# The effects of temperature on offspring provisioning in a cooperative breeder

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While most current predictive models agree that the climate is changing, it is not yet clear what impact these changes will have on animal populations. It is vital to determine the potential consequences in order to develop future management and conservation strategies. Climate change may impact population stability by prompting changes in breeding behaviour. For example, if above-average temperatures negatively affect adult body condition, this will increase the cost of parental care. Theory suggests that under this scenario, individuals may trade off their own body condition and survival against that of their young. Despite convincing evidence that this parental care trade-off exists in nature, the potential impact of climate change on parental investment strategies has rarely been investigated. In cooperatively breeding species, group-living adults can gain group size benefits, such as assistance with raising young. These benefits may mediate the effects of climate change on adult condition and subsequent investment in young. Here, we investigated the extent to which high temperatures and rainfall variation affect (1) adult provisioning rates to dependent nestlings, (2) offspring development and (3) the cost of offspring care in the cooperatively breeding pied babbler, *Turdoides bicolor*. We found that overall, adults provisioned young significantly less on hot days. However, this pattern was affected by rank: dominant individuals provisioned significantly less while subordinates did not. Offspring development was negatively affected by heatwave events, suggesting that young suffer from reduced investment on hot days. However, there was no evidence that the cost of provisioning young increased during heatwave periods, perhaps owing to the reduction in investment by adults. This study provides some of the first evidence that higher temperatures affect investment decisions in cooperative breeders and that dominant and subordinate individuals respond differently to this stressor.

The way in which organisms respond to environmental change is fast becoming one of the most pertinent issues in biology due to the threat of rapid climate change. Climate change is globally recognized as one of the biggest threats to biodiversity (Foden et al., 2013; Parmesan & Yohe, 2003; Selwood, McGeoch, & Mac Nally, 2015). The Intergovernmental Panel on Climate Change's (IPCC, 2012) special report on global warming predicted substantial warming and higher temperature extremes by the end of the 21st century. The report concluded it is very likely that the length, frequency and intensity of extreme weather events such as heatwaves will increase over most land areas, with a 1-in-20 year hottest day likely to become a 1-in-2 year event by the end of the 21st century. This was corroborated in the 2014 synthesis report, where it was stated to be 'virtually certain that there will be more frequent hot, and fewer cold temperature extremes over most land areas on daily and seasonal timescales, due to an increase in global mean surface temperature' (IPCC 2014, p. 60). Determining the implications of these predicted climatic changes for animal populations is now a priority for ecological research if we are to implement appropriate future management strategies.

Physiological research has recognized that extreme environmental fluctuations may have detrimental effects on body size, breeding success and population density (Walther et al., 2002; Williams & Tieleman, 2005). However, the direct impacts of rising temperatures on the ability of species to effectively forage, breed and interact are poorly understood. In hot and arid

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environments, some (particularly smaller) bird species rapidly exceed their physiological tolerance limits (McKechnie & Wolf, 2010). Following a 2009 mass die-off of budgerigars, *Melopsittacus undulatus*, during a heatwave in Western Australia, McKechnie & Wolf (2010) suggested that the frequency and intensity of extreme weather events over short time periods can be more important than long-term temperature rise. It has therefore become critical to document the direct effects extreme weather events are having on species, and to consider the ramifications of such impacts for future population management.

The impact of environmental variation on life history, physiology and population growth rate has been addressed in several influential papers on noncooperative species (Bickford, Howard, Ng, & Sheridan, 2010; Ozgul et al., 2010; Saether et al., 2000), but comparative data are not available for cooperative breeders. Cooperatively breeding species normally have group-structured populations (Nelson-Flower, Hockey, O'Ryan, & Ridley, 2012; Rollins et al., 2012), and therefore their population dynamics differ from those of conventional breeders (Courchamp, Grenfell, & Clutton-Brock, 1999). Cooperative species may respond differently to external stressors than nonsocial species, because reproductive success and survival can be affected by group size and the behaviour of other group members, rather than a pair or single individual. In defined and generally stable groups (Brown, 1978; Emlen, 1997), task-partitioning behaviours (such as antipredator defence, hunting, territory defence and raising young) often occur, which provide individual fitness benefits (Clutton-Brock, 2009; Raihani & Ridley, 2007b).

In some cases, breeders may reduce their investment in young, facilitated by the presence of helpers, a behaviour known as load lightening (Crick, 1992; Johnstone, 2011; Meade, Nam, Beckerman, & Hatchwell, 2010). Load-lightening behaviour can have a positive effect on parental survival and condition by reducing the cost of parental care without young receiving less care overall (Allainé, Brondex, Graziani, & Coulon, 2000; Cockburn et al., 2008; Woxvold & Magrath, 2005). The presence of helpers could to some extent buffer the effects of variation in environmental conditions on reproductive success, through task-partitioning and load-lightening behaviours (Heinsohn, 2004; Ridley & Raihani, 2008). Therefore, we may expect that individuals in large groups are less likely to be affected by environmental stressors when making reproductive investment decisions, than individuals in smaller groups.

