limit their off-bout duration and spend more time at the nest engaging in cooling and shielding behaviours to protect the eggs from the heat. In previous studies it is often overlooked that the relationship between incubation behaviour and temperature may not be linear (Conway & Martin 2000). Therefore, in this study, a quadratic relationship of temperature will also be considered.

Secondly, it is predicted that food provisioning will also be negatively influenced when temperatures increase due to lower food availability and an increase in energy costs for the birds. This reduction in food provisioning is especially expected at days when temperature exceeds 35.5 °C (du Plessis et al. 2012). Both these effects of temperature on incubation and provisioning behaviour might be less visible in cooperative breeding species. In cooperative breeders, helpers may act as a buffer against changes in incubation patterns and a decline in food provisioning to offspring by breeding parents during extreme temperatures. Furthermore, it is also expected that the effect of temperature on incubation and provisioning behaviour in larger groups will be less noticeable than compared to smaller groups or birds with biparental care due to the buffer effect of helpers.

## Methods

### Study sites and study species

#### Study species and Mbuluzi Game Reserve

Three different passerine bird species from Eswatini were studied: arrow-marked babbler (*Turdoides jardineii*; hereafter; ‘babblers’), white-crested helmetshrike (*Prionops plumatus*; hereafter; ‘helmetshrikes’) and dark-capped bulbul (*Pyconotus tricolor*; hereafter; ‘bulbuls’). Babblers are a cooperatively breeding species and are extremely social birds. They live in groups ranging from 6 to 9 individuals (Smith 1836). The birds mainly inhabit an open grassy environment and almost exclusively nest in low thorny bushes. Babblers mostly feed on insects but may also forage for seeds and fruits. Clutches consists of 2 to 5 eggs (Smith 1836). Helmetshrikes are also a cooperative breeding species which lives in groups from 2 to 10 members. They are an insectivorous species. Helmetshrikes build their nests mostly in high trees and clutch sizes consist of 3 to 4 eggs (Hockey et al. 2005). Bulbuls have a biparental care system. They mostly build their nest in low bushes with thorns and clutch sizes ranges from 1 to 3 eggs (Hockey et al. 2005). Bulbuls are an omnivorous bird species and forage for both fruit, flowers and insects.

Data of the Eswatini birds was collected during the breeding seasons (October till November) of 2018 (bulbul) and 2019 (helmetshrike, babbler) in Eswatini, Mbuluzi Game Reserve and was part of The Social Savannah Project. The area is characterised by a low altitude, dry savannah habitats and extreme weather, such as severe drought and extreme temperatures (Anderson 2018). Day temperature during the breeding season of 2018 ranged from 11 to 43 °C and in 2019 the temperature ranged from 14 to 46 °C.

#### Study species and Lysterfield park

The superb fairy-wren (*Malurus cyaneus*; hereafter; ‘fairy-wrens’) is an insectivorous passerine bird species which is endemic to Australia. It is a sexual dimorphic bird species where males may change seasonally from a brown plumage to a bright nuptial plumage (Rowley 1965; Peters 2000). Fairy-wrens breed either in pairs or cooperative breed in groups of 3 to 4 individuals. Clutches consists of 2 to 4 eggs (Dunn & Cockburn 1998).

Data on the fairy-wrens was collected during the breeding season of 2020/2021 (September–February) in Australia, Victoria, Lysterfield Park. Daytime temperature during the breeding season in this area ranges from 5 to 30 °C. In the National parks in Victoria different habitats can be found such as grasslands, forests and grassy woodlands where birds may breed (<https://www.parks.vic.gov.au>).

### Nest monitoring

#### Fieldwork in Mbuluzi Game reserve, Eswatini

At the onset of spring (late August/begin September), nests were located via transect searches at 50m (or less when the vegetation was too dense to clearly inspect suitable nesting habitats). Once nests were found, they were regularly checked. The stage of the nest was noted down and every 3 to 4 days nests were checked again to monitor their progress. During the egg laying stage, date of first egg and clutch size was noted down. Once the eggs hatched, the hatch date and brood size was collected. Nestlings were ringed on different days from recording days or at the end of a recording to not disturb the birds before behavioural observations. Incubation and provisioning behaviour were recorded with GoPros for the bulbuls and babblers which were close to the nests (<2 m). For the helmetshrikes, camcorders were used which were located ca. 20m from the nest and zoomed in on the nest (for

durations of observations per species see below). For incubation behaviour, nests were filmed around day 3,7 and/or 14 after the first egg was laid. Day of provisioning recordings varied between the observations for each species. For the bulbuls, nests were mostly filmed when the nestlings were 7 days old. Nests were monitored until brood failure or when nestlings had fledged.

### **Field work in Lysterfield park, Australia**

During the breeding season (September till January), each territory was visited at least once a week to check for (breeding) activity of the fairy-wrens. Most of the adult birds were colour banded. Dominant females were followed for at least 40 minutes and observed for any breeding behaviour. If no breeding activity was observed during those 40 minutes, the group was visited one week later to check for any breeding activity again. Once a nest was found, the stage of the nest was noted down and at least every 3 days the nest was checked to observe the progress and status. If the nest contained nestlings, age and number of nestlings were noted down. Nestlings were banded around day 6 till 8 and was done at different moments from recording days to not disturb the behavioural observations. For the observations of provisioning behaviour, motion triggered cameras (CopCam) were placed in front of the nest at day 6 or/and 8. The cameras were covered with green tape for camouflaging and placed in front of the nest on a pole or branch.

### **Temperature measurement**

In Mbuluzi, Eswatini, a total of 12 USB thermo-loggers (Lascar Electronics EL-USB-2) were distributed throughout the area to measure the ambient temperature (°C) during the breeding season. These thermo-loggers where all placed in a similar situation, in the shadow close to a tree trunk and around 1.5m in height. Ambient temperature was recorded throughout the whole day and during the night (00:00-23:59) with an interval of 10 minutes, depending on the thermo-logger. For the analysis of incubation and provisioning behaviour, the nearest thermo-logger was linked to the nest closest to that specific thermo-logger (average distance between nest and thermo-logger was 500m and ranged from 93m to 808m).

In Lysterfield Park, Australia during the breeding season, weather data was collected by using a Davis Vantage Pro2 (wireless) weather station from November 2020 till January 2021. Temperature was measured throughout the day and night with intervals of 5 minutes. Temperature data before November 2020 (e.g., October 2020) was obtained from the website of the Bureau of Meteorology, Australia Government (<http://www.bom.gov.au>).

### **Behavioural observations**

Video analysis of recordings of incubation and provisioning behaviour was done with VLC Media Player 3.0.11 (Vetinari). Both incubation behaviour and provisioning behaviour were used as a proxy for investment in offspring in this study.

#### **Incubation observations**

Incubation behaviour was defined as time (in minutes) of an on- or off-bout during the filming period. On-bouts were defined as time spending on the nest incubating and an off-bout was defined as no bird on the nest. For each recording, the first and last bout observation was removed to account for any disturbance during placing or removing the cameras and for the fact that the on- or off-bout duration was unknown when first placing the cameras. For each observation the following data was collected: unique identity of the nest under observation (NestID), date of the observation, start and end time of observation, start and end time of an on/off-bout, number of on- and off-bouts and exposure to direct sunlight (yes or no). The direct exposure of the nest to sunlight was incorporated in order to

investigate the effect on incubation behaviour. Whether or not a nest was exposed to sunlight was visual inspected during the video analysis. Moreover, mean on- and off-bout duration of the entire observation was also calculated. Additional factors such as time spend shading the eggs from the heat by individuals and time spent brooding were also noted down for each observation. Table 1 shows a summary of data used in this study.

#### *Babbler incubation observations*

Incubation behaviour was monitored for 5 babbler nests (10 recordings) and in total 70 filming hours. The start of the observations ranged between 07:00-09:00 and ended between 15:00-17:00. Mean duration of the observations was 7 hours per observation (duration ranged from 4 hours to 11 hours).

#### *Helmetshrike incubation observations*

Incubation behaviour was monitored for 7 helmetshrike nests (16 recordings). In total 36 filming hours were obtained during the breeding season. Observations started around 06:00-07:00 and ended between 10:00-11:00. Recordings of the helmetshrikes lasted for an average of 4 hours (duration ranged from 2.5 hours to 4 hours).

#### *Provisioning observations*

Provisioning rate was defined as number of feeds per hour in a certain time period (entire day, morning, afternoon or evening) and was calculated by number of feeds during filming period divided by the number of filming hours in that period. For every video the following data was collected: NestID, date of observation, start and end time of observation, number of feeds during filming hours and temperature during filming hours. For the Eswatini birds, the first and last feed were excluded to standardize the provisioning data. Other factors that may influence the provisioning behaviour such as age of nestlings, number of nestlings and whether the nest was exposed to direct sunlight were also noted down per nest. Sex was not determined for the Eswatini birds since those bird species are monomorphic and it is therefore not possible to identify the sex by visual inspection only.

#### *Babbler provisioning observations*

Data of provisioning behaviour of 8 babbler nests (10 recordings) and in total 96 filming hours were used in this study. Observations started around 07:00-08:00 and ended between 15:00-17:00. Mean duration of the observations was 9.5 hours per observation (duration ranged from 8 hours to 11 hours). The observations of babblers were either recorded with a time lapse recording where 4 seconds of video represents 1 minute in real time or without a time lapse.

#### *Helmetshrike provisioning observations*

Provisioning behaviour of 4 helmetshrike nests (6 recordings) and in total 18 filming hours were used. The provisioning behaviour of helmetshrikes was only recorded in the afternoon. Mean duration of the observations was 3 hours per observation (duration ranged from 2.5 to 3 hours). Observations started between 14:30-15:00 and ended between 18:00-18:30.

#### *Bulbul provisioning observations*

Provisioning data from 7 bulbul nests (7 recordings) was collected during the breeding season of 2018. A total of 67 filming hours were recorded. Each recording lasted on average 9.5 hours (duration

ranged from 8.5 to 11 hours). Observations started between 06:00-08:00 and ended between 15:00-17:00.

#### *Fairy-wren provisioning observations*

Data from 38 fairy-wren nests (38 recordings) and in total 156 filming hours were used in this study. Duration of a single observation was on average 4 hours (duration ranged from 2 to 6 hours). These observations mostly started around 09:00 -10:00 and ended around 15:00-16:00. The first feed was not removed for the fairy-wren data since the first hour was already removed from each observation. In addition, the sex of the bird (determined based on the bright plumage of males and brown colour of females and on the colour rings) was also noted down during video analysis, since there might be a shift in care of either male or female.

