Can sociality buffer the impacts of climate change on a cooperatively-breeding bird, the southern pied babbler *Turdoides bicolor*?

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SUMMARY

Increasingly harsh and unpredictable climate regimes are affecting animal populations everywhere and understanding how species respond to current environmental variability is important for predicting vulnerability to climate change over longer timescales. Species living in characteristically harsh and unpredictable arid and semi-arid ecosystems are useful models for studying impacts of climate variability and change because these ecosystems are experiencing rapid increases in both average and maximum temperatures, as well as increased interannual rainfall variation, as a result of anthropogenic climate change. That animals living in highly variable environments are disproportionately more likely to engage in cooperative breeding implies that this strategy may buffer individuals against the negative effects of adverse climate conditions. An aspect of species' vulnerability to climate change that remains relatively unexplored is whether responses to environmental stressors might therefore be mitigated by sociality, particularly in those species in which group members are highly cooperative.

In this thesis, I use behaviour, morphology, and physiology data that I collected over three consecutive austral summer field seasons (2016-2019) and A. Prof. Amanda Ridley's 15-year life history dataset (2003-2019, to which I contributed the last three years of data) for a cooperatively-breeding bird, the southern pied babbler *Turdoides bicolor*. I investigate the impacts of temperature, rainfall, and group size on interannual survival, behaviour, physiology, growth, and reproduction in southern pied babblers, taking a multidisciplinary approach combining behavioural ecology, life history, and ecophysiology. In order to avoid disturbance to the study population, I validated and implemented a non-invasive method for collecting physiological measurements (daily energy expenditure and water turnover). I also tested for the influence of interactions between weather and

group size variables because the presence of significant interactions would provide evidence in support of a moderating effect of sociality.

I found that exposure to high temperatures significantly constrained successful breeding and the interannual survival of both breeding adults and juvenile birds, and explored the mechanisms behind these observed relationships: adjustments in parental care behaviour, body mass loss, reduced nestling growth rates, and the physiological costs of care at high temperatures. Higher rainfall and larger groups sizes were generally associated with higher reproductive success and survival, but I found no evidence for an interaction between weather variables and group size: individuals across all group sizes experienced similar effects of conditions. I therefore conclude that 1) pied babblers will increasingly face challenges for population recovery and persistence in the near future as survival and reproduction are increasingly compromised by ever higher temperatures, and 2) a life history strategy that relies on the presence of helpers for successful breeding is unlikely to buffer individual group members against climatic variability and climate change in this cooperatively breeding species.

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In writing this thesis, I've used the word 'I' liberally to describe 'my' undertakings and findings. In truth this work could not have been completed without the active involvement of a very large number of people and institutions in addition to those listed above. Every time I use the word 'I' in the pages that follow it is used in the most global of senses and should be understood as acknowledging the fundamental contribution of each and every one of the people listed above and below:

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CONFERENCE PRESENTATIONS

Bourne AR, Cunningham SJ, Spottiswoode CN, Ridley AR. *Can sociality buffer environmental stress in a cooperative breeder?* Australasian Ornithological Conference, Darwin, Australia. July 2019

Rose S, **Bourne AR,** Moagi LL, Ridley AR, Cunningham SJ. *Can thermal landscapes buffer the costs of keeping cool?* Australasian Ornithological Conference, Darwin, Australia. July 2019

Bourne AR, Ridley AR, Spottiswoode C, Cunningham SJ. *Hot nests don't hatch: high temperatures negatively affect nest success in Southern Pied Babblers.* International Ornithological Congress, Vancouver, Canada. August 2018

Bourne AR, Ridley AR, McKechnie AE, Karasov WH, Cunningham SJ. *Field application of a non-invasive doubly labelled water technique for measuring physiological heat stress.* International Society of Behavioural Ecology Conference, Minneapolis, USA. August 2018

Bourne AR, McKechnie AE, Cunningham SJ, Ridley AR, Woodborne SM, Karasov WH. *A non-invasive method for measuring metabolic rate in habituated birds.* Learn About Birds Conference, Langebaan, South Africa. March 2018 (awarded Best Student Talk)

Bourne AR, McKechnie AE, Cunningham SJ, Ridley AR, Woodborne SM, Karasov WH. *Measuring metabolic rates with non-invasive doubly-labelled water.* Zoological Society of Southern Africa Conference, Pretoria, South Africa. July 2017

POPULAR ARTICLES

Bourne AR, Cunningham SJ. 2019. Non-invasive physiological measurements in wild animals. Quest magazine 15(4), p32-33, available here

Bourne AR, Pattinson NB. 2019. Hot birds in the top end. *Promerops 315: 26-27*

Bourne AR, Cunningham SJ. 2019. No touching please! Non-invasive physiological measurements in wild animals. Science Matters: UCT Science Faculty Newsletter, p15, available here

Bourne AR, Cunningham SJ, Nupen L, McKechnie AE, Ridley AR. 2019. Male and female southern pied babbler *Turdoides bicolor* nestlings respond similarly to heat stress. Report from a British Ornithologists Union funded project, available here

Bourne AR, Martin J, Nash A-E. 2018. Review of ISBE 2018 in Minneapolis. International Society for Behavioural Ecology Newsletter 30(2), available here.

Bourne AR. 2018. Sex can't help you when it's hot: high temperatures suppress growth equally in male and female Southern Pied Babbler nestlings. British Ornithologists Union blog, available here

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PUBLICATIONS ARISING FROM THESIS

Thesis chapters

Published prior to submission for examination:

Bourne AR, McKechnie AE, Cunningham SJ, Ridley AR, Woodborne SM, Karasov WH. 2019. Non-invasive measurement of metabolic rates in wild, free-living birds using doubly labelled water. *Functional Ecology 33(1): 162-174*

The data published in the above paper are presented in Chapter 2 of this thesis. The chapter additionally includes an unpublished figure, and unpublished table, and details of individual washout rates and discussions of gut processing times omitted from the published paper due to space restrictions. I have removed some sections that are dealt with in other chapters of the thesis (study site and species, directions for future research), and edited the chapter for consistency with the rest of the thesis, including adding references to the other relevant chapters. I made the largest contribution to the publication, including study design, most of the field work for the proof of concept section, all of the field work for the field application section, all of the lab work, analysis of the data, drafting of the manuscript, and responding to reviewers' comments. AEM and WHK were extremely involved in the design of the proof of concept and SJC and ARR with the design of the field application. SMW trained me in the lab and assisted with data processing. WHK assisted in the data analysis and initial interpretation. All co-authors were actively involved in reviewing and revising the manuscript.

Published after submission for examination:

Bourne AR, Cunningham SJ, Spottiswoode C, Ridley AR. 2020. High temperatures drive offspring mortality in a cooperatively breeding bird. *Proceedings of the Royal Society B 287: 20201140*

The data published in the above paper are presented in Chapter 3 of this thesis. The chapter additionally includes several unpublished figures and a Cox proportional hazards analysis. I have removed some published sections that are dealt with in other chapters of the thesis (e.g. study site and species, some general methods), and edited the chapter for consistency with the rest of the thesis, including adding references to the other relevant chapters. I made the largest contribution to the publication, including three years of field work, analysis of the data, drafting of the manuscript, and responding to reviewers' comments. ARR and SJC were extremely involved in the design of the study

and its implementation, and all co-authors were actively involved in reviewing and revising the manuscript.

Bourne AR, Cunningham SJ, Spottiswoode C, Ridley AR. 2020. Compensatory breeding in years following drought in a desert-dwelling cooperative breeder. *Frontiers in Ecology and Evolution 8: 190*

The data published in the above paper are presented in Chapter 6 of this thesis. The chapter additionally includes several additional analyses and figures. I have removed some published sections that are dealt with in other chapters of the thesis (e.g. study site and species, some general methods), and edited the chapter for consistency with the rest of the thesis, including adding references to the other relevant chapters. I made the largest contribution to the publication, including three years of field work, analysis of the data, drafting of the manuscript, and responding to reviewers' comments. ARR and SJC were extremely involved in the design of the study and its implementation, and all co-authors were actively involved in reviewing and revising the manuscript.