Parental care is a costly form of investment (Clutton-Brock, 1991; Ridley & Raihani, 2007; Smith & Fretwell, 1974; Smith & Wootton, 1995; Walker, Gurven, Burger, & Hamilton, 2008). Life history theory predicts that in species that produce many offspring but have low adult survival rates, parents should value current offspring survival over their own survival, whereas those that produce fewer offspring but have a greater likelihood of surviving to breed again should value their own survival over that of their current young (Ghalambor & Martin, 2001; Sofaer, Sillett, Peluc, Morrison, & Ghalambor, 2013; Trivers, 1972; Zanette, White, Allen, & Clinchy, 2011). Previous research has investigated switches in reproductive strategy in response to environmental change (Fontaine & Martin, 2006; Schwagmeyer & Mock, 2008), revealing that in several long-lived species (e.g. puffins, *Fratercula arctica*; albatross, *Diomedea exulans*), large annual variation in environmental conditions is reflected in highly variable reproductive effort (Erikstad, Fauchald, Tveraa, & Steen, 1998; Weimerskirch, Cherel, Cuenot-Chaillet, & Ridoux, 1997). Our study addresses offspring care strategies in cooperative breeders by assessing how the care of dependent young is

affected as a direct short-term behavioural response to environmental stressors. We investigated (1) individual short-term behavioural responses to an environmental variable (the effect of heat on brood provisioning rate), and (2) the relationship between two environmental variables (rainfall and temperature) and one offspring trait (nestling body mass).

One of the first detailed studies to directly measure the potential impact of increasing temperatures on behavioural patterns and the ability to maintain body mass in arid zone bird species confirmed that pied babblers, *Turdoides bicolor*, exhibit heat stress above a daytime temperature of 35.5 °C (du Plessis et al., 2012). Here, we further explored the ramifications of this observed critical temperature effect by (1) determining the ability of individuals to maintain provisioning rates to young (a costly activity, Ridley & Raihani, 2007b) during temperatures above 35.5 °C, and (2) determining the cost of provisioning young at different temperatures, in terms of body mass loss. We would expect higher temperatures to affect the cost of offspring care for adults, with consequent impacts on the growth and development of young. We also expect that a change in investment in response to environmental stressors could be affected by group size, with young from larger groups (where there are more adults providing offspring care) less affected by reduced provisioning rates at high temperatures.

## METHODS

### Study Site and Species

We investigated cooperative brood care in pied babbler groups at the Pied Babbler Research Project, based in the 33 km$^2$ Kuruman River Reserve (KRR) in the southern Kalahari region of South Africa (26°58′S, 21°49′E). The study site has a subtropical climate and is primarily semiarid grassland and acacia savanna (see Ridley & Thompson, 2011 for description of habitat types). The area has a mean annual rainfall of 197 mm, with most rain falling during mid–late summer in January and April (Kong, Marsh, van Rooyen, Kellner, & Orr, 2015). In mid-summer (January) mean daily maximum and minimum temperatures are 34.7 °C and 22.2 °C, respectively, but can reach highs of 45.4 °C (Steenkamp, Vogel, Fuls, van Rooyen, & van Rooyen, 2008).

### Temperature and rainfall

Temperature (°C) and rainfall (mm) data were collected daily from the weather station at the Kuruman River Reserve. High temperature extremes (>45.4 °C) have been recorded at the study site once in the decade 1996–2005 (1 day only) and six times in 4 different years, from 2006 to the current day (three 1-day events and three 3-day events). The average duration of the (six) more recent events was 1.92 days (see Appendix Table A1, weather station data, KRR). Rainfall was summed for each relevant provisioning period (i.e. total rainfall in the month prior to behavioural observations). One month was chosen due to the typical delay between rainfall and insect emergence in the Kalahari (Cumming & Bernard, 1997; Ridley & Child, 2009). Maximum temperature ($T_{max}$) was recorded daily at the study site. A hot day was defined as greater than 35.5 °C (hereafter referred to as $T_{crit}$), because this was the temperature du Plessis et al. (2012) recognized as critical for the pied babbler, beyond which foraging efficiency declined, heat dissipation increased exponentially and individuals were unable to maintain body weight. Furthermore, the number of days per year where the temperature was over 35.5 °C has

increased approximately two-fold in the last decade (see Appendix Fig. A1, weather station data, KRR). For comparison purposes, the temperature on normal (i.e. not 'hot') observation days had to be a minimum of 5 °C lower than this critical temperature point (du Plessis et al. (2012) revealed some heat stress behaviour beginning to occur in the low 30 s for this species). A heatwave event was defined as when the maximum temperature was over $T_{crit}$ (35.5 °C) on any particular day (sensu Cunningham, Kruger, Nxumalo, & Hockey, 2013). Frequency of heatwave events (over the first 11 days posthatch) was calculated for each brood we monitored to determine the effect of temperature on nestling body mass.