**Table 1**

Overview of data used in this study.

species	behaviour	season	n nests	n recordings	filming hours
Arrow-marked babbler	incubation	2019	5	10	70
Arrow-marked babbler	provisioning	2019	8	10	95
Dark-capped bulbul	provisioning	2018	7	7	67
Superb fairy-wren	provisioning	2020/21	38	38	156
White-crested helmetshrike	incubation	2019	7	16	35
White-crested helmetshrike	provisioning	2019	4	6	18

## Statistical analysis

For all the statistical analyses, the program RStudio 1.3.1093 (RStudio team 2020) was used. Normality of the residuals of the incubation and provisioning data was analysed by using Q-Q plots and the Shapiro-Wilk test. Data was checked with Cook's distance statistics to investigate the effect of single data points for each data set. Data was analysed by using Linear models (LM) and Linear mixed models (LMM) with the package 'lme4' (Bates et al. 2019) and fitted with Restricted Maximum Likelihood. Mixed models were used in order to account for both within-nest and across-nest variation because some nests had multiple recordings on different days. Therefore, the random factor NestID, which was the name given to a nest when found, was incorporated. LMs were used on data where there was one recording per nest available. Moreover, in most of the models, where sample size was relatively large, the interaction term between group size and temperature was incorporated to investigate the buffer effect of helpers during suboptimal circumstances. The threshold of  $p < 0.05$  was used as statistically significant result. Model selection was done by removing non-significant terms with backward step-wise elimination starting with non-significant interactions to construct the minimal model. Reported values of non-significant terms were obtained by including those in the minimal model.

## Incubation analysis

### *Babbler incubation analysis*

Data of the babblers were analysed with LMMs. The incubation data was analysed in two different ways: first, it was tested whether the mean on- or off- bout duration (min) was associated with the mean temperature ( $^{\circ}\text{C}$ ) across the whole observation, and secondly, it was tested whether the duration of individual on- or off-bouts were related to the mean temperature during that particular bout.

For the first analysis, mean on- or off-bout duration was used as response variable. The mean temperature, group size, the interaction between temperature and group size, number of eggs and exposure to sun was included as fixed effect. Nest ID was incorporated as random factor.

For the second analysis, the duration per on- or off-bout was used as predictor variable. The interaction with mean temperature during the whole observation and group size, a quadratic effect for temperature and exposure to sun (yes/no) was included as fixed effect. A quadratic effect of temperature was included in the model since it was expected that birds would decrease their incubation bouts up to a temperature of 36 °C and would increase incubation bouts again around 40 °C. This was not incorporated in the first analysis to avoid over-fitting of the model. Nest ID nested in observation number was incorporated as random factor.

#### *Helmetshrike incubation analysis*

Influence of ambient temperature on incubation bouts was investigated by using LMMs for the helmetshrikes ( $n=7$ , 16 observations). One outlier was removed from the incubation data of the helmetshrikes. This was a single case where the measured temperature was above the 40°C and where on-bout duration was extremely long and off-bout duration very short and therefore skewed the data. Furthermore, ‘on-bouts’ that lasted less than one minute were removed from the dataset. These short bouts on the nest were mostly used for nest building and maintenance activities by individuals. Data was analysed in the two different ways previously described in the babbler section.

For the first analysis, the mean on- or off-bout duration was used as response variable. The interaction with mean temperature and group size and exposure to sun were included as fixed effect. NestID was incorporated as random factor.

For the second analysis, the duration per on- or off-bout was used as response variable. The interaction with mean temperature and group size, a quadratic effect for temperature and exposure to sun was included as fixed effect. NestID nested in observation number was incorporated as random factor. However, results for this LMM analysis should be interpret with caution. The data was transformed with a log and square root transformation to try to normalize the model residuals, without success. Generalized linear models were also tried, without success. Results of the LMM are shown in the result section below.

#### **Provisioning analysis**

##### *Babbler provisioning analysis*

The effect of temperature on the provisioning rate of babblers was analysed with LMMs. The data was divided in four different time periods: entire period of observation, morning (07:00-10:00), afternoon (10:01-14:00) and evening (14:01-17:00). This division was made because temperature fluctuates throughout the day in Eswatini. Overall, the morning is the coldest period and afternoon and evening are the periods with the highest temperatures. Thus, four different models were constructed with the feeding rate during these different time periods as response variable. The interaction with temperature (during the corresponding time period) and group size, offspring age, number of offspring and exposure to sun were incorporated as fixed effects. NestID was included as random factor. In addition, data was also divided in just morning (07:00-11:00) and afternoon (11:01-17:00) to increase the observations during these time periods.

##### *Bulbul provisioning analysis*

Data of the bulbuls were analysed with LMs because one observation per nest was collected during the breeding season. Data was also divided in four different time periods as described above in the babbler provisioning section. Therefore, four different models were constructed again for entire observation, morning, afternoon and evening. Response variable was the feeding rate during these different time periods. The temperature during the corresponding time periods was incorporated as fixed effect. Moreover, data of the bulbuls was also divided in morning (07:00-11:00) and afternoon (11:01-17:00).

### *Helmetshrike provisioning analysis*

Since helmetshrike observations were only conducted in the afternoon, no division of time periods was made within a day. The data was analysed with LMMs. No interaction between temperature and group size was done to avoid over-fitting of the model. Only one model was constructed with feeding rate during the whole length of the observation as response variable. Predictor variables were temperature during observation and group size.

### *Fairy-wren provisioning analysis*

Data of the fairy-wrens ( $n=38$ , 38 observations) were analysed with LMs. Days were not divided in different periods because provisioning observations were mostly conducted in the late morning/ early afternoon.

One model was constructed with the provisioning rate during the whole duration of the observation as response variable. The interaction between temperature and group size, and the factors temperature during the observations, group size, nestling age and number of nestlings were included as predictor variable. In addition, a second model was constructed to investigate whether there was an interaction between sex and temperature. Individual provisioning rate (male and female) was included as response variable. Predictor variables were group size and the interaction between sex and temperature. NestID was incorporated as random factor.

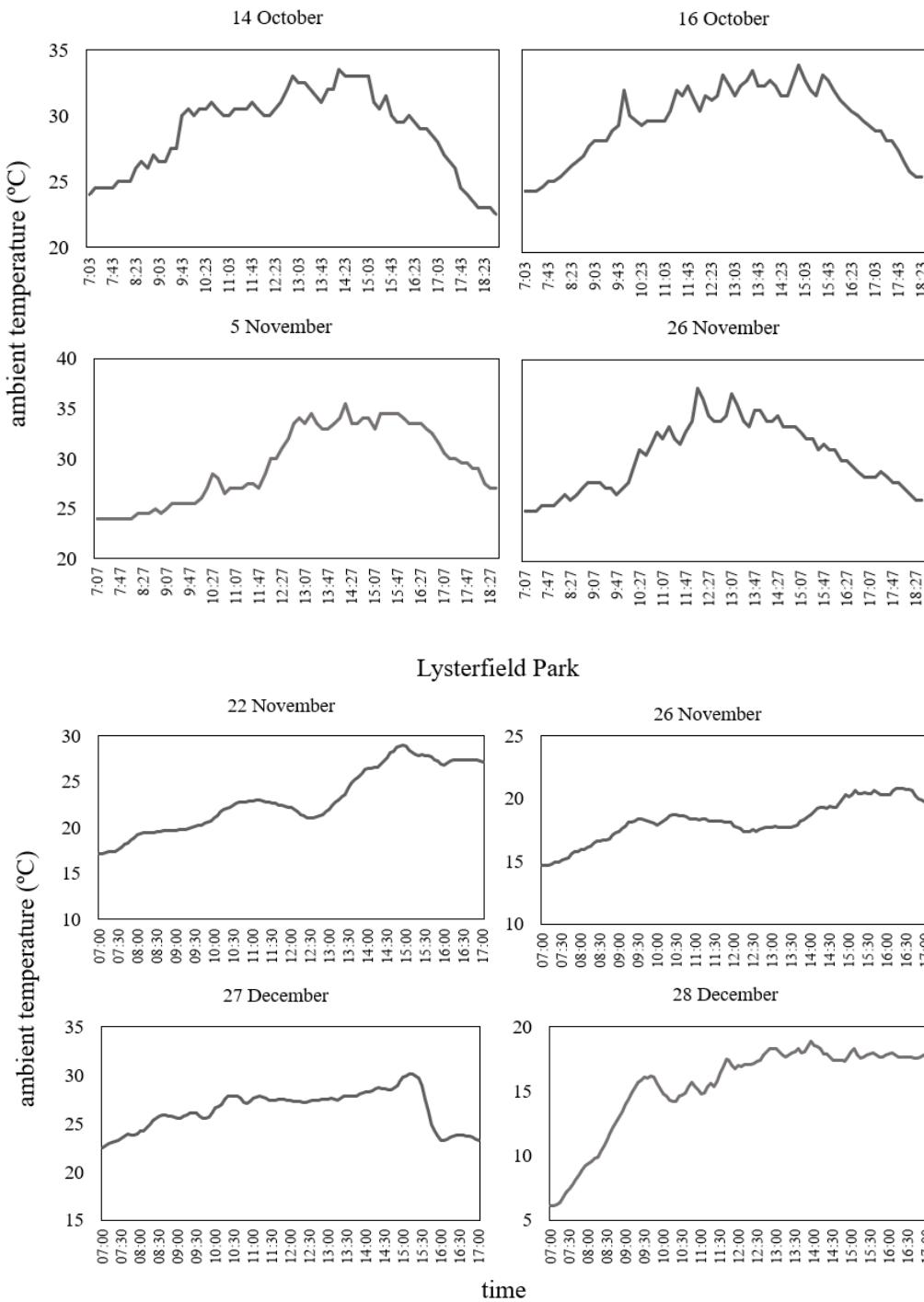
## Results

### **Temperature measurements**

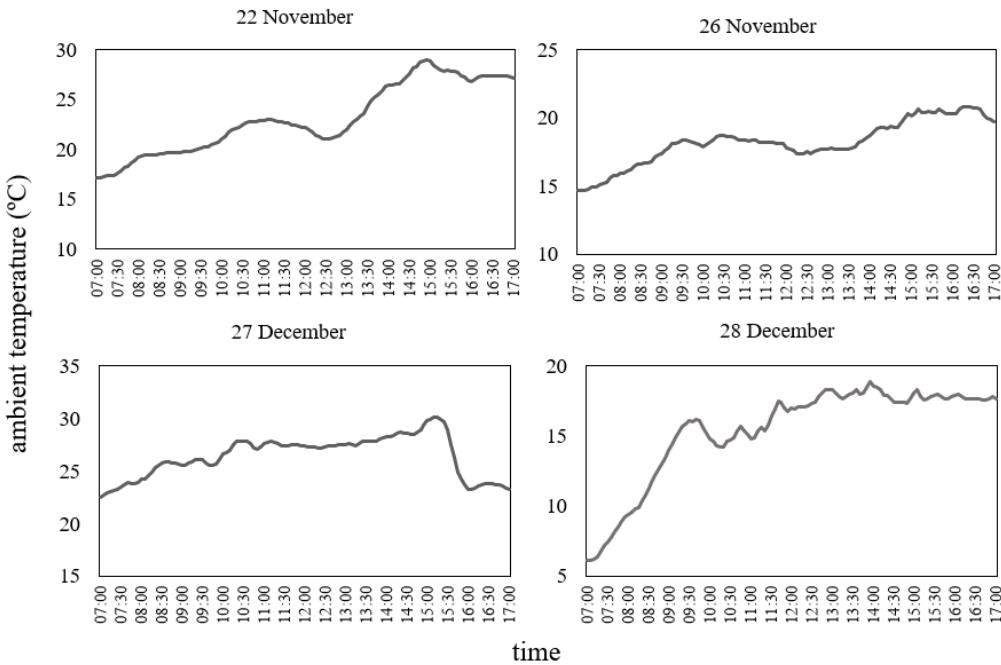
In Eswatini, the temperature ranged from  $\pm 20$  to  $40^{\circ}\text{C}$  during the day. Overall, temperature was lowest between 07:00 and 10:00 and temperature peaked between 10:00 and 14:00 and decreased after approximately 14:00-15:00 again (Fig. 1).