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Collaborations:

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DECLARATIONS

This thesis reports original research that I conducted while enrolled as a PhD student at the FitzPatrick Institute of African Ornithology, University of Cape Town. All assistance received was in line with normal support provided by supervisors and has been fully acknowledged. This work has not been submitted in any form for any degree at any other university.

I confirm that I have been granted permission by the University of Cape Town's Doctoral Degrees Board to include the following publication, with minor modifications (see above), in my PhD thesis, and where co-authorships are involved, my co-authors have agreed that I may include the publication:

Bourne AR, McKechnie AE, Cunningham SJ, Ridley AR, Woodborne SM, Karasov WH. 2019. Non-invasive measurement of metabolic rates in wild, free-living birds using doubly labelled water. *Functional Ecology 33(1): 162-174*

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CHAPTER 1: General introduction

Preamble

In this chapter, I present the thesis rationale, describing the overarching research question addressed in the data chapters that follow. This chapter also contains 1) brief literature reviews on the different elements of my research question, specifically the impacts of climate variability and change on wild animals and the relationship between cooperative breeding behaviour and environmental factors, 2) an introduction to the study site and system, 3) a summary of general methods applicable to all data chapters, and 4) the thesis outline, providing a brief overview of each data chapter.

1.1 Thesis rationale

The purpose of this doctoral research is to explore the relationship between social behaviour and vulnerability to climate change. Increasingly harsh and unpredictable climate regimes, resulting from rapidly advancing anthropogenic climate change, are affecting wildlife populations around the world (Allen, Breshears, & McDowell, 2015; Scheffers et al., 2016; Rey, Fuller, Mitchell, Meyer, & Hetem, 2017; Spooner, Pearson, & Freeman, 2018; Ripple, Wolf, Newsome, Barnard, & Moomaw, 2019). Understanding life history responses to current environmental conditions is increasingly important for accurately predicting vulnerability to climate change (Camacho et al., 2018; Conradie, Woodborne, Cunningham, & McKechnie, 2019). The discovery that animals living in climatically variable environments are more likely to engage in cooperative breeding (Rubenstein & Lovette, 2007; Lukas & Clutton-Brock, 2017) implies that cooperative breeding may buffer individuals against adverse weather conditions. Individuals living in groups are known to share tasks related to, for example, parental care, territory defence, or predator vigilance. These practices bring benefits for individual group members such as (i) less investment in each task per individual, a phenomenon known as load-lightening (Crick, 1992; Meade, Nam, Beckerman, & Hatchwell, 2010); (ii) additive contributions to tasks, leading, for example, to greater defence against predators or greater investment in young (Ridley & Raihani, 2007a; Canestrari, Chiarati, Marcos, Ekman, & Baglione, 2008; Pike, Ashton, Morgan, & Ridley, 2019; Guindre-Parker & Rubenstein, 2020); and (iii) task partitioning, leading to the more efficient execution of tasks by distributing work among group members (Clutton-Brock, Russell, & Sharpe, 2004; Ridley & Raihani, 2008). The benefits of cooperation may buffer against adverse weather because each individual group member may be able to invest more time in behaviours related to self-maintenance, such as foraging, resting, or behavioural thermoregulation (e.g. seeking shade), without compromising vigilance or parental care overall. Alternatively, or additionally, cooperation may buffer

against adverse weather by ensuring a greater reliability of resources, due to more group members being available to search for food, defend a territory, or care for dependent young.

Cooperation thus represents a breeding strategy with the potential to moderate impacts of climate change and is worthy of further investigation in this context. Yet, there are relatively few empirical studies explicitly testing for a buffering effect of cooperation against climate variability and change (Covas, Du Plessis, & Doutrelant, 2008; Langmore, Bailey, Heinsohn, Russell, & Kilner, 2016; Guindre-Parker & Rubenstein, 2018, 2020; van de Ven, Fuller, & Clutton-Brock, 2020). In this study, I investigated the relative influence of environmental (temperature, rainfall) and social (group size) factors on behaviour, physiology, reproduction and survival in southern pied babblers *Turdoides bicolor* (Ridley, 2016), hereafter referred to as 'pied babblers', a cooperatively breeding bird endemic to the Kalahari (Hockey, Dean, & Ryan, 2005). I have used a 15-year life history dataset (2003 to 2019), to which I contributed three years of data, along with three austral summers (Sept to March) of project-specific fieldwork with the same population (2016 to 2019). I have explored the effect of interactions between group size and weather throughout the thesis, wherever sample sizes allowed, because the presence of significant interactions indicating reduced impacts of adverse weather in larger groups would be consistent with a buffering effect of group size.

1.2 Contribution to knowledge

In this thesis, I address the question of whether and to what extent the presence of helpers in pied babbler groups provides a buffer against the impacts of climate variability and change. To do this, I have brought two quite different questions together into a single, multi-disciplinary study. The first, one of long-standing theoretical interest in evolutionary biology, is 'Why be social?' and, while there are many theories (Ricklefs, 1975; Crick, 1992; Cockburn, 2002; Koenig & Dickinson, 2004; Jetz &

Rubenstein, 2011; Riehl, 2013; Connelly, Bruger, McKinley, & Waters, 2016; Shen, Emlen, Koenig, & Rubenstein, 2017; Griesser, Drobniak, Nakagawa, & Botero, 2017; Kingma, 2017; Lukas & Clutton-Brock, 2018; Lin, Chan, Rubenstein, Liu, & Shen, 2019), this question remains under active investigation today (Cornwallis et al., 2017; Shen & Rubenstein, 2019; Downing, Griffin, & Cornwallis, 2020). The second, critical in conservation biology (Pearce-Higgins, Eglington, Martay, & Chamberlain, 2015; Camacho et al., 2018; Spooner et al., 2018; Buchholz et al., 2019; McKechnie, 2019), is concerned with what underlies species' vulnerability to climate change.

I collected detailed observations of individual behaviour (Altmann, 1974; Gilby, Pokempner, & Wrangham, 2010), measurements of energy expenditure and water turnover using a novel non-invasive doubly labelled water (DLW) technique (Anava, Kam, Shkolnik, & Degen, 2000; Bourne et al., 2019), nest and individual life histories (Ridley & van den Heuvel, 2012; Nelson-Flower, Wiley, Flower, & Ridley, 2018), body mass measurements (du Plessis, Martin, Hockey, Cunningham, & Ridley, 2012; Sharpe, Cale, & Gardner, 2019), and nestling daily growth rate data (Cunningham, Martin, Hojem, & Hockey, 2013; van de Ven, McKechnie, Er, & Cunningham, 2020). I worked with a unique, individually-marked and habituated, free-living study population (Ridley, 2016), collecting behaviour and physiology data concurrently in the same individuals and without having to handle the birds at all. Minimal handling during physiological research is often difficult to achieve in the wild (Cooper, Withers, Hurley, & Griffith, 2019; Smit, Woodborne, Wolf, & Mckechnie, 2019) yet is important both for animal welfare in research and for the improved biological relevance of data collected from wild animals, given that physiological responses to handling can be rapid and so can confound measurements of interest (Romero & Reed, 2005; Tomlinson, Maloney, Withers, Voigt, & Cruz-Neto, 2013; Pavlova et al., 2018; Závorka et al., 2018). This project thus also makes a novel

methodological contribution in support of much-needed concurrent animal behaviour and ecophysiology research in wild populations under natural conditions (Stillman, 2019).