The pied babbler is a cooperatively breeding, territorial, medium-sized (75—95 g) passerine, in which all adult group members contribute to the provisioning of nestlings and fledglings (Ridley & Raihani, 2007a). Since 2003, a study population consisting of uniquely ringed individuals has been habituated, monitored and maintained at the study site. Pied babblers are predominantly terrestrial foragers and habituated groups tolerate observers within 2—3 m while they forage undisturbed, so that extremely detailed behavioural observations can be made (Ridley & Raihani, 2007a). Pied babblers live in stable groups, consisting of a dominant breeding pair, which produce the majority of offspring (Nelson-Flower et al., 2011), and sexually mature (over 1 year old posthatching) subordinate helpers. The dominant pair are identifiable through behavioural traits, including aggressive behaviour towards other group members, extended time allopreening and investment in nest-building behaviour (Nelson-Flower et al., 2013; Ridley & Raihani, 2008). Subordinates are identified by submissive behaviours, including bill gaping, crouching, looking away and/or fleeing during dominant individual approach (Raihani, Ridley, Browning, Nelson-Flower, & Knowles, 2008). The study population typically comprises 18 habituated groups of pied babblers each year, with an average group size of $3.9 \pm 1.3$ adults (Ridley, Wiley, & Thompson, 2014). For a small food reward, individuals will hop onto a small (Ohaus) top-pan scale to be weighed. In this way, body condition can be monitored throughout each individual's lifetime noninvasively, thus avoiding any need for recapture.

Pied babblers build, incubate then provision one nest per breeding attempt, but may attempt to breed several times during a breeding season (Raihani, Nelson-Flower, Moyes, Browning, & Ridley, 2010). All group members help to both incubate and provision dependent young while in the nest (14—18 days) and postfledging, until they reach independence (40—97 days postfledging, Ridley & Raihani, 2007b). Data for this study were collected from March 2009 to December 2014 in consecutive breeding seasons, which typically run from September to April.

### Ethical Note

purposes only, which will occur only once for each bird). Immigrant adult birds to the population are caught using walk-in traps, which are never left unattended, and the bird is released in the exact same place it was captured. The whole ringing procedure takes less than 5 min. Nestling birds are retrieved from the nest at a young age (11 days), before they are too old to force-fledge or show a disturbed behavioural response to the ringing process. Each bird is ringed with two rings on each leg and the tarsi are measured using a digital calliper. A small sample of blood (50 μl) is taken from the brachial vein for sexing and determination of parentage.

### Data Collection

#### Behavioural data

To determine provisioning rates to young and foraging efficiency of provisioning adults, 20 min time—activity focal observations were carried out on all adult individuals in each group over the course of a breeding event (where a breeding event is defined as the time from when a brood hatches until young are no longer dependent on adults for the majority of their food supply; Raihani & Ridley, 2007b). Daily $T_{max}$ was allocated to each focal observation, from the on-site weather station data. Focal observations on different adult group members were all conducted on the same day to allow standardized comparisons relative to chick age and environmental conditions, and each adult had multiple focal observations collected over the course of a breeding event. Daily focal order was random such that the effect of time of day on focal results was minimized. All food items found while foraging were noted, as well as size and food type (Lepidoptera, Orthoptera, etc.), and whether items were eaten by the focal individual or fed to young. Food sizes were classified by observers according to previous definitions for this population as described in Raihani and Ridley (2007a) and each size was given a biomass value (for calculations see Ridley & Raihani, 2007). Foraging efficiency and the proportion of food captured that was subsequently given away to young was calculated for each individual per focal follow. Morning weight (taken at dawn, before 30 min of foraging time had elapsed for the day) was measured for each individual being observed, for each observation session. A 'lunch' weight was also taken at the end of an observation session, typically 3—4 h after observations begin, and always after at least 90 min of foraging. The difference between morning and lunch weights allowed a calculation of weight gain per h for each provisioning adult. All nestlings were ringed, measured and weighed at 11 days posthatching to allow a standardized comparison between chicks from different nests.

For this analysis, we used 90 behavioural focal observations from 41 individuals in 16 groups to determine foraging efficiency and provisioning rates. We used nestling weight data at 11 days of age for 124 chicks.

To determine which parameter (s) affected adult weight change, over the course of an entire breeding event, we had body mass data for 69 adult individuals, where we had an adult weight for immediately before a brood hatched (Body Mass A) and fledged (Body Mass B, average time between Body Mass A and $B = 14 \pm 4$ days). We also included body mass data from 20 adult individuals over the same period, but in nonbreeding groups, to account for the possibility that weight loss was seasonal and not due to the costs of provisioning young. Body mass change was calculated as [(Body

Mass B − Body Mass A)/number of days between Body Mass A and Body Mass B]. All body mass measures for this analysis were collected at dawn, before 30 min of foraging time had elapsed for the day.

### Statistical Analysis

All data were analysed in SPSS (v 22.0, IBM, Armonk, NY, U.S.A.). To determine the parameters that influenced brood-provisioning rates in adults we used a linear mixed model (LMM) approach with model selection. Our dependent variable was the proportion of food that the (focal) individual found that they gave away to young. We fitted repeated measures in our data set as random terms, thus accounting in part for nonindependence of data. Individual and group identity were included as random terms in all models. The variables tested were adult age, adult group size (total number of adult birds in the group), brood size (number of chicks in the nest), $T_{max}$ (on day of focal), sex (of adult), rank (dominant or subordinate) and individual foraging efficiency (biomass of prey caught/time spent foraging).