In Australia, temperature ranged from 5 to  $30^{\circ}\text{C}$  during the day (Fig. 1).

### Mbuluzi Game Reserve



### Lysterfield Park



**Fig. 1.** Temperature measurement of several randomly chosen days during the breeding season in October, November and December in Mbuluzi Game Reserve, Eswatini during the breeding season of 2019 and Lysterfield Park, Australia during the breeding season of 2020.

## Influence of ambient temperature on incubation behaviour

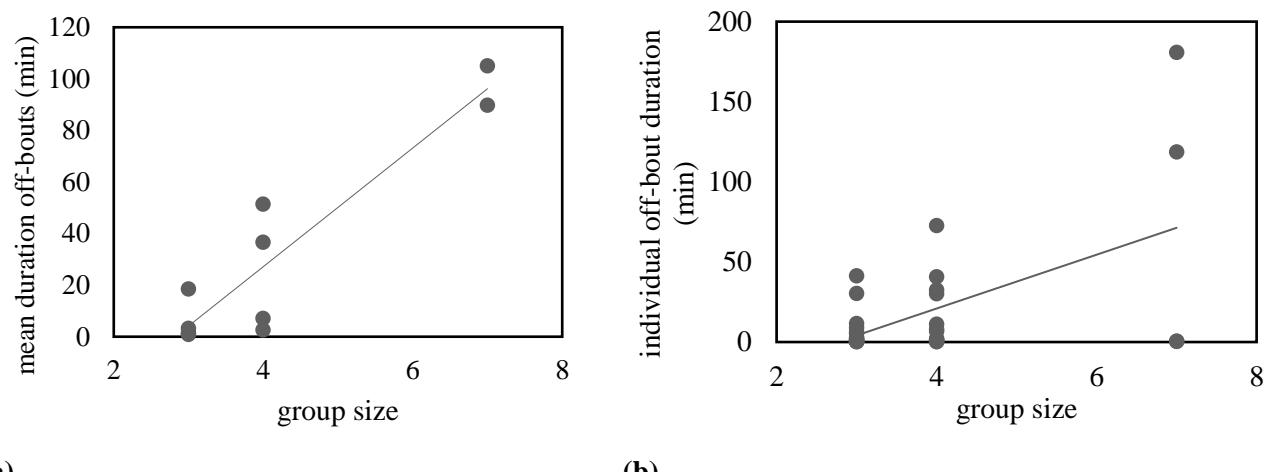
### Babbler incubation analysis

Mean temperature during on-bouts was 29 °C (ranged from 24 to 40 °C) and during off-bouts was 29 °C as well (ranged from 22 to 34 °C). Mean group size was 5 individuals per nest and mean clutch size was 2 eggs. The mean on-bout duration across nests ranged from 28 to 361 minutes. Off-bout duration from nests ranged from 1 to 105 minutes.

In the first analysis, the interaction between temperature and group size was not significant and was removed from the model. Exposure to sunlight and number of eggs also had no significant influence on mean on-bout duration and were removed from the model as well (See appendix I for full model results of LMMs with non-significant terms). No significant influence of mean on-bout temperature and group size on mean on-bout duration was observed (Table 2). Also, no interaction between off-bout temperature and group size was found. Exposure to sunlight and number of eggs had no significant effect on mean off-bout duration and were removed from the model as well (Table 2). Group size, however, was a significant predictor for off-bout duration. The mean off-bout duration was longer at nests with more individuals than when compared to nests with smaller group sizes (Fig 2a).

For the second analysis per individual on-bout, no significant quadratic relationship of temperature was found and no interaction between temperature and group size and thus were removed from the model. Exposure to sunlight also showed no significant relationship. No effect of on-bout temperature and group size on on-bout duration was observed (Table 3).

No significant quadratic effect was observed and no interaction between group size and off-bout temperature was observed. Number of eggs and exposure to sunlight were also removed from the model. However, a significant positive relationship between group size on off-bout duration was observed (Table 3), which is in line with the previous results of the mean off-bout duration (Fig 2b). Nests with large groups were left unattended for a longer period than nests with smaller groups.



**Fig. 2.** (a) Relationship between mean duration off-bout duration (min) and group size (n=5, observations =10) in arrow-marked babblers. (b) Relationship between duration per individual off-bout and group size (n=5, observations =34).

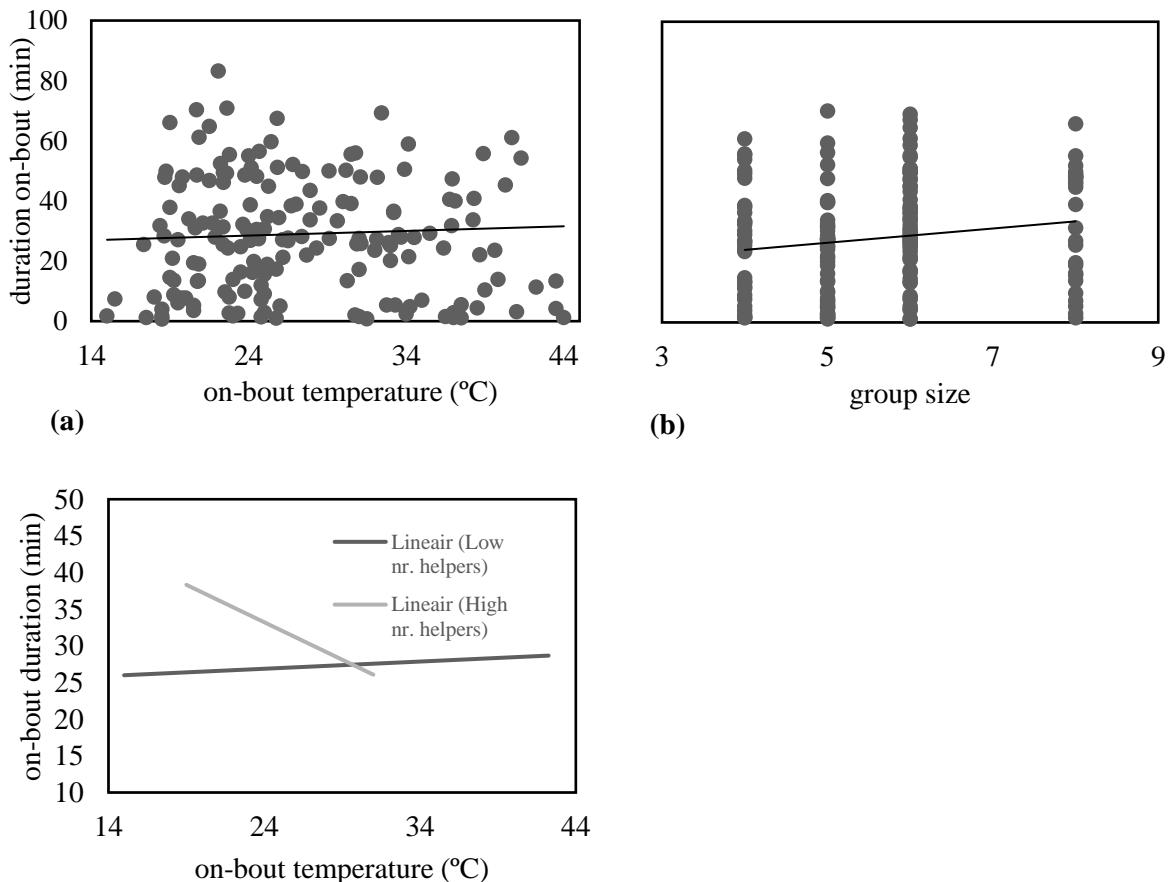
## Helmetshrike incubation analysis

Mean temperature during on- and off-bouts was 28 °C (ranged from 19 to 40 °C). Mean group size of the helmetshrikes was 5 and mean clutch size was 3 eggs. Mean on-bout duration across nests ranged from 12 to 36 minutes and mean off-bout duration ranged from 3 seconds to 7 minutes.

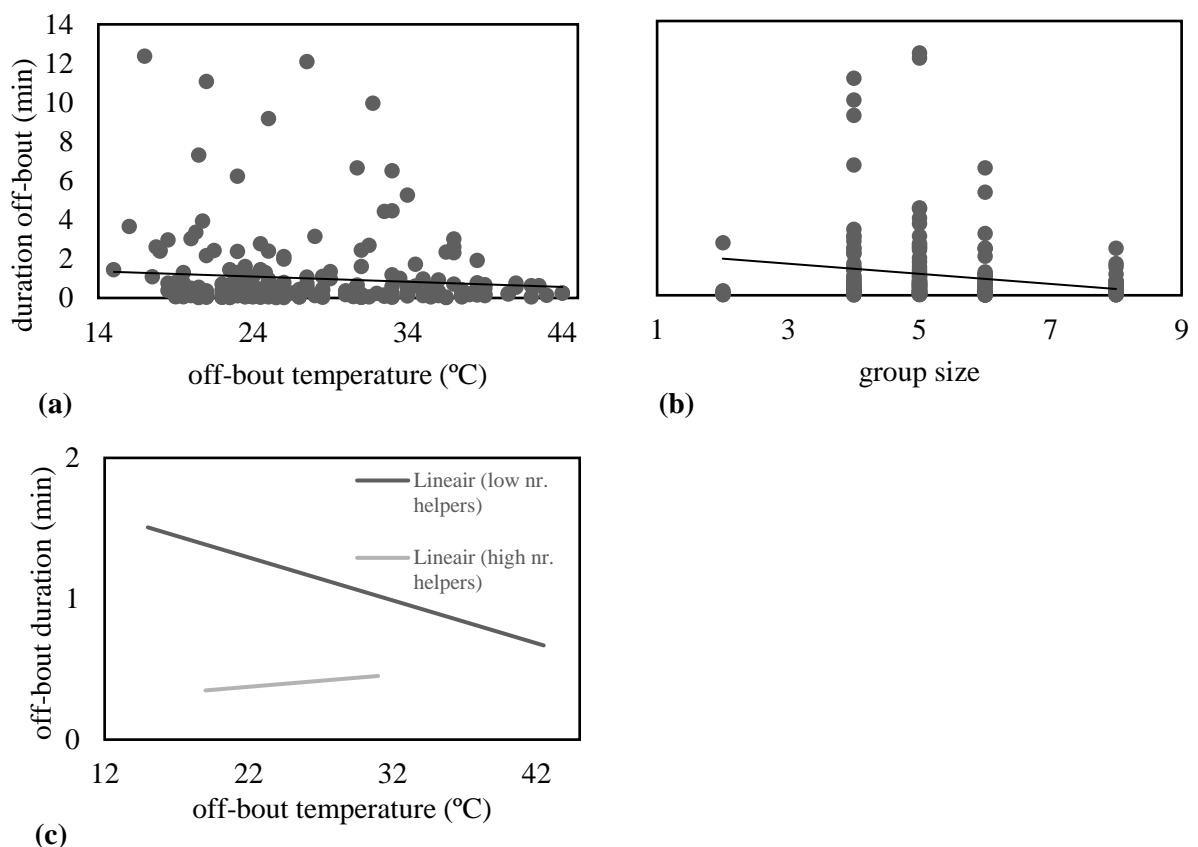
For the first analysis, no significant interaction between temperature and group size was found. Exposure to sunlight was also removed from the model. Results of the final model also showed no significant interaction with mean on- and off-bout duration with mean temperature during on- and off-bout and group size (Table 2).