1.3 Impacts of climate change

Globally, average temperatures are increasing at an unprecedented rate and are projected to continue to increase over most land masses in the future (IPCC, 2007, 2013). Current climate models predict a dramatic increase in the frequency, intensity, and duration of high temperature extremes, including heat waves (Easterling et al., 2000; Meehl & Tebaldi, 2004; Stillman, 2019). Changes to the timing and predictability of rainfall (Golodets et al., 2013; van Wilgen, Goodall, Holness, Chown, & McGeoch, 2016) and the frequency and intensity of extreme rainfall events (MacKellar, New, & Jack, 2014; Wise & Lensing, 2019) are also being observed. Such climatic changes are affecting wildlife populations in measurable ways, altering population abundance, species range distributions, reproductive strategies, and local extinction rates (Parmesan & Yohe, 2003; Thomas et al., 2004; Saino et al., 2011; Scheffers et al., 2016; Spooner et al., 2018).

Many studies have considered the impacts of climate variability and change on birds (Pearce-Higgins & Green, 2014; Dunn & Møller, 2019; McKechnie, 2019). Impacts directly attributable to adverse weather and changing climate regimes include higher risk of mortality (McKechnie & Wolf, 2010; Sharpe et al., 2019), reduced breeding success (Skagen & Yackel Adams, 2012; Cunningham et al., 2013; Conrey, Skagen, Yackel Adams, & Panjabi, 2016; Cruz-McDonnell & Wolf, 2016), compromised body condition and immunocompetence (du Plessis et al., 2012; Edwards, Mitchell, & Ridley, 2015; Wingfield et al., 2017; Xie, Romero, Htut, & McWhorter, 2017; Gardner, Rowley, Rebeira, Rebeira, & Brouwer, 2018), declining populations (Saino et al., 2011; Riddell, Iknayan, Wolf, Sinervo, & Beissinger, 2019), range changes (Hockey, Sirami, Ridley, Midgley, & Babiker, 2011;

Huntley, 2019), and potentially maladaptive behavioural adjustments to foraging (Cunningham, Martin, & Hockey, 2015; Pattinson & Smit, 2017; Bladon et al., 2019; Cooper et al., 2019; Funghi, McCowan, Schuett, & Griffith, 2019), parental care (Wiley & Ridley, 2016; Clauser & McRae, 2017; van de Ven, 2017; R. L. Carroll et al., 2018), and migration (Dunn, Robertson, Winkler, Whittingham, & Hannon, 2010; Samplonius et al., 2018).

Species living in arid and semi-arid environments are useful models for studying the impacts of climate change, because these ecosystems are (i) already characterised by extremes in temperature and rainfall (McKechnie, Hockey, & Wolf, 2012; Kruger & Sekele, 2013; Tokura, Jack, Anderson, & Hoffman, 2018), and (ii) are experiencing rapid increases in temperature and the interannual variability of rainfall as a result of anthropogenic climate change (Feng & Fu, 2013; Huang et al., 2016; Huang, Yu, Dai, Wei, & Kang, 2017; van Wilgen et al., 2016; Mayaud, Bailey, & Wiggs, 2017; Li, Wu, Liu, Zhang, & Li, 2018). High temperatures and low rainfall are already known to impact on behaviour, body condition, growth, and survival in a suite of arid-zone bird species (Cunningham et al., 2013; Sunday et al., 2014; Gardner et al., 2017; Iknayan & Beissinger, 2018; Oswald, Lee, & Smit, 2018; van de Ven, McKechnie, & Cunningham, 2019).

1.4 Benefits of cooperation

Cooperative breeding, where more than two individuals invest in rearing a single brood (Cockburn, 2002), occurs in ~9% of bird species globally (Cockburn, 2006; Riehl, 2013). In such systems, helpers care for young that may not be their own (Cockburn, 2002). Kin selection - when individuals living in cooperatively breeding groups increase their inclusive fitness by helping genetic relatives (Riehl, 2013) - is regarded as an important process in the evolution of avian cooperative breeding because most groups consist of family members (Koenig & Dickinson, 2004). Kinship, or

relatedness to the breeding pair, influences helper decisions in many species (Napper & Hatchwell, 2016; Groenewoud et al., 2018). Helpers are, however, not always related to the dominant pair and may immigrate from outside the family group (Raihani, Nelson-Flower, Golabek, & Ridley, 2010; Groenewoud et al., 2018). In such cases, kin selection cannot explain why helpers provide energetically costly care to unrelated offspring, and direct fitness benefits of group-living may be far more important than previously suspected (Koenig & Dickinson, 2004; Kingma, 2017). These direct fitness benefits include cooperative vigilance and resultant lower predation rates (Ridley, Nelson-Flower, & Thompson, 2013; Ostreiher & Heifetz, 2019), opportunities to inhabit better quality territories and the prospect of inheriting a territory (Nelson-Flower & Ridley, 2016; Kingma, 2017), and the opportunity to practice parenting skills (Komdeur, 1996).

In cooperative breeders, survival of young often improves with increasing group size (Canestrari, Marcos, & Baglione, 2008; Ridley, 2016). Larger groups may provision more regularly (Meade et al. 2010; but see Wiley & Ridley 2016), better detect and repel predators (Ridley & Raihani, 2007a), or gain access to higher quality territories or nest sites (Mumme, Bowman, Pruett, & Fitzpatrick, 2015). Other benefits of cooperation for avian reproduction include earlier fledging age and more broods raised per season than non-cooperatively breeding species (Ridley & van den Heuvel, 2012); reduced costs of breeding, resulting in higher interannual survival rates for females (Cockburn et al., 2008; Langmore et al., 2016); enhanced egg investment (Valencia, Mateos, de la Cruz, & Carranza, 2016); increased recruitment of fledglings into the adult population (Canestrari, Marcos, et al., 2008; Meade et al., 2010); and the ability to raise overlapping broods (Ridley & Raihani, 2008; Guindre-Parker & Rubenstein, 2018). The investment in young provided by helpers may be additive (Canestrari, Chiarati, et al., 2008; Pike et al., 2019), increasing the amount of care provided to young, or compensatory (Savage, Russell, & Johnstone, 2015; van Boheemen et al., 2019), enabling breeders

to reduce their investment while young receive a similar amount of care overall, a phenomenon known as 'load-lightening' (Crick, 1992; Langmore et al., 2016). As I have not conducted experiments, I cannot determine whether any observed association between group size and reproductive success is due to direct effects of the presence of helpers and the help they provide or occurs as a result of higher quality individuals in the breeding pairs being more likely to attract or retain helpers or access and maintain control over higher quality territories (Stacey & Ligon, 1991; Mumme et al., 2015; Nado, Kasova, Kristin, & Kanuch, 2018; van Boheemen et al., 2019). For the purposes of this study, I have assumed that the presence of helpers boosts productivity rather than that helpers accumulate on productive territories (Cockburn et al., 2008).

Theory suggests that a combination of ecological constraints (Emlen, 1982), environmental conditions (Lin et al., 2019; Shen & Rubenstein, 2019) and benefits of philopatry (Stacey & Ligon, 1991) favour individuals maintaining a subordinate position within an established territory instead of dispersing to breed independently (Nelson-Flower et al., 2018). Several non-mutually exclusive hypotheses concerning the evolution of cooperative breeding emphasise the collective action benefits of cooperative breeding in harsh conditions or in fluctuating environments (Lin et al., 2019; Shen & Rubenstein, 2019). The 'ecological constraints' hypothesis suggests that cooperative breeding may evolve in stable environments due to habitat saturation and high population densities leading to limited breeding and territory vacancies, or in fluctuating environments due to the high costs of reproduction in harsh years (Emlen, 1982; Shen et al., 2017). The 'benefits of philopatry' hypothesis suggests that cooperative breeding may have evolved where the natal territory provides better benefits than can be found elsewhere, and that influence survival, reproduction, and future breeding opportunities of individuals (Stacey & Ligon, 1991; Komdeur, 1996; Groenewoud et al., 2018). Other hypotheses focused on environmental conditions include the 'hard life' hypothesis (Koenig & Mumme, 1987;

Koenig, Walters, & Haydock, 2011), the 'fission-fusion' hypothesis (Emlen, 1982; Rubenstein & Lovette, 2007) and the closely related 'temporal variability' (Rubenstein & Lovette, 2007) and 'bet-hedging' hypotheses (Orzack & Tuljapurkar, 2001; Rubenstein, 2011; Müller, Hense, Fuchs, Utz, & Pötzsche, 2013). See Table 1.1 for definitions and associated predictions for each hypothesis in terms of the research questions in this thesis.