Model selection (using the Akaike information criterion corrected for small sample sizes, AICc) was employed to determine the model/s that best explained the patterns of variation in the data. Using AICc (with maximum likelihood estimation) a series of models were tested, with each model representing a biological hypothesis. Once an AICc score had been generated for each model, $\Delta$AICc scores were generated. A subset of best-supported models (defined as all models within 5 AICc of the 'best' model) were selected. Where there were several candidate models with similar AICc scores, Akaike weights ($\omega_i$) were calculated to determine the relative likelihood of each model. Akaike weights across candidate models were summed to 1 and models that had weights approaching 1 received the most support, relative to other models, and were selected as top models, as per methods outlined in Johnson and Omland (2004). Only those model terms whose confidence intervals did not intersect zero were considered to explain significant patterns within our data (as per Grueber, Nakagawa, Laws, & Jamieson, 2011).

To determine which variables affected nestling weight, we analysed data using LMMs, with nestling weight (at day 11 post-hatch) as the dependent variable. We then used model selection to determine a top model data set, employing model averaging to ascertain the best predictor term, as described for brood-provisioning rates above. Group identity, individual identity and brood identity were included as random terms in all models. The parameters investigated were frequency of $T_{crit}$ (in 11 days post-hatch), Julian date (number of days since first breeding attempt in the population for each year), rainfall (mm recorded in the month prior to hatch), rainfall squared (mm), brood size, sex of nestling and adult group size.

**Table 1**
The top model set for the terms influencing the proportion of food provisioned to young

| Model term | | AICc | $\Delta$AICc | $\omega_i$ |
|---|---|---|---|---|
| Basic | | 44.315 | 8.125 | |
| Rank+$T_{max}$ | | 36.19 | 0 | 0.8 |
| $T_{max}$ | | 39.052 | 2.862 | 0.2 |
| Effect size of significant explanatory terms | | Effect | SE | 95% CI |
| Constant | | 0.345 | 0.032 | 0.27/0.41 |
| Rank+$T_{max}$ | (Rank) | 0.1 | 0.06 | 0.02/0.25 |
| | ($T_{max}$) | −0.02 | 0.006 | −0.027/−0.006 |
| $T_{max}$ | | −0.02 | 0.006 | −0.027/−0.004 |

For a full list of models tested, refer to Appendix Table A2.
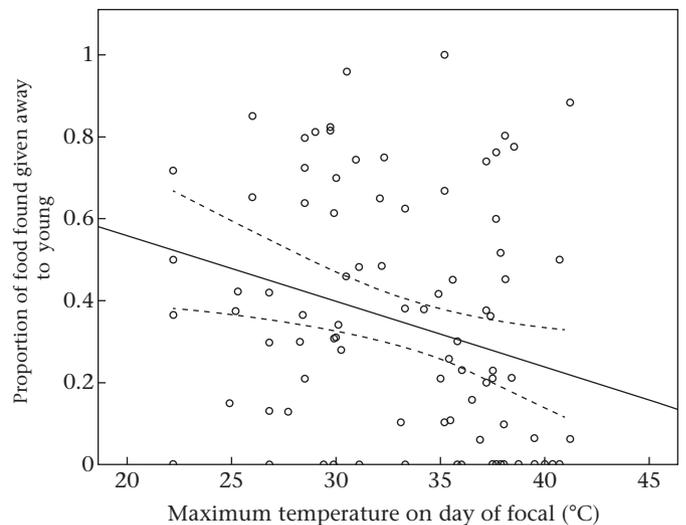


**Figure 1.** The relationship between the proportion of food given away to young by adults and $T_{max}$ on the day of the observation (solid line represents the output generated from the LMM (Table 1); dotted lines are 95% confidence intervals).

To determine the cost to adults of provisioning young from hatching date to fledging date (mean duration of nestling period = 14.69 +3.31/−5.69 days), we analysed adult weight change data using LMMs, and employed the model selection approach as detailed above (using AICc) to determine the parameters that influenced adult weight change over the nestling period. The following predictors were tested: adult rank, adult group size, frequency of $T_{crit}$ and breeding (yes/no). Adult weight change (g/day) was the dependent variable, with individual and group identity included as random terms in all models.

## RESULTS

### Provisioning Rates

Temperature ($T_{max}$) on the day of the focal observation affected adult provisioning rates (Table 1), with a significant reduction in the amount of food adults gave away to young as temperature increased (Fig. 1).
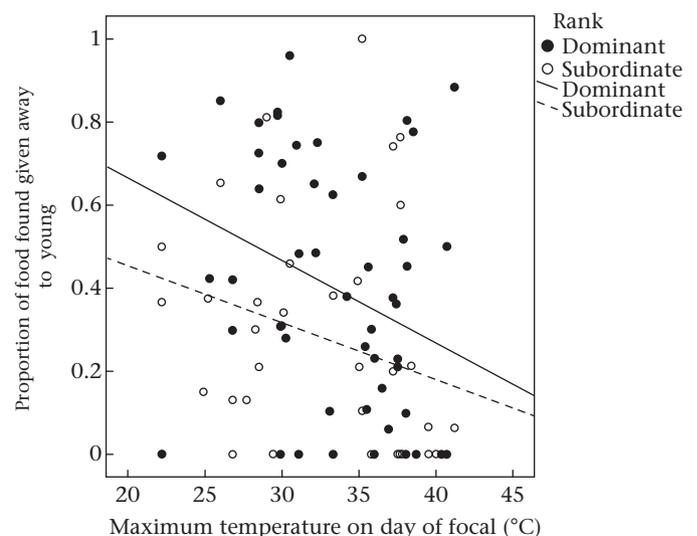


**Figure 2.** The change in proportion of food given away to young according to the rank of the individual and daily $T_{max}$.