For the second analysis, no quadratic effect of temperature was observed for both on- and off-bouts and thus was removed from the model. Exposure to sunlight was removed as well from the model. In general, birds tend to spend more time on the nest when temperature increased (Fig 3a). Also, on-bout duration at the nest increased with increasing group size (Fig 3b). However, an interaction between on-bout temperature and group size was observed as well (Table 3). Birds in larger groups tend to spend more time on the nest when temperature was relative low when compared with birds in smaller groups (Fig 3c). When temperature increased, however, birds in larger groups spend similar amount of time on nests when compared to birds with less helpers.

On the other hand, the off-bout duration from nests decreased with increasing temperatures (Fig 4a). Moreover, nests with more helpers were left unattended for a shorter period than nests with fewer helpers (Fig 4b). A weak interaction between group size and temperature was also found. Off-bouts duration at the nest of the birds decreased when temperature increased which was especially visible at nests with smaller groups (Fig 4c).



**Fig. 3.** (a) Relationship between individual on-bout duration and group size (b) Relationship between duration per on-bout (min) and the ambient temperature (°C) during on-bouts in white-crested helmetshrikes. (c) Interaction between on-bout temperature and group size. Dark grey = low number of helpers (2,3 or 4). Light grey = high number of helpers (6).



**Fig. 4** **(a)** duration of individual off-bout and off-bout temperature in white-crested helmetshrikes. **(b)** Duration single off-bouts and group size. Each point represents a single bout. **(c)** Interaction between off -bout temperature and group size. Dark grey = low number of helpers (2,3 or 4). Light grey = high number of helpers (6).

**Table 2**

LMM of mean duration incubation bouts helmetshrikes (n=6, 16 observations) and babblers (n=5, 10 observations). Temperature is in Celsius (°C). Significant terms are displayed in bold.

<b>response variable</b>	<b>species</b>	<b>predictors</b>	<b>estimate±se</b>	<b>t-value</b>	<b>p-value</b>
mean duration on-bout (min)	White-crested helmetshrike	mean on-bout temperature	0.037±0.26	0.14	0.89
		group size	0.51±0.92	0.56	0.58
	Arrow-marked babbler	mean on-bout temperature	-0.43±3.42	-0.13	0.91
		group size	13.93±39.12	0.36	0.74
mean duration off-bout (min)	White-crested helmetshrike	mean off-bout temperature *group size	0.034±0.02	1.88	0.08
		mean off-bout temperature	-0.19±0.10	-1.86	0.09
		group size	-1.09±0.52	-2.09	0.06
	Arrow-marked babbler	mean off-bout temperature (°C)	-1.11±1.91	-0.58	0.58
		<b>group size</b>	<b>21.77±4.17</b>	<b>5.22</b>	<b>0.001</b>

**Table 3**

LMM duration per bout during incubation of helmetshrikes (n=6, 157 observations) and babblers (n=5, 36 observations). Temperature is in Celsius (°C). Significant terms are displayed in bold.

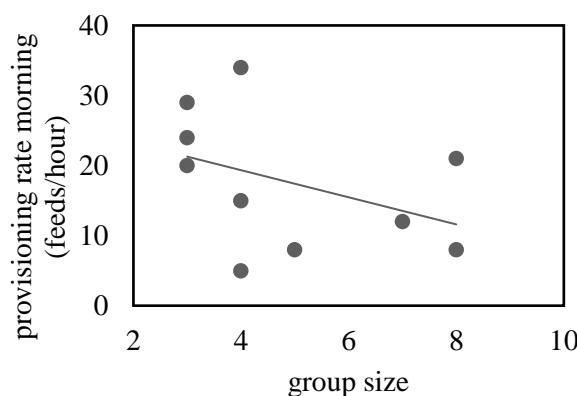
<b>response variable</b>	<b>species</b>	<b>predictors</b>	<b>estimate±se</b>	<b>t-value</b>	<b>p-value</b>
duration on-bout (min)	White-crested helmetshrike	<b>on-bout temperature *group size</b>	<b>-0.61±0.19</b>	<b>-3.11</b>	<b>0.03</b>
		<b>temperature on-bout</b>	<b>3.38±1.04</b>	<b>3.26</b>	<b>0.03</b>
		<b>group size</b>	<b>14.67±5.84</b>	<b>2.51</b>	<b>0.01</b>
	Arrow-marked babbler	on-bout temperature	1.79±2.09	0.85	0.41
		group size	11.74±18.24	0.64	0.52
		<b>number of eggs</b>	<b>-98.36±40.28</b>	<b>-2.44</b>	<b>0.02</b>
duration off-bout (min)	White-crested helmetshrike	off-bout temperature *group size	0.04±0.02	1.88	0.06
		<b>temperature off-bout</b>	<b>-0.25±0.12</b>	<b>-2.14</b>	<b>0.03</b>
		<b>group size</b>	<b>-1.47±0.60</b>	<b>-2.47</b>	<b>0.01</b>
	Arrow-marked babbler	off-bout temperature	-0.70±1.19	-0.58	0.56
	<b>group size</b>	<b>17.52±5.22</b>	<b>3.38</b>	<b>0.003</b>	

## Influence of ambient temperature on provisioning rates

### Babbler provisioning analysis

Mean temperature during provisioning was 29.5 °C (ranged from 24 to 33 °C). No interaction effect was found between group size and temperature during the different time periods (duration observation, morning, afternoon or evening). Other predictors, such as number of nestlings, nestling age, exposure to sunlight also had no significant effect on provisioning rates and were removed from the model (Appendix II for full model with p-values). No significant effect was found on provisioning rates and temperature of different time periods (Table 4). However, it was found that group size was a predictor for provisioning rates in the morning. Individuals in larger groups had a lower provisioning rate than individuals in smaller groups, however this was only visible during morning hours (Fig 4).

In addition, the provisioning data was also subdivided into morning (07:00-11:00) and afternoon (11:01-17:00). However, no differences were observed between subdividing the day this way (final model and results are shown in appendix III) and subdividing it in three different parts.



**Fig. 4.** Relationship between provisioning during morning hours and group size in arrow-marked babblers.

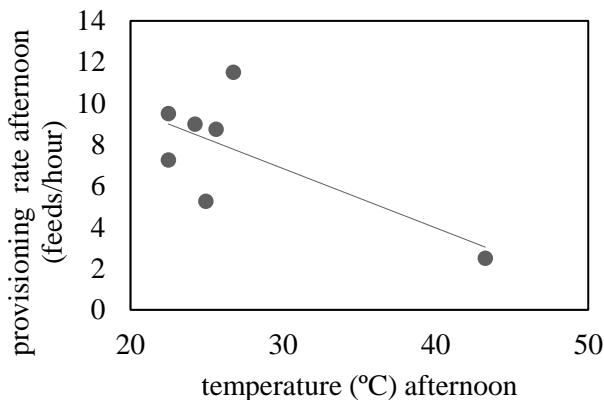
**Table 4**

Results LMM of provisioning rate (feeds per hour) of babblers (N=8, observations =10). Temperature is in Celsius (°C). Significant terms are displayed in bold.

response variable	species	predictors	estimate±se	t-value	p-value
provisioning rate entire day	Arrow-marked babbler	temperature entire observation	0.072 ±0.23	0.31	0.77
		group size	-0.60 ±0.44	-1.38	0.23
provisioning rate morning		temperature morning	0.05 ±0.09	0.60	0.57
		<b>group size</b>	<b>-0.37 ±0.15</b>	<b>0.16</b>	<b>0.05</b>
provisioning rate afternoon		temperature afternoon	-0.17 ±0.23	-0.74	0.49
		group size	-0.46 ±0.42	-1.10	0.35
provisioning rate evening		temperature evening	0.12 ±0.18	0.64	0.53
		<b>group size</b>	<b>-0.44 ±0.38</b>	<b>-1.17</b>	<b>0.27</b>

### Bulbul provisioning analysis

Mean temperature during provisioning was 26 °C (ranged from 21 to 43 °C). No significant relationship between overall provisioning rate and time of day was observed. However, the temperature in the afternoon was a weak predictor for the provisioning rate in the afternoon (Table 5). When afternoon temperature increased, the provisioning rate of individuals in the afternoon decreased (Fig. 5). Note, however, that this outcome was due to one point in the data set. On this particular day, the temperature in the afternoon was 43°C whereas on the other days the temperature ranged between 20 °C and 30 °C.