Cooperative breeding has been observed in both stable and fluctuating environments (Rubenstein & Lovette, 2007; Gonzalez, Sheldon, & Tobias, 2013), and not all species facing the same ecological constraints and inhabiting the same environments are cooperative breeders (Covas & Griesser, 2007; Ridley & van den Heuvel, 2012). One aspect of research into the benefits of cooperation for individual group members, suggested by the theories mentioned above but relatively little explored empirically, is the extent to which sociality could mitigate the effects of variation in weather conditions on reproduction and survival. A moderating effect of sociality could operate by, for example, enabling individual group members to allocate more time to self-maintenance without compromising reproductive output or survival probabilities within the group overall.

1.5 Cooperation as a buffer

Global comparative studies have shown that the distribution of cooperatively-breeding (Rubenstein & Lovette, 2007; Jetz & Rubenstein, 2011; Lukas & Clutton-Brock, 2017; Shen et al., 2017) and group-living (Griesser et al., 2017) birds and mammals is associated with harsh environments characterised by high spatial and temporal variability in rainfall, such as arid and semi-arid systems (although see Gonzalez, Sheldon, & Tobias, 2013 for a counter-example). This association suggests that the presence of additional group members buffers against environmental uncertainty (Jetz & Rubenstein, 2011; Russell, 2016; Cornwallis et al., 2017), at least up to an optimal group size (Markham, Gesquiere,

Alberts, & Altmann, 2015; Ridley, 2016). Several hypotheses have been proposed to explain the observed association, including that cooperative breeding evolved in such environments (Rubenstein & Lovette, 2007; Lukas & Clutton-Brock, 2017), facilitated the colonisation of such environments (Cornwallis et al., 2017), or lowered the probability of extinction under changing ecological conditions (Russell, 2016; Griesser et al., 2017). One prominent explanation for the occurrence of cooperative breeding in birds is that it represents a 'bet-hedging' strategy (Rubenstein, 2011), whereby breeding individuals share the costs of reproduction with helpers and are thus able to reduce interannual variation in reproductive success in response to unpredictable rainfall and food availability (Rubenstein & Lovette, 2007), see Table 1.1.

The theory of cooperation as a bet-hedging strategy has its basis in the phenomenon known as load-lightening (Crick, 1992), observed in a number of cooperatively-breeding species (Hatchwell, 1999; Mumme et al., 2015; Langmore et al., 2016). The term load-lightening describes individual reductions in workload in response to the presence of additional group members. Load-lightening results in, for example, young receiving adequate care overall even though each group member reduces their individual contribution in response to resource constraints, such as those imposed by drought, and may increase individual fitness of group members by reducing their investment in costly reproduction (Meade et al., 2010). Cooperation may also moderate impacts of environmental variability via task-partitioning (Clutton-Brock et al., 2004; Ridley & Raihani, 2008) or by ensuring improved access to resources (Golabek, Ridley, & Radford, 2012; Ebensperger et al., 2016).

Table 1.1: Outlines the non-mutually exclusive hypotheses concerning the evolution of cooperative breeding which emphasise the collective action benefits of cooperative breeding in harsh conditions or in fluctuating environments. With the possible exception of the 'benefits of philopatry' hypothesis, all of these hypotheses predict that helpers will be disproportionately more beneficial in harsh years than in benign years for cooperatively-breeding species living in spatially and temporally variable environments.

Hypothesis	*Definition*	*Prediction*	*Reference*
Ecological constraints	In stable environments, habitat saturation and high population densities lead to limited breeding and territory vacancies and delayed dispersal. In fluctuating environments, helpers mitigate the high costs of reproduction in harsh years.	Buffering effect of larger group size in harsh years.	Emlen (1982) Canario et al. (2004) Beauchamp (2014)
Benefits of philopatry	Natal territory provides greater benefits that can increase survival, reproduction, future breeding opportunities of individuals than elsewhere.	Competition over resources may result in smaller groups in harsh years.	Stacey & Ligon (1991) Komdeur (1996) Groenewoud et al. (2018)
Hard life	Individuals maintain stable groups through different environmental conditions and benefits such as cooperative provisioning of young are more important in hard times.	Buffering effect of larger group size in harsh years.	Koenig & Mumme (1987) Koenig et al. (2011)
Fission fusion	Individuals adjust breeding group size to current environmental conditions forming larger groups in bad years in order to access collective action benefits.	Buffering effect of larger group size in harsh years.	Emlen (1982) Rubenstein & Lovette (2007)
Bet-hedging	Unpredictability in highly variable environments favours cooperative breeding by reducing interannual variation in reproductive success.	Buffering effect of larger group size in harsh years.	Rubenstein (2011) Müller (2013) Sæther (2015)
Temporal variability	Cooperative breeding is likely to be adaptive in temporally variable environments because it allows for both reproduction in harsh years and sustained breeding during benign years.	Buffering effect of larger group size in harsh years.	Rubenstein & Lovette (2007)

A small number of recent studies empirically test the benefits of cooperation for reproduction across varying environmental conditions (Covas et al., 2008; Langmore et al., 2016; Guindre-Parker & Rubenstein, 2018; van de Ven, Fuller, et al., 2020), looking for interactions between measures of cooperation, such as group size or the number of helpers present, and environmental conditions. Only one study to date (Guindre-Parker & Rubenstein, 2020) extends the scope of these analyses to consider the implications of larger group sizes for adult survival, showing that larger groups sizes enhance survival by reducing predation risk rather than buffering against variation in rainfall in a highly social bird. Most empirical tests of the buffering effect of cooperation consider reproduction and

survival in response to variation in rainfall. The influence of temperature is rarely included, despite the fact that thermoregulatory benefits of group living have been demonstrated (Paquet et al., 2016; Mares, Doutrelant, Paquet, Spottiswoode, & Covas, 2017), but load-lightening behaviours might also buffer social animals against the fitness costs of variation in temperature (Sinervo et al., 2010; Cunningham et al., 2015) by enabling individuals to allocate more time to self-maintenance activities. For example, larger groups may be able to maintain overall incubation constancy at nests or maintain the amount of biomass provisioned to young during hot weather while also enabling each individual to spend more time on self-directed behaviours such as thermoregulation (e.g. increasing rest, seeking shade) or balancing energy and water requirements (e.g. increasing foraging time, reducing provisioning rates). Individuals in larger groups may therefore suffer fewer consequences of trade-offs between self-maintenance during adverse weather and investing in parental care, allowing not only higher reproductive success under challenging environmental conditions, but also better mass maintenance and a higher individual survival probability. Benefits and trade-offs associated with cooperation may vary between breeders and helpers, in part due to relatedness to the brood, as well as between species.