**Table 2**
The top model set for the terms influencing nestling weight at 11 days posthatching

| Model term | | AICc | ΔAICc | $\omega_i$ |
|---|---|---|---|---|
| Basic | | 814.397 | 10.651 | 0 |
| Freq $T_{crit}$+Rainfall | | 799.953 | 0 | 0.87 |
| Freq $T_{crit}$ | | 803.746 | 3.793 | 0.13 |
| Effect size of significant explanatory terms | | Effect | SE | 95% CI |
| Constant | | 38.2 | 0.87 | 36.4/39.9 |
| Freq $T_{crit}$+Rainfall | (Freq $T_{crit}$) | −7.98 | 2.21 | −12.43/−3.54 |
| | (Rainfall) | 0.051 | 0.02 | 0.01/0.09 |
| Freq $T_{crit}$ | | -8.9 | 2.32 | −13.57/−4.24 |

Data were based on body mass measurements from 124 11-day-old nestlings. For a full list of models tested, refer to Appendix Table A3.
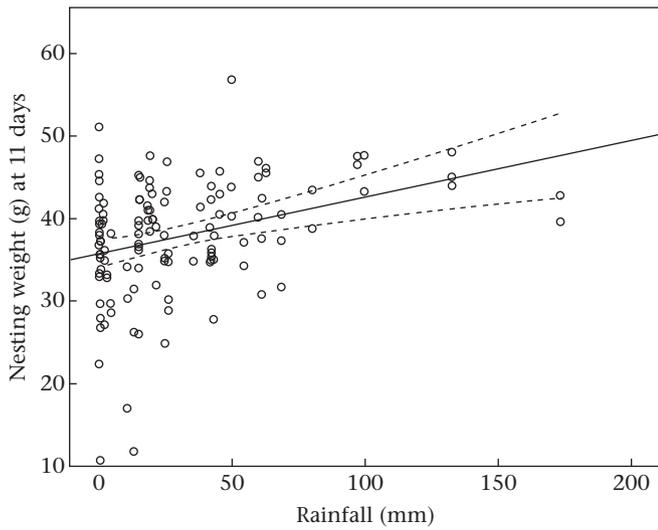
**Figure 3.** The relationship between the amount of rainfall (mm) in the month previous to hatching and the weight of 124 nestlings at 11 days old (solid line represents output from LMM (Table 2); dotted lines are 95% confidence intervals).
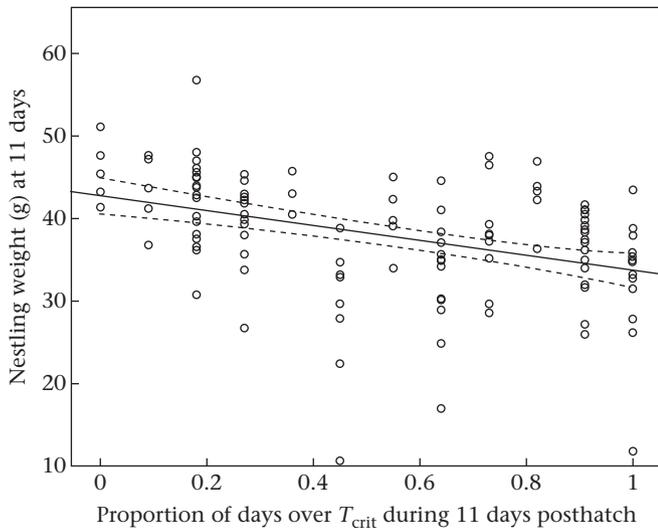
**Figure 4.** Nestling weights of 124 nestlings at 11 days posthatching, shown in relation to the proportion of days over $T_{crit}$ threshold temperature during the nestling period (dotted lines are 95% confidence intervals).

In addition, as temperature increased, dominant individuals reduced the amount they gave away significantly more than subordinates (Fig. 2).

### Nestling Body Mass

Nestlings were heavier at 11 days posthatching during periods of high rainfall (Table 2, Fig. 3). In addition, nestlings were heavier when raised during 'normal' temperature periods than when raised during 'hot' periods (with a higher frequency of days where temperature exceeded $T_{crit}$, Table 2, Fig. 4). There was no effect of group size on nestling weight (Table 2).