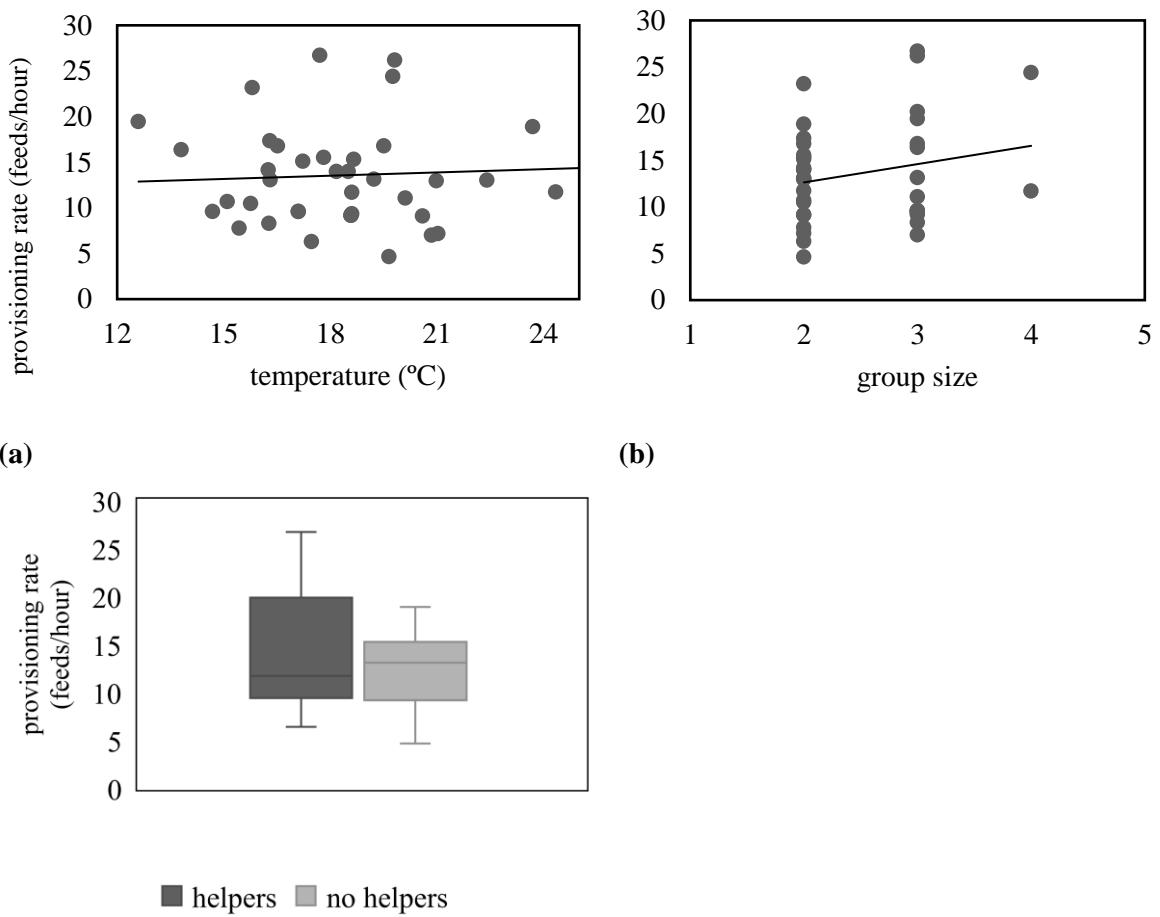
**Fig. 5.** Provisioning rate in feeds per hour and temperature in the afternoon in the dark-capped bulbuls.

### Helmetshrike provisioning analysis

The mean temperature during provisioning in the afternoon was 29 °C (ranged from 23 to 39 °C) For the helmetshrikes, no significant relationship between provisioning rate in the afternoon and ambient afternoon temperature was found. Group size also did not significantly affect the provisioning rate (Table 5).

### Fairy-wren provisioning analysis

Mean temperature during provisioning observations was 19 °C (ranged from 14 to 30 °C). No interaction was observed between temperature and group size and was removed from the model. Also, number of nestlings and nestling age did not significantly influence the provisioning rate (see for model with non-significant terms appendix IV). Ambient temperature and group size did not significantly influenced the provisioning rate of the fairy-wren. (Table 5; Fig 6a and 6b) Moreover, there was no significantly difference in provisioning rates between parental pairs with helpers and pairs without helpers (Fig 6c).



**Fig. 6.** **(a)** Relationship between provisioning rate and temperature ( $^{\circ}\text{C}$ ) during filming hours in superb fairy-wrens. **(b)** Relationship between provisioning rate (feeds per hour) and group size in the superb fairy-wrens. **(c)** Provisioning rates of breeding pairs with helpers versus no helpers.

**Table 5**

Results LM of provisioning rates helmetshrikes (N=4, observations =6), bulbuls (N=7, observations =7) and fairy-wrens (N=38, observations=38). Significant terms are displayed in bold.

<b>response variable</b>	<b>species</b>	<b>predictors</b>	<b>estimate±se</b>	<b>t-value</b>	<b>p-value</b>
provisioning entire observation	White-crested helmetshrike	temperature entire observation	-0.29±0.11	-2.65	0.23
		group size	0.11±1.81	0.06	0.96
provisioning rate entire day	Dark-capped bulbul	temperature entire observation	-0.22 ±0.12	-1.81	0.13
		temperature morning	-0.17±0.17	-1.03	0.35
provisioning rate morning		temperature afternoon	-0.29±0.13	-2.19	0.08
		temperature evening	-0.12±0.23	-0.51	0.63
provisioning rate entire day	Superb fairy-wren	temperature entire observation	0.16±0.27	0.61	0.55
		group size	2.22±1.45	1.53	0.13

In addition, overall provisioning rate of males and female was not significantly influenced by temperature and group size (Table 6).

**Table 6**

Results LMM provisioning rate (feeds/hour) superb fairy-wrens for female and male (n=37).

<b>Response variable</b>	<b>species</b>	<b>predictors</b>	<b>estimate±se</b>	<b>t-value</b>	<b>p-value</b>
Individual provisioning rate (male and female)	Superb fairy-wren	temperature entire observation*sex	-0.29±0.27	-1.07	0.29
		sex	2.92±5.11	0.57	0.57
		Temperature entire observation	0.51±0.43	1.20	0.23
		group size	0.078±1.11	0.07	0.94

## Species characteristics

For incubation behaviour, it was found that the duration of on-and off-bouts of babblers were longer than the bouts of helmetshrikes (Table 7). Provisioning rate was highest in the fairy-wrens which ranged from approximately 12 to 15 feeds per hour. The provisioning rates from species in Eswatini ranged from 4 to 7 feeds per hour (Table 7).

**Table 7**

Summary of species characteristics. Group size, clutch size, provisioning rate (feeds/hour), incubation on- and off-bout (min) are averages of data that was used in this study.

species	breeding system	geographical location	diet	group size	clutch size	provisioning rate	mean on-bout	mean off-bout
Arrow-marked babbler	cooperative	Eswatini	insects	5	2	4.43	158.64	31.74
Dark-capped Bulbul	biparental	Eswatini	insects/fruit	2	3	6.81	-	-
Superb fairy-wren	cooperative biparental	Australia	insects	3 2	3 3	14.45 12.27	- -	- -
White-crested helmetshrike	cooperative	Eswatini	insects	5	3	5.81	27.09	1.11

## Discussion

Overall, it was found that the influence of ambient temperature and group size on incubation and provisioning behaviour varies between the different bird species from Eswatini and Australia (Table 8). It was shown that mean bout duration and provisioning rates, in most species but not all, were not significantly influenced by ambient temperature and group size. However, a change in behavioural pattern due to either group size or temperature was especially detectable during days with extremely high temperatures (40 to 43 °C). This was also what initially was expected since days with extreme temperatures are per definition outliers. The findings are first discussed between species and secondly discussed per species. The results should at this stage, however, be interpreted with caution due to the low sample sizes of the Eswatini bird species.

**Table 8**

Summary of results found in this study for all species from Eswatini and Australia.

0 is no effect. + is a positive effect. - is a negative effect.

species	behaviour	temperature*group size	temperature	group size
Arrow-marked babbler	incubation on-bout duration	No	0	0
	- per on-bout	No	0	0
	incubation off-bout duration	No	0	+
	- per off-bout	No	0	+
	provisioning rate morning	No	0	-
Dark-capped bulbul	provisioning rate afternoon	NA	-	NA
Superb fairy-wren	provisioning rate	No	0	0
White-crested helmetshrike	incubation on-bout duration	No	0	0
	- per on-bout	Yes <sup>1</sup>	+	+
	incubation off-bout duration	No	0	0
	- per off-bout	Yes <sup>2</sup>	-	-
	provisioning rate	No	0	0

<sup>1</sup> Overall on-bout duration on nests were longer in larger groups and especially when temperatures were relatively low.

<sup>2</sup>Nests with a large number of helpers were left less time unattended when compared to nests with smaller groups.

## Incubation behaviour

Babblers and helmetshrikes differed in their incubation patterns. It was found that incubation bouts were longer in babblers compared to helmetshrikes. Babblers also tend to leave the nest unattended for longer periods than helmetshrikes. A possible explanation of differences in incubation patterns may be the location of nests. Babblers mainly nest in low thorny bushes with a lot of coverage (Smith 1836), whereas helmetshrikes build their nest in high trees without much vegetation coverage (Hockey et al. 2005). This may force helmetshrikes to spend more time on the nest, protecting the eggs from environmental circumstances such as heat and direct sunlight. Moreover, a difference in incubation patterns might also be due to the differences in filming days between babblers and helmetshrikes. The sensitivity of the embryo to temperature varies between different developmental stages (Webb 1987). Therefore, parents might need to adjust their incubation behaviour depending on the development stage of the eggs. A differences in incubation patterns could also be sex specific. For example in the study of Vincze et al. (2017), researchers investigated parental cooperation during

incubation in fluctuating environments in 36 plover species (*Charadrius spp.*) with biparental care and across six continents. The researchers used data previously collected across different breeding seasons and investigated various factors (mean temperature, temperature fluctuations between years and temperature differences during breeding seasons) that may influence parental care. They found that environmental temperature and fluctuations of temperature affect parental care division and especially influence the degree of male care. It was shown that males increase their care relative to that of females during the incubation period. A shift in care between male and female may increase conflict between parents where one or both parents adjust their workload and this may have consequences for the fitness for the parents (Vincze et al. 2017). However, in this study the sex of the birds was unknown since the bird species from Eswatini were all monomorphic and therefore not distinguishable by observations only. Thus, further research is needed to investigate what affects the incubation patterns of babblers and helmetshrikes.

### Arrow-marked babbler

Surprisingly, in babblers, it was found that nests with larger groups were left unattended for a longer period than nests with smaller groups. This finding was in contrast with the expectation that nests with more individuals would have a higher incubation constancy, since there are more individuals available to occupy the nest. However, the temperature on this particular day peaked around 40 °C and this may have had consequences for the incubation patterns of the birds. It is known that at higher temperatures, the trade-off between self-maintenance and care that the offspring demands of parents may be stronger (DuRant et al. 2019). At a temperature of 40 °C, birds may leave the nest for longer periods of time between incubations bouts and spend more time on self-maintenance and foraging. In consequence, a mismatch between care that offspring need and care that individuals are willing to give occurs, which eventually may lead to decrease in fitness of the offspring and parents (Vincze et al. 2017; DuRant et al 2019).

Moreover, an increase in off-bout duration of nests with more individuals could also be a group-level coordination problem. It has been shown for provisioning behaviour in chestnut-crowned babblers that larger groups were visiting nests more asynchronously on days when mean temperature was high (Nomano et al. 2019). This coordination problem in large groups may also occur during incubation of the eggs during high temperatures where the cost of parental care is relatively high.

Another possible explanation might be that this nest has been disturbed (e.g. predators or humans) throughout this particular day, which forced the birds to take longer off-bouts from their nest. Taken together, these findings suggest that temperature may negatively affect incubation patterns especially in large babbler groups.

### White-crested helmetshrike

In helmetshrikes, nests with a larger group of individuals were in general occupied for longer periods when compared to nests with smaller groups however, this was especially visible when temperatures were relatively low. Duration of incubation bouts of birds in smaller groups remained constant throughout different temperature ranges. These findings are also in line with previous studies. In the study of Morentsen & Reed (2018), researchers investigated the incubation patterns and the influence of group size in White-breasted Thrasher (*Ramphocinclus brachyurus*). They found that larger social groups had a higher incubation constancy than nests with pairs. Incubation constancy also remained high after a certain threshold temperature of 30 °C (Mortensen & Reed 2018). Moreover, results in this study suggests that especially at lower temperatures overall time spent on a nest is higher in nests with more helpers. This may suggest that larger groups may have a bigger advantage during lower temperatures instead of during extremely high temperature.