1.6 Study site

Fieldwork was conducted at the Kuruman River Reserve (KRR; 33 km2; 26°58'S, 21°49'E; Fig. 1.1), a summer-rainfall site in the southern Kalahari with mean daily summer maximum air temperatures of 34.7 ± 9.7°C, and mean annual precipitation of 186.2 ± 87.5mm for the period 1995–2015 (van de Ven et al., 2019). The region is characterised by hot summers and periodic droughts (van Wilgen et al., 2016). Rainfall is extremely variable between years (MacKellar et al., 2014). For example, between 2003 and 2019 (the duration of the Pied Babbler Research Project data collection period – see below), rainfall at the study site ranged from 62.4 to 291.2 mm (mean = 172.2 ± 68.3 mm) among austral summers (October – March). Over the last 20 years, high temperature extremes within the region have

increased in both frequency and severity (Kruger & Sekele, 2013; van Wilgen et al., 2016). The landscape consists of alternating sand dunes, sparsely treed plains, and dry riverbeds (Kong, Marsh, van Rooyen, Kellner, & Orr, 2015; Fig 1.2). The Kalahari is an arid savanna system where the dominant plant species are camelthorn trees *Vachellia erioloba* and sour grass *Schmidtia kalahariensis* (Steenkamp, Vogel, Fuls, van Rooyen, & van Rooyen, 2008). Other common plant species include blackthorn *Senegalia mellifera*, driedoring *Rhigozum trichotomum*, grey camelthorn *Vachellia haemotoxylon*, and shepherd's tree *Boscia albitrunca*.

The KRR is home to a large behavioural ecology research station and several long term studies of habituated animals native to the region, including pied babblers (Ridley, 2016), meerkats *Suricata suricatta* (Maag, Cozzi, Clutton-Brock, & Ozgul, 2018), southern yellow-billed hornbills *Tockus leucomelas* (van de Ven et al., 2019), Cape ground squirrels *Xerus inauris* (Samson & Manser, 2016), fork-tailed drongos *Dicrurus adsimilis* (Olinger, 2017), bat-eared foxes *Otocyon megalotis* (Welch, le Roux, Petelle, & Périquet, 2018), slender mongoose *Galerella sanguinea* (Graw & Manser, 2017), and crimson-breasted shrikes *Laniarius atrococcineus* (Ridley & van den Heuvel, 2012).

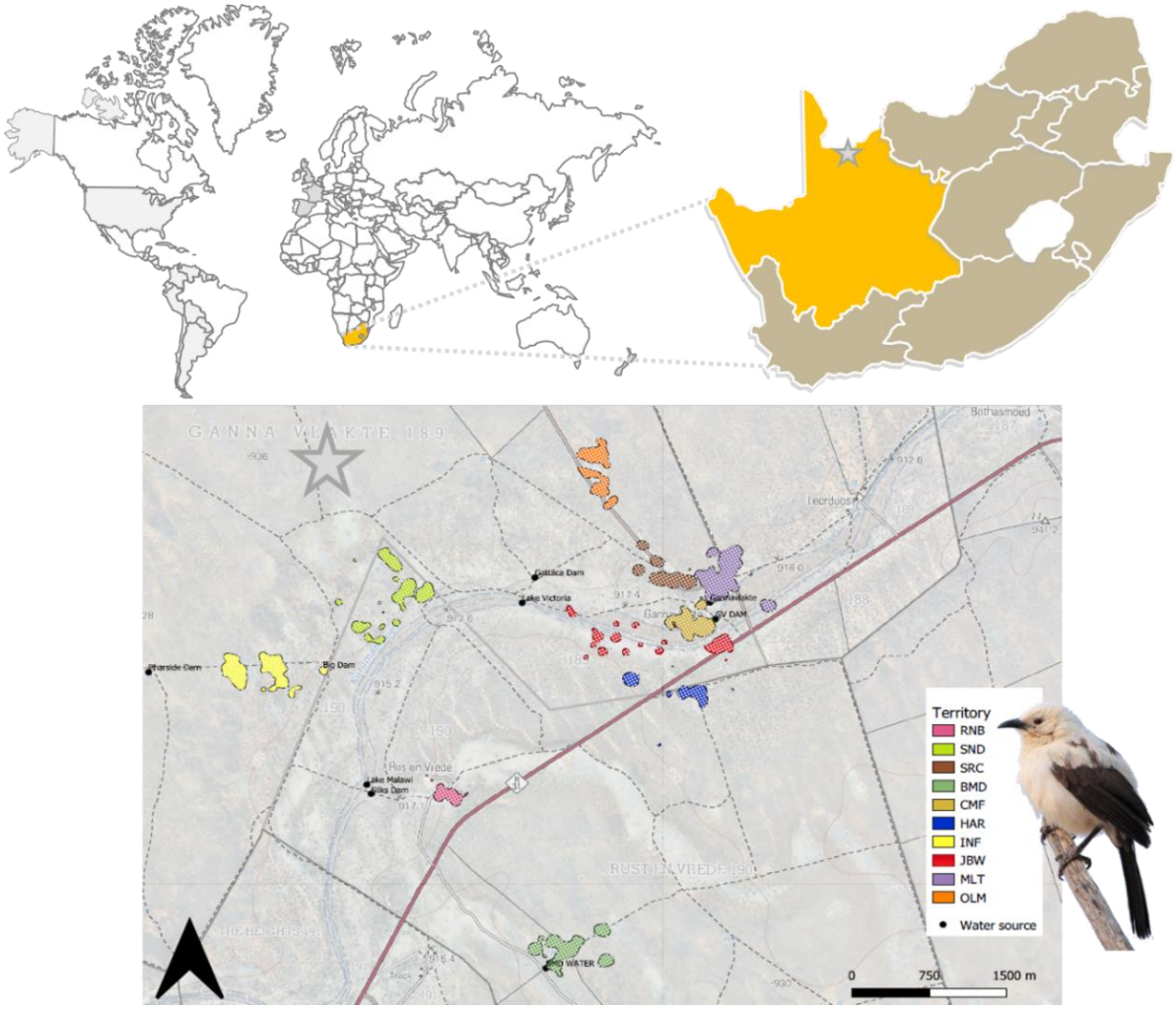


Figure 1.1: Map of the study site. The study site is located in the Northern Cape of South Africa (top right, highlighted in orange in the map of South Africa map, with the study site marked by a grey star). An indicative map of 10 southern pied babbler Turdoides bicolor *territories at the study site is shown on the lower panel. The world map and South Africa map were sourced from www.presentationmagazine.com and the territory map was created by Sanjo Rose from GPS data that I collected.*

Figure 2.2: Southern Pied Babblers Turdoides bicolor *are endemic to the Kalahari, a summer rainfall arid savannah ecosystem characterised by alternating sand dunes, sparsely treed plains, and dry riverbeds. Photographs by Nicholas B. Pattinson.*

1.7 Study system

1.7.1 Study species

Pied babblers are medium-sized (60–90 g), cooperatively-breeding passerines endemic to the Kalahari (Hockey et al., 2005). They are highly social, living in groups ranging in size from 3-15 adults (Raihani & Ridley, 2007b). Groups are territorial and consist of a single breeding pair with subordinate helpers that are usually, but not always, the offspring of the breeding pair (Raihani et al., 2010; Nelson-Flower et al., 2011; Ridley, 2016). A population pedigree, generated from genotyping nine highly variable microsatellite loci, parentage analyses and life- history data (Nelson-Flower et al., 2011), has previously shown that pied babbler groups are highly kin structured. Most subordinates are closely related to one another and to the breeding pair (mean relatedness ~0.38), such that help is almost invariably directed

toward close relatives and helping confers indirect fitness benefits on subordinates. All adult group members (individuals > 1 year old; Fig. 1.3) participate in cooperative behaviours, including territory defence, sentinel duties, and parental care (Ridley & Raihani, 2007b; Ridley, 2016). In addition to indirect fitness benefits, subordinate individuals gain direct benefits of philopatry via increased survival and high likelihood of eventual acquisition of a breeding position (Nelson-Flower et al., 2018).

Dominant pairs monopolise > 95% of breeding activity, and subordinates rarely breed even when unrelated potential breeding partners are present in the group (Nelson-Flower et al., 2011). Dominant individuals can be identified through their breeding behaviour. For example, only dominant females incubate the nest overnight (Ridley, 2016), and dominant pairs have distinctive duets (Wiley & Ridley, 2018). However, pied babblers are sexually monomorphic and sex cannot be reliably determined from external characteristics (Ridley, 2016).