### Adult Weight Loss During Provisioning Period

Whether a group was breeding or not affected adult body mass change, with individuals only losing weight if they were provisioning young over the measured period, revealing a significant cost of nestling care. The inclusion of weight change data at the same time of year for individuals that were not breeding revealed that body mass loss was probably related to provisioning effort rather than seasonal weight loss because nonbreeding adults did not lose weight (Fig. 5, Table 3). In addition, adults in larger groups lost less weight than those in smaller groups, during a breeding attempt (Fig. 6).
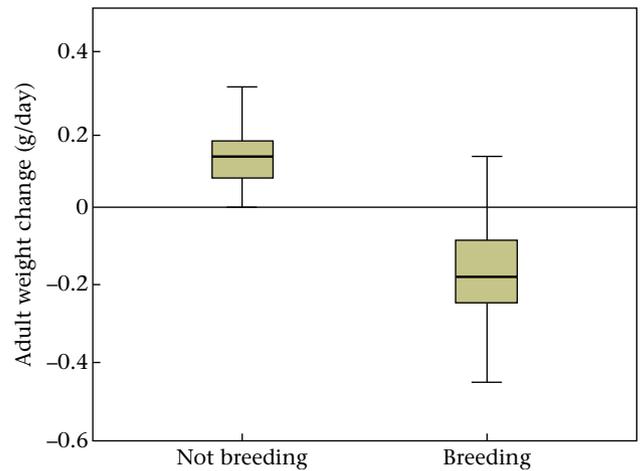
**Figure 5.** Adult weight change over a provisioning period for both nonbreeding and breeding groups. Each box represents weight change for a group of adults, nonbreeding or breeding, respectively. The median (horizontal dark line in each box), quartiles (top and bottom of box), and the 0.05 and 0.95 quantiles (vertical whiskers) are shown for each group.

**Table 3**
The top model set for the terms associated with adult weight change after time spent provisioning a nest

| Model term | | AICc | ΔAICc | $\omega_i$ |
|---|---|---|---|---|
| Basic | | 43.222 | 53.814 | |
| Breeding (yes/no) | | 93.728 | 3.308 | 0.16 |
| Adult group size+Breeding (y/n) | | 97.036 | 0 | 0.84 |
| Effect size of significant explanatory terms | | Effect | SE | 95% CI |
| Constant | | −0.12 | 0.03 | −0.17/−0.06 |
| Adult group size+Breeding (y/n) | (Group size) | 0.03 | 0.01 | 0.006/0.04 |
| | (Breeding y/n) | 0.3 | 0.03 | 0.24/0.37 |
| Breeding (yes/no) | | 0.3 | 0.04 | 0.23/0.38 |

Body mass data were collected from 72 individuals from 19 groups. For a full list of models tested, refer to Appendix Table A4.
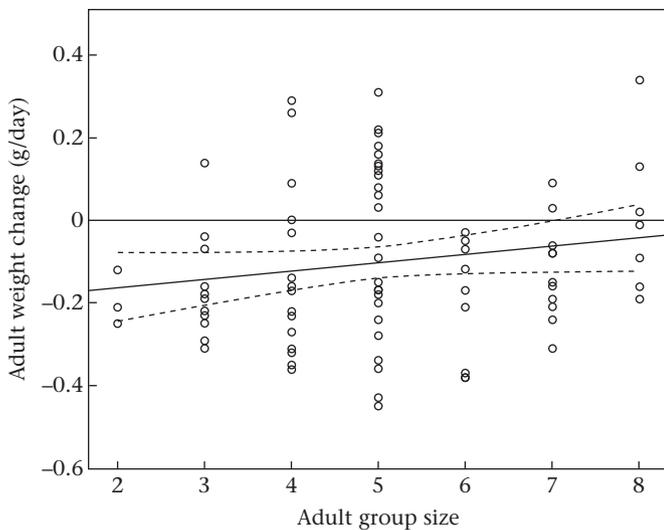
**Figure 6.** The relationship between weight change and group size for adults over a provisioning period (solid line represents LMM output (Table 3); dotted lines are 95% confidence intervals).

## DISCUSSION

Our results provide empirical evidence that hotter temperatures are related to a reduction in parental (dominant but not subordinate helper) investment in offspring. The decline in investment in young at high temperatures suggests a higher cost of parental investment at these temperatures. This cost was unlikely to be due to a decline in food availability or ability to forage at high temperatures, since our analysis revealed no change in weight due to temperature. Rather, the decline in offspring care may suggest an alternative physiological cost to adults, such as overheating when flying back and forth from the nest or an increased cost to adults of maintaining body condition on hot days (e.g. similar to that observed in sparrow-weavers, *Plocepasser mahali*, by Smit, Harding, Hockey, & McKechnie, 2013). Therefore, on hot days, when adults are at the limit of being able to offload heat and thus regulate body temperature (du Plessis et al., 2012), they may face the choice of trading off their own condition against that of their young, with some individuals showing a preference for themselves.

The difference in investment between dominants and subordinates supports previous empirical evidence in superb fairy-wrens, *Malurus cyaneus* (Russell, Langmore, Gardner, & Kilner, 2008), pied babblers (Ridley & Raihani, 2008) and ground tits, *Pseudopodoces humilis* (Li et al., 2015) that one benefit of group living for parents is that they can reduce investment in their own young when subordinate helpers are present to provide additional care (the load-lightening effect, Crick, 1992). In support of the load-lightening hypothesis (Blackmore & Heinsohn, 2007; Brown, 1978; Crick, 1992) we found that individuals from large groups lost less body mass over the offspring provisioning period than individuals from smaller groups. This difference could be for two possible reasons: (1) individuals in large groups occupy better territories with access to a higher quality or quantity of food resources (Clutton-Brock, 2009), or (2) each individual in large groups contributes less work overall to the brood, such that the brood receives the same level of care, but each adult invests less of its time in raising young than adults in smaller groups (Ridley & Raihani, 2008; Savage, Russell, & Johnstone, 2015). We consider option (2) to be most likely, since an analysis of nestling body mass found no

effect of group size on nestling body mass, and previous research on pied babblers has suggested that load lightening occurs in this species (Raihani & Ridley, 2008; Ridley & Raihani, 2008). A positive effect of adult group size on nestling mass would be expected in scenario (1), but not scenario (2).