Off-bout duration of nests with smaller groups decreased when temperature increased. Whereas, time spent off the nest in larger cooperative breeding groups remained constant during

different temperatures and was overall less when compared to birds in smaller groups. This is in line with the hypothesis that when ambient temperature increases, off-bout duration will decrease, as birds might need to engage in more cooling behaviour and shielding the eggs from over exposure to heat (Courtney et al. 1999). This decrease in overall off-bout duration during high temperatures may suggest that individuals are able to spend less time on self-maintenance, which might affect the condition of the birds. Other studies showed that incubation behaviour may be plastic as well. In a study conducted on Northern bobwhite (*Colinus virginianus*) and scaled quail (*Callipepla squamata*) researchers found that for both species, individuals were able to adjust their parental incubation behaviour to ensure an optimal development temperature. This was even observed during extreme temperature fluctuations (Carroll et al. 2018). Also in this study, helmetshrikes showed that incubation behaviour may be flexible across a different range of temperatures.

## Provisioning behaviour

Overall provisioning rate in fairy-wrens was higher than the provisioning rate of the birds from Eswatini. These differences in provisioning rates may be due to species characteristic differences and the life history of a species. Also, geographical differences (e.g. habitat quality, precipitation) and temperature differences between the two locations may also play a role. The mean temperature in Eswatini was 10 °C higher than in Australia during the breeding seasons. Therefore, the energetic costs for birds may be higher when foraging for food in Eswatini and thus provision less than the fairy-wrens. Higher temperatures in Eswatini may also negatively affect the food availability, which makes it more difficult to find food resources. Thus, there may be various factors contributing to differences in provisioning behaviour between birds from Eswatini and Australia.

When considering only birds from Eswatini, bulbuls had overall the highest provisioning rates compared to the other two cooperative breeding species. Bulbuls often feed their offspring small insects or fruits such as berries. These food items are low in caloric value (Izhaki & Safriel 1989) and therefore bulbuls may need to provision the offspring more regularly. In this study, it was observed that helmetshrikes and babblers often feed their offspring with larger prey such as grasshoppers and other large arthropods which are high quality in terms of calories and protein content (Razeng & Watson 2015). Therefore, helmetshrikes and babblers may be able to feed the offspring less regularly than bulbuls.

It may also be the case that certain individuals in the cooperative breeding groups contribute less to the care of offspring due to an increase in conflict in cooperative breeding groups (Ridley & Raihani 2008; Nomano et al. 2019). Previous studies showed that dominance rank may play a crucial role in the adjustment of parental care. It was shown that helpers may have a load-lightening effect (Crick 1992) in superb fairy-wrens (Russel et al. 2008) and pied babblers (Ridley et al. 2008). This enables parents to decrease their own investment in offspring while helpers also provide care for the young. For example, Wiley & Ridley (2016) investigated the influence of temperature on provisioning of offspring in pied babblers. Here, the researchers took the dominance hierarchy within a group into account. They found that dominant birds significantly provisioned less on days with high temperatures whereas subordinate birds did not decrease their provisioning rates (Wiley & Ridley 2016). In this study however, individual bird identity and dominance rank was not known and therefore it could not be distinguished which individual was a dominant or helper bird.

## Arrow-marked babbler

Birds in larger groups provisioned overall less, during the morning, when compared to smaller groups. This was initially not what was expected since it was hypothesized that the overall provisioning rate would be higher in larger groups because of more individuals that can forage for food and provisioning the offspring. How the provisioning behaviour is compromised in larger groups is open

for discussion, since temperature was not particular extreme during observations. A possible explanation might be that this nest has been disturbed by predators and therefore, individuals may have been forced to reduce their activity around the nest (Griesser & Ekman 2008; Iserbyt et al. 2019). Moreover, this reduction in provisioning in larger groups could also be a group-coordination problem. Group-coordination is important to reduce conflict of care between individuals. However, when group-coordination is not optimal, the amount of care may decrease and could have severe consequences for the offspring (Nomano et al. 2019). Thus, in babblers it was shown that a larger group may not automatically result in higher provisioning rates.

### Dark-capped bulbul

In the bulbuls, the provisioning rate in the afternoon decreased when temperature increased (up to 43°C). It is known that foraging efficiency declines with higher temperatures and especially after 35.5 °C (du Plessis et al. 2012). This decline in provisioning rates and foraging efficiency may be due to a trade-off between behaviour that allows heat to dissipate from the body and foraging for food (du Plessis et al. 2012; Wiley & Ridley 2016). In addition, a decrease in food availability during extreme temperatures could also play a role in a decreased overall provisioning rate (Rauter et al. 2000; Carey 2009). These results suggest that the provisioning rate in bulbuls is influenced by high temperatures. Ultimately, this decrease in food provisioning of parents to offspring may negatively impact the development of offspring and even their survival chance.

### White-crested helmetshrike

In contrast to the bulbuls, helmetshrikes did not visible alter their food provisioning patterns in response to high temperature. The absence of an observable effect of temperature on provisioning rates in helmetshrikes is in contrast with several earlier conducted studies, where ambient temperature was found to influence the provisioning rates (Wiley & Ridley 2016; DuPlessis et al. 2012).

A possible explanation could be that helmetshrikes are insensitive to high temperatures and therefore do not respond to temperature changes. Helmetshrikes build their nests high in trees without much coverage and are very exposed to environmental influences such as heat and direct sunlight. Therefore, offspring may be more vulnerable to changes in the environment and need constant provisioning of food to compensate for water loss (DuPlessis et al 2012). This constant rate of food provisioning to offspring, even during extremely high temperatures, may have severe consequences for the body condition of parents and helpers.

### Superb fairy-wren

Fairy-wrens also did not alter their provisioning rate in response to temperature or group size. In a previous conducted study, it was shown that pied babblers decreased their provisioning rate at a critical temperature of 35.5 °C (du Plessis et al 2012). However, in this study, the mean temperature during the breeding season in Australia ranged from 20 to 30 °C. Thus, there were no days above this critical temperature where birds might need to adjust their provisioning behaviour due to extreme temperatures.

## Conclusion

In this study, it was shown that different bird species from Eswatini and Australia varied in their response to ambient temperature. Overall, bout duration and provisioning rates were not extremely influenced by ambient temperature and group size in most of the bird species. Some bird species, however, showed a stronger behavioural response to extreme temperature and group size. These

results might suggest that parental behaviour can be resilient, to a certain extent, against extreme temperatures in bird species with different breeding systems. On the other hand, it may also suggest that birds may not be able to change their parental behaviour in response to extreme temperatures. This inflexibility might have a negative impact on the physiology of parents and may hamper their ability to breed in the next season and even decrease survival. For future studies it is therefore crucial to investigate these effects of temperature on parental care patterns at a more individual level, per dominance rank (Crick 1992; Russel et al. 2008; Ridley et al. 2008) and for male and female separately (Vincze et al. 2017). In this study, overall parental behavioural patterns were considered, however, body condition and survival rate of offspring may also be affected by extreme temperatures. Therefore, in light of the currently rapid changing climate (IPCC 2013), it is important to keep investigating and increase our understanding in the cost of parental care and behavioural changes of bird species with different breeding systems.

## Acknowledgments

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Despite not going to Eswatini, I really enjoyed video watching all the birds doing their thing and it felt like I was still a little bit doing fieldwork!

## References

- Amininasab, S. M., Kingma, S. A., Birker, M., Hildenbrandt, H., & Komdeur, J. (2016). The effect of ambient temperature, habitat quality and individual age on incubation behaviour and incubation feeding in a socially monogamous songbird. *Behavioral Ecology and Sociobiology*, 70(9), 1591–1600. <https://doi.org/10.1007/s00265-016-2167-2>
- Anderson, B. D. (2018). *Factors Driving Sugar Cane Production in the Kingdom of Eswatini*. 1–123. Retrieved from <https://scholarworks.uark.edu/etd>
- Bates D, Maechler M, Bolker B (2019) Linear mixed-effects models using “Eigen” and S4. R package version 1.1.21
- Blackmore, C. J., & Heinsohn, R. (2007). Reproductive success and helper effects in the cooperatively breeding grey-crowned babbler. *Journal of Zoology*, 273(3), 326–332. <https://doi.org/10.1111/j.1469-7998.2007.00332.x>
- Both, C., Bouwhuis, S., Lessells, C. M., & Visser, M. E. (2006). Climate change and population declines in a long-distance migratory bird. *Nature*, 441(1), 81–83. <https://doi.org/10.1038/nature04539>
- Cant, M. A. (2012). C H A P T E R 12 Cooperative breeding systems. *The Evolution of Parental Care*, 206–225
- Carey, C. (2009). The impacts of climate change on the annual cycles of birds. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 364(1534), 3321–3330. <https://doi.org/10.1098/rstb.2009.0182>
- Carroll, R. L., Davis, C. A., Fuhlendorf, S. D., Elmore, R. D., DuRant, S. E., & Carroll, J. M. (2018). Avian parental behavior and nest success influenced by temperature fluctuations. *Journal of Thermal Biology*, 74, 140–148. <https://doi.org/10.1016/j.jtherbio.2018.03.020>
- Clark, C.W., and Mangel, M. (1986) The evolutionary advantages of group foraging. *Theoretical Population Biology*, p. 1994)..
- Conradie, S. R., Woodborne, S. M., Cunningham, S. J., & McKechnie, A. E. (2019). Chronic, sublethal effects of high temperatures will cause severe declines in southern African arid-zone birds during the 21st century. *Proceedings of the National Academy of Sciences of the United States of America*, 116(28), 14065–14070. <https://doi.org/10.1073/pnas.1821312116>
- Conway, C. J., & Martin, T. E. (2000). Effects of ambient temperature on avian incubation behavior. *Behavioral Ecology*, 11(2), 178–188. <https://doi.org/10.1093/beheco/11.2.178>
- Crick, H.Q.P. (1992). Load-lightening in cooperatively breeding birds and the cost of reproduction. *Ibis*, 134(1), 56–61
- Dodsworth, G., Nixon, D., & Sweet, C. (1990). An assessment of drip irrigation of sugar cane on poorly structured soils in Swaziland. *Agricultural Water Management*, 17(1–3), 325–335. [https://doi.org/10.1016/0378-3774\(90\)90082-A](https://doi.org/10.1016/0378-3774(90)90082-A)
- Dunn, P. O., & Cockburn, A. (1998). *Costs and Benefits of Extra-Group Paternity in Superb Fairy-Wrens Author ( s ) : Peter O. Dunn and Andrew Cockburn Source : Ornithological Monographs , No . 49 , Avian Reproductive Tactics : Female and Male Published by : American Ornithological Society S. (49) , 147–161.*
- du Plessis, K. L., Martin, R. O., Hockey, P. A. R., Cunningham, S. J., & Ridley, A. R. (2012). The costs of keeping cool in a warming world: Implications of high temperatures for foraging, thermoregulation and body condition of an arid-zone bird. *Global Change Biology*, 18(10), 3063–3070. <https://doi.org/10.1111/j.1365-2486.2012.02778.x>
- Durant, S. E., Hopkins, W. A., Hepp, G. R., & Walters, J. R. (2013). Ecological, evolutionary, and conservation implications of incubation temperature-dependent phenotypes in birds. *Biological Reviews*, 88(2), 499–509. <https://doi.org/10.1111/brv.12015>
- DuRant, S. E., Willson, J. D., & Carroll, R. B. (2019). Parental Effects and Climate Change: Will Avian Incubation Behavior Shield Embryos from Increasing Environmental Temperatures? *Integrative and Comparative Biology*, 59(4), 1068–1080. <https://doi.org/10.1093/icb/icz083>
- Easterling, D. R., Meehl, G. A., Parmesan, C., Changnon, S. A., Karl, T. R., & Mearns, L. O. (2000). *Climate Extremes: Observations, Modeling, and Impacts*. 289(September), 2068–2075.