Pied babblers breed during the austral summer, typically between August and April, when it is hottest (Ridley, 2016; Bourne, Cunningham, Spottiswoode, & Ridley, 2020b). They construct open-cup grass nests in camelthorn or blackthorn trees, usually at heights of 3-10 m (Ridley & van den Heuvel, 2012; Wiley, 2017). Pied babbler females lay one egg per day on consecutive days and begin incubation once the clutch is complete. Modal clutch size is three (Ridley, 2016). Clutches are incubated by all adult group members. Although pied babbler groups typically attend to one nest at a time, they may attempt to breed several times within a single breeding season (Raihani et al., 2010) and the dominant pair may initiate and incubate a new clutch while the group is still feeding dependent fledglings from the previous breeding attempt (Ridley & Raihani, 2008). Stable pair bonds between mated dominant individuals are associated with improved reproductive success and group stability (Wiley & Ridley, 2018) as well as an improved ability to recover from extreme weather events such as droughts (Wiley, 2017). Previous research on this species has shown that high temperatures and

drought affect population demographics, increasing the risk of localised extinction (Wiley, 2017), reducing offspring provisioning rates (Wiley & Ridley, 2016), and constraining foraging behaviour (du Plessis et al., 2012). High temperatures are also associated with an inability to maintain body mass between consecutive days (du Plessis et al., 2012), lower energy expenditure (Bourne et al., 2019), and reduced effort to defend territories (Golabek et al., 2012) in this species.

Figure 1.3: Southern pied babblers Turdoides bicolor *are sexually monomorphic cooperative breeders. Pictured here, an adult subordinate female (left) feeds a male juvenile (right, with mottled brown plumage). Individuals in the study population are identifiable by the unique combination of metal and colour rings on their legs. Sex is determined from blood samples using a molecular sexing technique.*

1.7.2 Pied Babbler Research Project

The Pied Babbler Research Project (PBRP) was established at the KRR in 2003, by Associate Professor Amanda Ridley, and long-term monitoring of pied babbler life history and cooperative

behaviour has been conducted at the site ever since (Ridley, 2016). The study population comprises 10-20 habituated pied babbler groups each year, with an average group size (± one standard deviation) of 4.4 ± 1.5 adults (range: 2–10 adults). Pied babblers in the study population are habituated to observation by humans at distances of 1–5 m (Ridley & Raihani, 2007b).

As part of ongoing research, habituated groups are visited approximately weekly during the peak breeding season (austral summer) to check group composition, weigh the birds, and record life history events such as breeding, immigration, and dispersal. Groups are highly territorial and can therefore be reliably located by visits to each territory (Golabek et al., 2012; Ridley, 2016). Birds in the study population are marked as nestlings with a unique combination of metal and colour rings, allowing for individual identification throughout their lifetimes (Fig. 1.2).

1.8 General methods

The long-term life history data used for analyses presented in Chapter 3 and Chapter 6 of this thesis were collected by the PBRP during each austral summer breeding season between September 2005 and February 2019. Data additional to the ongoing, long-term monitoring of this population, which were collected specifically for this study and are presented in Chapters 2, 4, and 5, were collected over three austral summer breeding seasons between September 2016 and February 2019.

1.8.1 Sexing

Blood samples for molecular sexing were collected from nestlings by brachial venipuncture and stored in lysis buffer. Nuclear DNA was extracted from blood samples and molecular sexing techniques used to determine the sex of individuals (sensu Fridolfsson & Ellegren, 1999; Nelson-Flower et al., 2011). This procedure was also occasionally conducted for immigrant adults of unknown sex, after they had been successfully habituated.

1.8.2 Body mass measurements

All nestlings were weighed to 0.1 g on a top-pan scale at 11 days post hatching, at the same time as ringing and blood sampling. Body mass data were collected from fledglings and adult birds by enticing individuals to stand on a top pan balance in exchange for a small food reward (Ridley, 2016). All adult body mass measures used in this thesis were collected at dawn, representing pre-foraging body mass.

1.8.3 Life history data

During weekly visits, information on breeding status, including nest-building, copulation, egg-laying, incubation, provisioning, and fledging, were recorded. Information on group composition, inter-group interactions, and immigration, emigration, or prospecting behaviour were also recorded every time a group was encountered. Group size varied between groups and breeding seasons, but did not differ significantly between drought and not-drought years ($F_{1,164} = 0.754$, $p = 0.387$). Between 2005 and 2019, the largest group on average consisted of 5.4 ± 2.3 adult group members (range across 11 breeding seasons: 2.3–9), while the smallest group on average consisted of 3.3 ± 0.9 members (range across 12 breeding seasons: 2–5). Relatively large or small groups on average were not consistently larger or smaller than other contemporary groups across all breeding seasons (Fig. 1.4).

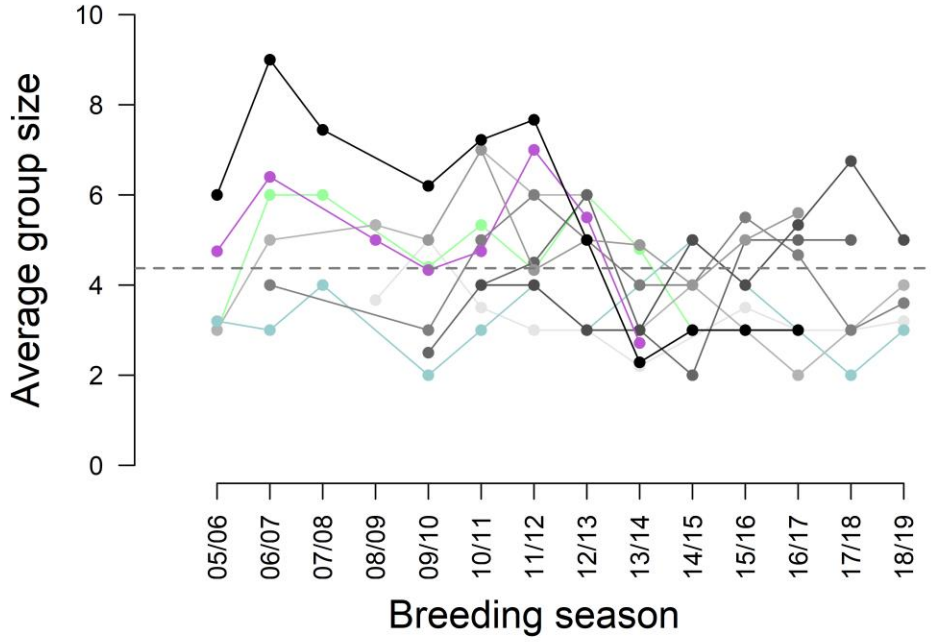


Figure 1.4: Southern pied babblers Turdoides bicolor *groups were not consistently large, small, or average-sized in comparison to other contemporary groups between austral summer breeding seasons. The figure shows average group size during the breeding season for the ten groups monitored most consistently at the study site, over 8-12 consecutive breeding seasons. Each colour represents a different group. The dashed horizontal line represents mean group size for the 10 groups shown across all of the breeding seasons.*

1.8.4 Temperature and rainfall

Daily maximum temperature (°C) and rainfall (mm) data were collected from an on-site weather station (Vantage Pro2, Davis Instruments, Hayward, USA) at the KRR. Missing data from 2009, 2010, and 2011 were sourced from a nearby South Africa Weather Services weather station at Van Zylsrus (28 km). I found significant, high repeatability between the temperature measurements recorded by the two weather stations (Lin's concordance correlation coefficient r_c = 0.957, 95% CI: 0.951–0.962), and moderate repeatability between rainfall measurements (r_c = 0.517, 95% CI: 0.465–0.566). Lower repeatability for rainfall is unsurprising given that rainfall in the region is characterised by localised thunderstorms. Differences in rainfall measured (in mm) between the two stations were small (average

difference between individual rainfall events = 0.045 ± 3.075mm, 95% CI = -5.981–6.072mm), suggesting that both weather stations adequately detected wet vs. dry periods.