There is already strong evidence from studies linking body condition and temperature, for example, in Alpine chamois, *Rupicapra rupicapra*, body mass declines steadily with increasing temperature (Mason et al., 2014) and in pied babblers, beyond a critical temperature point, foraging efficiency declines to the point where adults cannot maintain their body weight (du Plessis et al., 2012). In long-lived species, life history theory predicts that when ecological conditions are harsh, breeders should be more likely to favour their own survival over that of their young, to mitigate the direct immediate cost to themselves (Canestrari, Chiarati, Marcos, Ekman, & Baglione, 2008; Ghalambor & Martin, 2001; Weimerskirch et al., 1997). This strategy allows individuals to maintain body condition to enhance chances of survival for future breeding attempts. In pied babblers, since dominant individuals tend to be heavier (Ridley, Raihani, & Nelson-Flower, 2008), and thus have higher energy demands, decisions to invest less in young could be somewhat adaptive and depend directly on the current environmental and social situation, i.e. they may choose to maintain weight to retain competitive ability (Brockelman, 1975), breeding condition (Nelson-Flower et al., 2011) and ensure dominance tenure (Clutton-Brock, 1988). However, the behaviour of subordinates may be guided by different motivations in pied babblers, owing to the presence of high reproductive skew in this species (Nelson-Flower et al., 2011). When there are limited breeding opportunities, subordinates may adopt a 'pay-to-stay' strategy (Bergmüller, Heg, & Taborsky, 2005), resulting in their investing in young at a high level even when breeders do not, thus maximizing the fitness benefits of cooperation for helpers. Where the help provided by subordinates benefits dominant individuals, they may punish those that decrease or cease to help. In these scenarios, subordinates should pre-empt and avoid potentially costly punishment in aggressive encounters with breeding individuals, through helping and submissive social behaviour (Bergmüller & Taborsky, 2004; Mulder & Langmore, 1993). If this is the case in pied babblers, this could explain why subordinates do not reduce investment as dominants do, when experiencing higher temperatures. Alternatively, nonbreeding subordinates could gain direct fitness benefits by aiding group augmentation and subsequently increasing the occurrence of by-product mutualistic behaviours seen in group living, such as sentinel behaviour, territory defence and antipredator behaviours (Kokko, Johnstone, & Clutton-Brock, 2001).

Our findings provide some of the first empirical evidence that higher temperatures are affecting reproductive investment decisions in a cooperatively breeding species. Our data support theoretical predictions that during periods of environmental stress, some adults will trade off maintenance of their own condition against that of their young (Ghalambor & Martin, 2001). In pied babblers, this appears to only be true for the reproductive pair within a group, which suggests that group living and the presence of helpers can greatly impact offspring care strategies and the life history trade-offs that breeding adults face. Our findings imply that the causal relationship between fitness benefits (here defined as adult survival and reproductive success) and behavioural plasticity (level of investment in young) is mediated by cooperative group living and the number of helpers available, suggesting that decisions regarding shifts in parental care strategy show a level of adaptive plasticity (Koenig, Walters, & Haydock, 2009; Meade et al., 2010; Paquet, Covas, Chastel, Parenteau, & Doutrelant, 2013).

Our study highlights several important potential consequences of predicted climate change that require future consideration. If higher temperatures are occurring more frequently and impacting on reproductive investment decisions, this could have repercussions for understanding and modelling future population dynamics. For example, these could include (1) the need to be able to determine whether continued investment by helpers makes them less vulnerable to sublethal temperature effects, (2) whether the decline in parental care seen at high temperatures suggests that at even higher temperatures, parents may not initiate a breeding attempt at all, and (3) whether there are long-term impacts of declining adult investment in young during high temperatures. Even though subordinates did not significantly reduce their investment, neither did they increase it to compensate for the decline in investment by dominants at high temperatures, resulting in an overall decline in provisioning rate to nestlings at high temperatures. This may therefore be why nestlings weighed less at day 11 during periods of high temperatures, and suggests that a potential 'downstream effect' of high temperatures is the production of smaller, lower quality young that may have higher mortality rates, lower recruitment or be less likely to gain a breeding position in a social group as adults (Ridley & Raihani, 2007a). Although parental care investment decisions can (and do) show a level of flexibility in adapting to environmental conditions (Lima, 2009; Mönkkönen, Forsman, Kananoja, & Ylönen, 2009), these strategies are unlikely to be without limits. Further investigation into the impacts of increasing temperatures is vital to understand how to manage populations of cooperative breeders in a changing climate.