- Eggers, S., Griesser, M., & Ekman, J. (2008). Predator-induced reductions in nest visitation rates are modified by forest cover and food availability. *Behavioral Ecology*, 19(5), 1056–1062.  
<https://doi.org/10.1093/beheco/arn063>
- Gaston, J.A. (1978). *The Evolution of Group Territorial Behavior and Cooperative Breeding*  
*Published by : The University of Chicago Press for The American Society of Naturalists Stable URL : https://www.jstor.org/stable/2460350.* 112(988), 1091–1100.
- Guthery, F. S., Land, C. L., & Hall, B. W. (2001). Heat Loads on Reproducing Bobwhites in the Semiarid Subtropics, *Journal of Wildlife Management*, 65(1), 111–117.  
<http://www.jstor.org/stable/3803282>,
- Hanssen, S. A., Hasselquist, D., Folstad, I., & Erikstad, K. E. (2005). Cost of reproduction in a long-lived bird: Incubation effort reduces immune function and future reproduction. *Proceedings of the Royal Society B: Biological Sciences*, 272(1567), 1039–1046.  
<https://doi.org/10.1098/rspb.2005.3057>
- Hatchwell, B. J. (1999). Investment Strategies of Breeders in Avian Cooperative Breeding Systems. *The American Naturalist*, 154(2), 205–219. <https://doi.org/10.1086/303227>
- Hatchwell, B. J., & Davies, N. B. (1990). Provisioning of nestlings by dunnocks, *Prunella modularis*, in pairs and trios compensation reactions by males and females. *Behavioral Ecology and Sociobiology*, 27(3), 199–209. <https://doi.org/10.1007/BF00180304>
- Hatchwell, B. J., & Komdeur, J. (2000). Ecological constraints, life history traits and the evolution of cooperative breeding. *Animal Behaviour*, 59(6), 1079–1086.  
<https://doi.org/10.1006/anbe.2000.1394>
- Heist, C. A., & Ritchison, G. (2016). Effects of variation in nestling hunger levels and begging on the provisioning behavior of male and female Eastern Phoebe (Sayornis phoebe). *The Wilson Journal of Ornithology*, 128(1), 132–143. <https://doi.org/10.1676/wils-128-01-132-143.1>
- Hockey, P.A.R., Dean, R., & Ryan, P. (2005). *Roberts Birds of Southern Africa* (7<sup>th</sup> ed.).
- Huggins, R. A. (1941). Egg temperature of wild birds under natural conditions. *Ecology* 22:148- 157
- Huntley, B., & Barnard, P. (2012). Potential impacts of climatic change on southern African birds of fynbos and grassland biodiversity hotspots. *Diversity and Distributions*, 18(8), 769–781.  
<https://doi.org/10.1111/j.1472-4642.2012.00890.x>
- IPCC, 2013: *Climate Change 2013: The physical Science Basis, Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* [Stocker, T.F., D. Qin, G-K. Plattner, M. Tignor, S.K. Allen, J.Boschung, A. Nauels, Y. Xia, V. Bex and P.M. Midgley (eds.)] Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, 1535 pp.
- Izhaki, I., & Safriel, U. N. (1989). *Why Are There So Few Exclusively Frugivorous Birds ? Experiments on Fruit Digestibility*, Wiley on behalf of Nordic Society Oikos, 54(1), 23–32.
- Kokko, H., Johnstone, R. A., & Clutton-Brock, T. H. (2001). The evolution of cooperative breeding through group augmentation. *Proceedings of the Royal Society B: Biological Sciences*, 268(1463), 187–196. <https://doi.org/10.1098/rspb.2000.1349>
- MacColl, A. D. C., & Hatchwell, B. J. (2003). Sharing of caring: Nestling provisioning behaviour of long-tailed tit, *Aegithalos caudatus*, parents and helpers. *Animal Behaviour*, 66(5), 955–964.  
<https://doi.org/10.1006/anbe.2003.2268>
- McKechnie, A. E., & Wolf, B. O. (2010). Climate change increases the likelihood of catastrophic avian mortality events during extreme heat waves. *Biology Letters*, 6(2), 253–256.  
<https://doi.org/10.1098/rsbl.2009.0702>
- Mortensen, J. L., & Reed, J. M. (2018). Parental incubation patterns and the effect of group size in a Neotropical cooperative breeder. *Auk*, 135(3), 669–692. <https://doi.org/10.1642/AUK-17-236.1>
- Nomano, F. Y., Savage, J. L., Browning, L. E., Griffith, S. C., & Russell, A. F. (2019). Breeding Phenology and Meteorological Conditions Affect Carer Provisioning Rates and Group-Level Coordination in Cooperative Chestnut-Crowned Babblers. *Frontiers in Ecology and Evolution*, 7(November), 1–16. <https://doi.org/10.3389/fevo.2019.00423>
- Olson, V. A., Liker, A., Freckleton, R. P., & Székely, T. (2008). Parental conflict in birds: Comparative analyses of offspring development, ecology and mating opportunities.

- Proceedings of the Royal Society B: Biological Sciences*, 275(1632), 301–307.  
<https://doi.org/10.1098/rspb.2007.1395>
- Peters, A., Astheimer, L. B., Boland, C. R. J., & Cockburn, A. (2000). Testosterone is involved in acquisition and maintenance of sexually selected male plumage in superb fairy-wrens, *Malurus cyaneus*. *Behavioral Ecology and Sociobiology*, 47(6), 438–445.  
<https://doi.org/10.1007/s002650050688>
- Rauter, C. M., Brodmann, P. A., & Reyer, H. U. (2000). Provisioning behaviour in relation to food availability and nestling food demand in the Water Pipit *Anthus spinoletta*. *Ardea*, 88(1), 81–90.
- Razeng, E., & Watson, D. M. (2015). Nutritional composition of the preferred prey of insectivorous birds: Popularity reflects quality. *Journal of Avian Biology*, 46(1), 89–96.  
<https://doi.org/10.1111/jav.00475>
- Remeš, V., Freckleton, R. P., Tökölyi, J., Liker, A., & Székely, T. (2015). *The evolution of parental cooperation in birds*. <https://doi.org/10.5061/dryad.02jk0>
- Ridley, A. R., & Raihani, N. J. (2008). Task partitioning increases reproductive output in a cooperative bird. *Behavioral Ecology*, 19(6), 1136–1142. <https://doi.org/10.1093/beheco/arn097>
- Ridley, A. R., Raihani, N. J., & Nelson-Flower, M. J. (2008). The cost of being alone: The fate of floaters in a population of cooperatively breeding pied babblers *Turdoides bicolor*. *Journal of Avian Biology*, 39(4), 389–392. <https://doi.org/10.1111/j.2008.0908-8857.04479.x>
- Rowley, I. (1965). The life history of the superb blue wren (*Malurus cyaneus*). *Emu* 64:251–297
- RStudio Team (2020). RStudio: Integrated Development for R. RStudio, PBC, Boston, MA  
URL <http://www.rstudio.com/>
- Russell, A. F., Langmore, N. E., Gardner, J. L., & Kilner, R. M. (2008). Maternal investment tactics in superb fairy-wrens. *Proceedings of the Royal Society B: Biological Sciences*, 275(1630), 29–36.  
<https://doi.org/10.1098/rspb.2007.0821>
- Savage, J. L., Russell, A. F., & Johnstone, R. A. (2015). Maternal allocation in cooperative breeders: Should mothers match or compensate for expected helper contributions? *Animal Behaviour*, 102, 189–197. <https://doi.org/10.1016/j.anbehav.2015.01.015>
- Skagen, S. K., & Adams, A. A. Y. (2012). Weather effects on avian breeding performance and implications of climate change. In *Ecological Applications* (Vol. 22, Issue 4).  
<http://www.wrcc.dri.edu/>
- Smith, A. (1836). Rep.Exped. Expl. Cent. Afr., p45
- Sorato, E., Gullett, P. R., Griffith, S. C., & Russell, A. F. (2012). Effects of predation risk on foraging behaviour and group size: Adaptations in a social cooperative species. *Animal Behaviour*, 84(4), 823–834. <https://doi.org/10.1016/j.anbehav.2012.07.003>
- Thompson, L. J., Brown, M., & Downs, C. T. (2015). The potential effects of climate-change-associated temperature increases on the metabolic rate of a small Afrotropical bird. *Journal of Experimental Biology*, 218(10), 1504–1512. <https://doi.org/10.1242/jeb.116509>
- Trivers, Rober, L. (1972). Parental investment and sexual selection. *Sexual Selection & the Descent of Man*, Aldine de Gruyter, New York.136-79.
- Trivers, Robert, L. (1974). Parent-Offspring Conflict Author. *American Zoologist*, 14(1), 249–264.
- van de Ven, T. M. F. N., McKechnie, A. E., Er, S., & Cunningham, S. J. (2020). High temperatures are associated with substantial reductions in breeding success and offspring quality in an arid-zone bird. *Oecologia*, 193(1), 225–235. <https://doi.org/10.1007/s00442-020-04644-6>
- Vincze, O., Kosztolányi, A., Barta, Z., Küpper, C., Alrashidi, M., Amat, J. A., Argüelles Ticó, A., Burns, F., Cavitt, J., Conway, W. C., Cruz-López, M., Desucré-Medrano, A. E., dos Remedios, N., Figuerola, J., Galindo-Espinosa, D., García-Peña, G. E., Gómez Del Angel, S., Gratto-Trevor, C., Jönsson, P., ... Székely, T. (2017). Parental cooperation in a changing climate: fluctuating environments predict shifts in care division. *Global Ecology and Biogeography*, 26(3), 347–358.  
<https://doi.org/10.1111/geb.12540>
- Visser, M. E. (2008). Keeping up with a warming world; assessing the rate of adaptation to climate change. In *Proceedings of the Royal Society B: Biological Sciences* (Vol. 275, Issue 1635, pp. 649–659). Royal Society. <https://doi.org/10.1098/rspb.2007.0997>
- Webb, D. R. (1987). Thermal Tolerance of Avian Embryos: A Review. *The Condor*, 89(4), 874–898.  
<https://doi.org/10.2307/1368537>