1.8.5 Statistical analyses

Statistical analyses were conducted in R v 3.4.1 and R v 3.6.0 (R Core Team, 2017), making use of specific versions and packages as stated for each analysis in each chapter. Throughout this thesis:

1) all continuous explanatory variables were scaled by centering and standardising by the mean, allowing coefficients to be interpreted as effect sizes (Schielzeth, 2010; Harrison et al., 2018a);
2) all explanatory variables were tested for correlation with one another, using Variance Inflation Factor > 2 as cut-off values indicating significant correlation between continuous variables (Fox & Monette 1992), and ANOVA and chi-square tests to indicate significant correlation between a continuous and a categorical predictor and two categorical predictors respectively (Harrison et al., 2018a);
3) correlated variables were not included in the same additive models but interactions between correlated variables were tested when these interactions formed part of the central hypothesis (Harrison et al., 2018a);
4) sample sizes reflect complete data sets after removing records containing any missing values;
5) summary statistics are presented as mean ± one standard deviation, unless otherwise indicated in the text;
6) quadratic terms for continuous variables were included as explanatory variables only when no linear main effect was found ***and*** visual inspection of the data suggested a non-linear relationship;

7) where I included repeat sampling of the same individuals, broods, and groups, I attempted to fit random factors for all of the relevant repeated measures. When this resulted in unstable models due to unbalanced sampling, I selected the random term/s that explained the greatest proportion of variation while avoiding destablising the models (Grueber, Nakagawa, Laws, & Jamieson, 2011; Harrison et al., 2018b).
8) linear model fits were evaluated using Normal Q-Q plots and histograms of residuals; and
9) binomial and Poisson model fits were evaluated against the dispersion parameter, using the package *RVAideMemoire* (Herve, 2019).

Interactions between group size and weather effects on development would be consistent with a buffering effect of group size on survival. I therefore conducted sensitivity power analyses in each of the relevant chapters (Chapter 3, 4, and 6) to identify the minimum determinable effect of two-way interactions given the available sample sizes (Cohen, 1988; Greenland et al., 2016), using the R package *pwr* (Champely et al., 2018). For regression models, I used the function *pwr.f2.test*(u =, v =, f^2 =, sig.level =, power =), where u = numerator degrees of freedom, v = denominator degrees of freedom, α (the signficance level; probability of finding an effect that is not there) = 0.05, and power (probability of finding an effect that is there) = 0.8. The calculated value, Cohen's f^2, represents the measure of determinable effect size. I assumed a fourfold increase in required sample size to adequately detect interactions in mixed-effects models (Leon & Heo, 2009). Cohen (1988) suggested that f^2 values of ~ 0.02, ~0.15, and ~0.35 represent the ability to detect small, medium, and large effect sizes respectively.

1.9 Thesis outline

The objective of this research is to understand the extent to which the presence of helpers can provide a buffer against the impacts of climate variability and change, specifically high temperatures and low or unpredictable rainfall. I have used the southern pied babbler, a cooperatively breeding passerine endemic to a hot and dry environment, as a model species. The results of this study provide insight into the behavioural and physiological responses of this species to current environmental variability, the benefits of cooperative breeding strategies, and the potential for cooperation, as indicated by the number of adult group members present, to moderate the effects of adverse weather conditions. I address this research objective in five data chapters, structured as follows:

CHAPTER 2: presents the proof of concept study and field test of the non-invasive DLW method developed for measuring energy expenditure and water turnover without having to capture or handle the habituated study animals. The technique is applied in Chapter 4. The data from this chapter have been included in a publication in *Functional Ecology* (Bourne et al., 2019).

CHAPTER 3: presents data on the influence of temperature, rainfall, group size, and the interactions between weather and group size on survival of young during three stages of early development: egg, nestling, and fledgling. This chapter draws on the 15-year PBRP nest life history and individual life history datasets. Data from this chapter have been included in a publication in *Proceedings of the Royal Society B: Biological Sciences* (Bourne et al., 2020b).

CHAPTER 4: presents data on the influence of temperature, rainfall, group size, and the interactions between weather and group size on the behaviour and physiology of adult birds incubating clutches, in order to understand the mechanisms behind low hatching success at high temperatures (identified in Chapter 3). In this chapter, I present analyses of three field seasons of data, including

detailed observations of behaviour and simultaneous measurements of physiological responses in known individuals using the non-invasive DLW technique described in Chapter 2. Data from this chapter have been included in a manuscript currently in revision for *Conservation Physiology*.

CHAPTER 5: presents data on the influence of temperature, rainfall, and group size on nestling growth and the behaviour of adult birds provisioning nestlings in order to understand the mechanisms behind low fledging rates at high temperatures (identified in Chapter 3). Interactions were not explored in detail due to sample size constraints. In this chapter, I present analyses of three field seasons of data, including detailed, intra-individual repeated measurements of nestling size and growth and observations of parental care behaviour.

CHAPTER 6: presents data on the influence of temperature, rainfall, group size, and the interactions between weather and group size on interannual survival of breeding adults and of young birds in their first year (indicating recruitment into the adult population). This chapter draws on the 15-year PBRP individual life history dataset. Data from this chapter have been included in two publications, in *Frontiers in Ecology and Evolution* (Bourne, Cunningham, Spottiswoode, & Ridley, 2020a) and *Ecology Letters* (Bourne, Cunningham, Spottiswoode, & Ridley, 2020c).

The data chapters are followed by a synthesis and discussion chapter, Chapter 7. All literature cited throughout the thesis is compiled in a single list, which is located towards the end of the document, after Chapter 7. Appendices for each of the relevant chapters (Chapter 3, 4, 5, and 6) follow the complete list of literature cited, appearing at the end of the document in chapter order. Each chapter has been written in preparation for publication. As such, a degree of repetition with regards to framing and methods is unavoidable.

CHAPTER 2: Non-invasive measurement of metabolic rates in wild, free-living birds using doubly labelled water.

Preamble

In this primarily methodological chapter, I present a proof of concept study and a field test of a novel non-invasive doubly labelled water technique I developed as part of my doctoral research. The approach relies on oral dosing and faecal sampling and thus avoids the need to handle the study animal at all in order to collect measurements of energy expenditure and water turnover. The data from this chapter are published. I applied the technique in Chapter 4, to evaluate my research question in terms of the physiological responses of incubating birds to variation in temperature, rainfall, and group size.

Bourne AR, McKechnie AE, Cunningham SJ, Ridley AR, Woodborne SM, Karasov WH. 2019. Non-invasive measurement of metabolic rates in wild, free-living birds using doubly labelled water. *Functional Ecology 33(1): 162-174*.

2.1 Abstract

Doubly labelled water (DLW) is routinely used to measure energy expenditure and water turnover in free-ranging animals. Standard methods involve capture, blood sampling for baseline measurement, injection with isotopic tracers, captivity for an equilibration period, post-dose blood sampling, release, and subsequent re-capture for final blood sampling. Single sampling methods that minimise disturbance by reducing capture and handling time have been developed and tested. Sampling faeces rather than blood could further reduce disturbance to study animals in a range of species and study systems. However, the extent to which estimates of metabolic rate derived from blood and faecal samples diverge has not been investigated.

I compared isotopic enrichment in blood and faecal samples taken concurrently from captive southern pied babblers *Turdoides bicolor*. Isotopic enrichment levels in faeces and in blood were used to calculate initial and final ratios of $\frac{\delta^{18}O_i}{\delta^{2}H_i}$ for each individual. I then used these ratios to calculate daily energy expenditure (DEE) and directly compared measurements from blood samples with those from faecal samples within individuals. I found that faecal sampling resulted in estimates of DEE that agree with those based on blood sampling.