## Acknowledgments

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## APPENDIX

**Table A1**

Data summarized here were collected from the weather station located at the field site on the Kuruman River Reserve, in the southern Kalahari region of South Africa (26°58′S, 21°49′E)

| Year | Maximum temperature (°C) per year | No. of days per year where temperature >35.5 °C | No. of extreme high temperature events >45.4 °C per year | Average duration of extreme temperature events (days) |
|---|---|---|---|---|
| 1996 | 39 | 12 | 0 | |
| 1997 | 43 | 61 | 0 | |
| 1998 | 42 | 28 | 0 | |
| 1999 | 42 | 96 | 0 | |
| 2000 | 42 | 89 | 0 | |
| 2001 | 50 | 72 | 1 | 1 |
| 2002 | 41 | 63 | 0 | |
| 2003 | 42 | 91 | 0 | |
| 2004 | 41 | 95 | 0 | |
| 2005 | 44 | 101 | 0 | |
| 2006 | 48 | 119 | 2 | 1.66 |
| 2007 | 46.5 | 163 | 2 | 2 |
| 2008 | 45.1 | 160 | 1 | 1 |
| 2009 | 45.6 | 139 | 1 | 3 |
| 2010 | 41.2 | 93 | 0 | |
| 2011 | 41.2 | 76 | 0 | |
| 2012 | 42.3 | 114 | 0 | |
| 2013 | 42.3 | 115 | 0 | |
| 2014 | 41.4 | 89 | 0 | |
| 2015 | 42.1 | 120 | 0 | |

**Table A2**

Model terms and interactions that were tested to determine which variables were affecting brood provisioning rates

| Model term | AICc | ΔAICc |
|---|---|---|
| Basic | 44.315 | 8.125 |
| $T_{max}$ | 39.052 | 2.862 |
| Adult group size | 42.187 | 5.997 |
| Rank | 42.628 | 6.438 |
| Sex | 45.143 | 8.953 |
| Foraging efficiency | 43.465 | 7.275 |
| Brood size | 46.489 | 10.299 |
| Age | 45.286 | 9.096 |
| Rank×$T_{max}$ | 43.658 | 7.468 |
| Rank+$T_{max}$ | 36.190 | 0 |
| Rank+Adult group size | 41.554 | 5.364 |
| Rank+$T_{max}$+Rank×$T_{max}$ | 38.079 | 1.889 |

Data were from 90 behavioural focal observations, from 41 individuals in 16 groups.

**Table A3**

All model terms and interactions that were tested as potential influences on nestling weight at 11 days posthatching

| Model term | AICc | ΔAICc |
|---|---|---|
| Basic | 814.397 | 10.651 |
| Freq $T_{crit}$ | 803.746 | 3.793 |
| Rainfall | 809.267 | 9.314 |
| Sex | 814.26 | 14.307 |
| Adult group size | 816.323 | 16.37 |
| Julian date | 814.427 | 14.474 |
| Brood size | 812.911 | 12.958 |
| Freq $T_{crit}$+Rainfall | 799.953 | 0 |
| Rainfall (squared) | 812.129 | 12.176 |
| Freq $T_{crit}$+Adult group size | 805.889 | 5.936 |
| Freq $T_{crit}$×Brood size+Freq $T_{crit}$+Brood size | 804.630 | 4.677 |
| Freq $T_{crit}$+Brood size | 802.591 | 2.638 |
| Freq $T_{crit}$×Adult group size | 808.161 | 8.208 |

Data were based on body mass measurements from 124 11-day-old nestlings from 21 groups in 10 years.

**Table A4**
Model terms and interactions which were tested to determine what factors influenced adult body mass change after time spent provisioning a nest

| Model term | AICc | ΔAICc |
| --- | --- | --- |
| Basic | −43.222 | 53.814 |
| Adult group size | −42.466 | 54.57 |
| Freq $T_{crit}$ | −42.091 | 54.945 |
| Rank | −41.086 | 55.95 |
| Breeding (yes/no) | −93.728 | 3.308 |
| Group size+Breeding (y/n) | −97.036 | 0 |
| Rank×Group size | −40.425 | 56.611 |
| Rank+Breeding (y/n) | −91.761 | 5.275 |

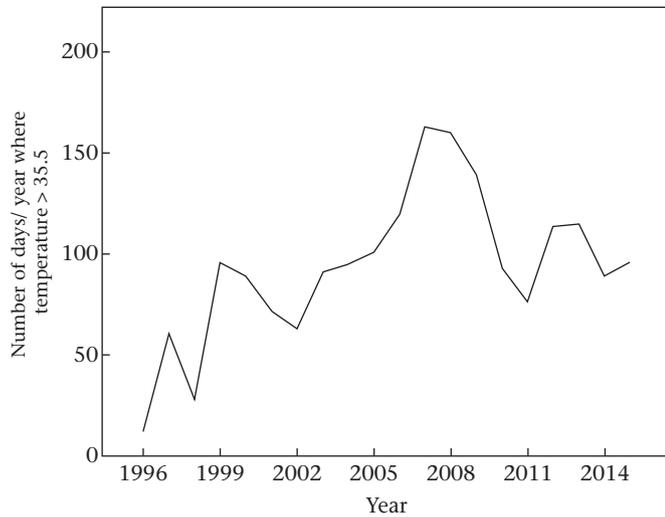Body mass data were collected from 89 individuals from 19 groups.



**Figure A1.** The number of days per year at the study site where the maximum temperature exceeded $T_{crit}$ (35.5 °C) for pied babblers in the years 1996–2015.