- Wesołowski, T. (2004). The origin of parental care in birds: A reassessment. *Behavioral Ecology*, 15(3), 520–523. <https://doi.org/10.1093/beheco/arh039>
- Wiley, E. M., & Ridley, A. R. (2016). The effects of temperature on offspring provisioning in a cooperative breeder. *Animal Behaviour*, 117, 187–195. <https://doi.org/10.1016/j.anbehav.2016.05.009>
- Williams, T. D. (2018). Physiology, activity and costs of parental care in birds. *Journal of Experimental Biology*, Vol. 221. <https://doi.org/10.1242/jeb.169433>

## Appendix I results incubation analysis babbler and helmetshrike full model without stepwise elimination

**Table 1**

LMM of mean duration incubation bouts helmetshrikes (n=6, 16 observations) and babblers (n=5, 10 observations). Temperature is in Celsius (°C). Significant terms are displayed in bold.

response variable	species	predictors	estimate±se	t-value	p-value
mean duration on-bout (min)	White-crested helmetshrike	mean on-bout temperature*group size	-0.28±0.19	-1.47	0.17
		mean on-bout temperature	1.66±1.07	1.55	0.15
		group size	8.17±5.38	1.52	0.16
		exposure to sun	-0.28±0.19	-1.47	0.17
		mean on-bout temperature*group size	-1.75±2.71	-0.65	0.58
	Arrow-marked babbler	mean on-bout duration	10.32±16.21	0.64	0.59
		group size	50.27±93.26	0.54	0.63
		number eggs	-147.14±148.95	-0.99	0.44
		exposure to sun	-1.75±2.70	-0.65	0.58
		<b>mean off-bout temperature*group size</b>	<b>0.03±0.02</b>	<b>1.80</b>	<b>0.01</b>
mean duration off-bout (min)	White-crested helmetshrike	mean off-bout temperature	-0.20±0.11	-1.76	0.11
		group size	-1.10±0.55	-2.01	0.07
		exposure to sun	0.075±0.47	0.16	0.87
		mean off-bout temperature*group size	0.63±1.11	0.56	0.60
		mean off-bout temperature	-2.98±5.21	-0.57	0.60
	Arrow-marked babbler	group size	6.25±30.19	0.21	0.85
		number of eggs	4.92±15.93	0.31	0.77
		exposure to sun	-31.37±22.98	-1.36	0.24

**Table 2**

LMM data duration (min) per bout incubation of helmetshrikes (n=6, 187 observations) and babblers (n=5, 36 observations). Temperature is in Celsius (°C). Significant terms are displayed in bold.

response variable	species	predictors	estimate $\pm$ se	t-value	p-value
duration on-bout (min)	White-crested helmetshrike	<b>on-bout temperature*group size</b>	<b>-0.63<math>\pm</math>0.20</b>	<b>-3.23</b>	<b>&lt;0.05</b>
		temperature on-bout	<b>6.25<math>\pm</math>2.29</b>	<b>2.73</b>	<b>&lt;0.05</b>
		temperature on-bout <sup>2</sup>	-0.05 $\pm$ 0.035	-1.41	0.16
		<b>group size</b>	<b>17<math>\pm</math>5.29</b>	<b>2.64</b>	<b>&lt;0.05</b>
		exposure to sun	-6.04 $\pm$ 3.57	-1.69	0.09
	Arrow-marked babbler	on-bout temperature* group size	-1.58 $\pm$ 2.69	-0.59	0.57
		temperature on-bout	10.03 $\pm$ 30.86	0.32	0.75
		temperature on-bout <sup>2</sup>	-0.008 $\pm$ 0.70	-0.01	0.99
		group size	60.23 $\pm$ 81.03	0.74	0.47
		exposure to sun	-30.14 $\pm$ 36.45	-0.83	0.42
		<b>number of eggs</b>	<b>-95.01<math>\pm</math>42.21</b>	<b>-2.25</b>	<b>0.03</b>
duration off-bout (min)	White-crested helmetshrike	off-bout temperature*group size	0.043 $\pm$ 0.02	1.90	0.06
		temperature off-bout	-0.21 $\pm$ 0.27	-0.77	0.44
		temperature off-bout <sup>2</sup>	-0.001 $\pm$ 0.004	-2.43	0.80
		<b>group size</b>	<b>-1.45<math>\pm</math>0.60</b>	<b>-2.43</b>	<b>0.02</b>
		exposure to sun	0.63 $\pm$ 0.43	1.47	0.14
	Arrow-marked babbler	off-bout temperature*group size	0.11 $\pm$ 1.02	0.11	0.91
		temperature off-bout	21.89 $\pm$ 13.89	1.57	0.14
		temperature off-bout <sup>2</sup>	-0.39 $\pm$ 0.29	-1.35	0.20
		group size	17.97 $\pm$ 30.42	0.59	0.56
		exposure to sun	-25.94 $\pm$ 18.05	-1.44	0.17
		number of eggs	7.13 $\pm$ 18.01	0.40	0.70

## Appendix II results provisioning babbler with all predictors

Table 3 shows the full model provisioning results for the babblers with all the predictors used.

**Table 3**

Results LMM of provisioning rate (feeds per hour) of babblers (N=8, observations =10). Temperature is in Celsius (°C). Significant terms are displayed in bold.

<b>response variable</b>	<b>species</b>	<b>predictors</b>	<b>estimate<math>\pm</math>se</b>	<b>t-value</b>	<b>p-value</b>
provisioning rate entire observation	Arrow-marked babbler	temperature entire observation*group size	0.23 $\pm$ 0.07	3.54	0.92
		temperature entire observation	-1.08 $\pm$ 0.60	-1.80	0.55
		group size	-0.36 $\pm$ 0.29	-1.25	0.24
		nestling age	-0.06 $\pm$ 0.24	-0.24	0.24
		exposure to sun	-0.51 $\pm$ 1.24	-0.41	0.69
		nestlings	0.95 $\pm$ 0.53	1.80	0.10
		temperature morning*group size	0.15 $\pm$ 0.11	1.40	0.31
		temperature morning	-0.05 $\pm$ 0.14	-0.37	0.73
		group size	-0.40 $\pm$ 0.22	-1.81	0.14
		nestling age	-0.08 $\pm$ 0.19	-0.43	0.69
provisioning rate afternoon		exposure sun at nest	0.97 $\pm$ 0.88	1.11	0.33
		nestlings	-0.11 $\pm$ 0.39	-0.28	0.80
		temperature afternoon *group size	0.19 $\pm$ 0.15	1.26	0.33
		temperature afternoon	0.022 $\pm$ 0.27	0.08	0.94
		group size	-0.36 $\pm$ 0.36	-0.10	0.34
		nestling age	-0.01 $\pm$ 0.31	-0.04	0.97
provisioning rate evening		exposure sun at nest	-2.051 $\pm$ 1.85	-1.11	0.29
		nestlings	0.75 $\pm$ 0.67	1.12	0.29
		temperature evening *group size	0.12 $\pm$ 0.18	0.64	0.53
		temperature evening	-0.54 $\pm$ 0.33	-1.66	0.20
		group size	-0.44 $\pm$ 0.38	-1.17	0.27

### Appendix III provisioning analysis data divided in morning and afternoon

The data of the provisioning analysis of the bulbuls and babblers were also divided in morning (07:00-11:00) and afternoon (11:01-17:00), which are in general the coldest and warmest period of the day (Table 2 and 3).

**Table 4**

Results LM of provisioning rates bulbuls (N=7, observations =7). Data divided in morning hours (07:00-11:00), and afternoon (11:01-17:00).

<b>response variable</b>	<b>species</b>	<b>predictors</b>	<b>estimate±se</b>	<b>t-value</b>	<b>p-value</b>
provisioning rate morning	Dark-capped bulbul	temperature morning (°C)	-0.19±0.14	-1.38	0.23
provisioning rate afternoon		temperature afternoon (°C)	-0.27±0.12	-2.34	0.07

**Table 5**

Results LMM of provisioning rate (feeds per hour) of babblers (N=8, observations =10). Data divided in morning hours (07:00-11:00), and afternoon (11:01-17:00).

<b>response variable</b>	<b>species</b>	<b>predictors</b>	<b>estimate±se</b>	<b>t-value</b>	<b>p-value</b>
provisioning rate morning	Arrow-marked babbler	temperature morning (°C)	0.054±0.13	0.41	0.69
		group size	-0.54±0.22	-2.51	0.25
		nestling age	0.15±0.14	1.10	0.37
		exposure sun at nest	-2.27±0.89	-2.55	0.04
		nestlings	0.74±0.35	2.084	0.07
provisioning rate afternoon		temperature afternoon (°C)	0.09±0.19	0.48	0.64
		group size	-0.36±0.31	-1.14	0.28
		nestling age	-0.0004±0.26	-0.001	0.10
		exposure sun at nest	-1.43±1.35	-1.057	0.32
		nestlings	1.15±0.59	1.95	0.29

## Appendix IV results provisioning fairy-wrens with all predictors

**Table 6**

Results LM of provisioning rates fairy-wrens (N=38, observations=38). Temperature is in Celsius (°C). Significant terms are displayed in bold.

response variable	species	predictors	estimate $\pm$ se	t-value	p-value
provisioning rate entire day	Superb fairy-wren	temperature entire observation*group size	0.24 $\pm$ 0.57	0.42	0.68
		temperature entire observation	-0.51 $\pm$ 1.55	-0.33	0.74
		group size	-2.61 $\pm$ 10.87	-0.24	0.81
		nestling age	-0.47 $\pm$ 1.05	-0.45	0.66
		nestlings	1.45 $\pm$ 1.43	1.02	0.32

Since the sex was known for the fairy-wrens, the provisioning rate of female and male were also investigated. Table 1 shows the full model without backward elimination of non-significant terms.

**Table 7**

Results LM of sex specific provisioning rates fairy-wrens (N=38, observations=38). Temperature is in Celsius (°C). Significant terms are displayed in bold.

response variable	species	predictors	estimate $\pm$ se	t-value	p-value
provisioning rate female	Superb fairy-wren	temperature entire observation*group size	0.23 $\pm$ 0.41	0.56	0.58
		temperature entire observation	-0.37 $\pm$ 1.12	-0.33	0.74
		group size	-3.87 $\pm$ 7.83	-0.49	0.62
		nestling age	0.13 $\pm$ 0.75	0.18	0.86
		nestlings	0.49 $\pm$ 1.03	0.48	0.64
provisioning rate male		temperature entire observation*group size	0.030 $\pm$ 0.41	0.07	0.94
		temperature entire observation	-0.21 $\pm$ 1.10	-0.19	0.85
		group size	1.02 $\pm$ 7.69	0.13	0.89
		nestling age	-0.79 $\pm$ 0.74	-1.06	0.30
		nestlings	1.10 $\pm$ 1.01	1.09	0.28