Additionally, I field-tested an oral dosing and faecal sampling protocol with a habituated population of babblers in the southern Kalahari Desert. During the field test, study animals were not captured or handled for either dosing or sampling. Field-testing confirmed the practical feasibility of non-invasive dosing and sampling techniques in free-living animals, and I obtained measurements of DEE that were used to test an *a priori* prediction that DEE is inversely related to air temperature. The data show decreasing DEE with increasing air temperature, a pattern consistent with studies testing similar predictions in birds using traditional DLW methods.

Faecal samples can substitute for blood when measuring DEE using DLW in an insectivorous bird, and, in this chapter, I provide a reproducible method that will allow field-based researchers to obtain sound physiological measurements while minimising handling and removal of study animals from their natural environments.

2.2 Introduction

Quantifying the energy and water requirements of free-living animals is necessary for understanding how physiological processes and behavioural patterns change in response to ecological conditions (Le Maho, 2002; McKechnie et al., 2012; Tomlinson et al., 2014). The doubly-labelled water (DLW) method is a routine technique for measuring energy expenditure in free-living animals via the introduction of two isotopically-enriched tracers into body water and the subsequent collection of samples of body fluids for the analysis of enrichment levels (Speakman & Hambly, 2016). The DLW method is particularly important for understanding energy fluxes in animals too small for heart rate telemetry, the other widely-used technique for quantifying energy expenditure in free-ranging populations (Butler, Green, Boyd, & Speakman, 2004). The isotopes most commonly used for DLW studies, and which I have used as "labels" here, are enriched with oxygen-18 (measured as $\delta^{18}O$) and deuterium (measured as $\delta^{2}H$).

In the study of non-human vertebrates, the DLW technique traditionally involves (1) capture of a study animal, (2) injection with an isotopically-enriched solution, (3) a period of captivity for equilibration of the injectate with body water prior to release, and (4) recapture (Speakman, 1997). Typically, three blood samples are drawn within a 24 h period (or multiple thereof): a baseline sample before enrichment, followed by an initial sample after equilibration and a final enriched sample 24 h

(or longer) after release (Nagy, 1983; Williams, 2001; Smit & McKechnie, 2015; Speakman & Hambly, 2016), known as the two-sample (TS) method (Speakman, 1997; Butler et al., 2004).

Handling, injecting, and blood sampling generally require temporarily removing animals from their natural environments. Most studies investigating the impact of stress associated with DLW procedures on derived measurements of energy expenditure have reported no significant differences between treated and control animals (Speakman, Racey, & Burnett, 1991; Part, Gustafsson, & Moreno, 1992; Weathers & Sullivan, 1993). However, some undesirable effects of standard DLW procedures, including reduced clutch size, nest abandonment, mass loss, behaviour change, and long absences from active nests, have been reported in birds (Culik & Wilson, 1992; Ward, 1996; Schultner, Welcker, Speakman, Nordøy, & Gabrielsen, 2010), and may alter energy expenditure. Other animal physiology studies have shown that handling time and sampling procedures affect measured cortisol levels, an indicator of stress (Romero & Reed, 2005; Hämäläinen, Heistermann, Fenosoa, & Kraus, 2014; Pavlova et al., 2018; Swierk & Langkilde, 2018).

Techniques that are less invasive, or entirely non-invasive, are therefore desirable to reduce any remaining risk of handling affecting physiological or concurrent behavioural measurements under otherwise natural conditions. Techniques relying on non-invasive dosing and/or sampling may be useful for researchers working with, for example, large animals that are difficult to capture and confine (Gotaas, Milne, Haggarty, & Tyler, 1997; Williams, Anderson, & Richardson, 1997; Scantlebury et al., 2014; King, Schoenecker, Fike, & Oyler-McCance, 2018), threatened species, as suggested by Speakman and Hambly (2016), institutionalised animals in research facilities such as zoos, game reserves, rehabilitation centers or captive breeding programmes (Ballantyne, Packer, Hughes, & Dierking, 2007), very small animals from which it may be difficult or not feasible to collect blood (Webster & Weathers, 1989; Chaverri, Schneider, & Kunz, 2008), agricultural (Samuels, Cupido,

Swarts, Palmer, & Paulse, 2015) or predator-naïve species (McLean, Hölzer, & Studholme, 1999; Courchamp, Chapuis, & Pascal, 2003; Blumstein & Daniel, 2005; Vitousek, Romero, Tarlow, Cyr, & Wikelski, 2010) that can be easily approached by humans, and/or habituated study populations used to such approaches (Lazaro-Perea et al., 2000; Pozis-Francois, Zahavi, & Zahavi, 2004; Samuni, Mundry, Terkel, Zuberbühler, & Hobaiter, 2014; Huchard, English, Bell, Thavarajah, & Clutton-Brock, 2016; Ridley, 2016; Samson & Manser, 2016; Ashton, Ridley, Edwards, & Thornton, 2018).

The DLW method has been extensively validated across multiple taxa (Congdon, King, & Nagy, 1978; Williams & Nagy, 1984; Schoeller et al., 1986; Speakman & Racey, 1986; Butler et al., 2004; Tomlinson et al., 2013; Speakman & Hambly, 2016), with typical differences of <10% in comparison with simultaneous alternative measures by other methods. Single-sample (SS) methods, in which initial isotope enrichments are determined from a separate control group of dosed animals and blood sampling of study animals is therefore limited to a single final sample (Weathers & Stiles, 1989; Lynn, Houtmann, Weathers, Ketterson, & Nolan, 2000), have also been validated and shown to produce measurements comparable to those obtained with TS procedures (Webster & Weathers, 1989; Speakman, 1997). Moreover, neither blood sampling nor injection of the dose are essential for using DLW to measure energy expenditure. Faecal samples have been used in several studies involving large mammals injected with DLW (Fairall & Klein, 1984; Klein & Fairall, 1986; Gotaas et al., 1997; Williams et al., 1997; Scantlebury et al., 2014) and one study involving birds dosed orally (Anava et al., 2000; Anava, Kam, Shkolnik, & Degen, 2002). Oral dosing and urine sampling are both routine practices in DLW studies involving human subjects (Speakman, 1997; Burrows, Martin, & Collins, 2010). Techniques using oral dosing and faecal sampling of animals in the field require that individuals be uniquely identifiable – for example by transponders, distinctive markings, dye-marks, or tags – and traceable.

In a recent review of the DLW method, Speakman and Hambly (2016) identified faeces as the most feasible non-invasive source of bodily fluids for sampling free-ranging animals, but noted that 1) oral dosing and faecal sampling risks being somewhat 'hit and miss' in the field, and 2) the extent of divergence between measurements derived from blood and faeces had not been investigated. There are only two studies involving direct comparisons between blood and faeces collected simultaneously in the same individuals (Gotaas et al., 1997; Williams et al., 1997). Both studies focused on large mammals injected with DLW (n = 4 Norwegian reindeer *Rangifer tarandus tarandus*, n = 1 aardwolf *Proteles cristatus* respectively), and found that time-matched measurements from blood and faeces were correlated. Oral dosing and faecal sampling have been used concurrently in a field study on two occasions previously (Anava et al., 2000, 2002, n = 78 Arabian babblers *Turdoides squamiceps*; Scantlebury et al., 2014, n = 2 cheetah *Acinonyx jubatus*), and neither study explicitly compared blood and faecal samples within the same individuals.

In this chapter, I report the results of a study that quantified the extent to which measurements derived from blood and faeces diverged in an arid-zone bird, the southern pied babbler *Turdoides bicolor*. Based on measurements in captive and free-living birds, I demonstrate the utility of a non-invasive dosing and sampling approach. To determine the efficacy of the non-invasive technique, doses of DLW were administered in food items to birds temporarily held in captivity and isotopic enrichments were measured in water derived from faecal samples and blood collected concurrently. These values were used to calculate daily energy expenditure (DEE) and compared directly. I tested two predictions: (i) the value of $\frac{\delta^{18}O_i}{\delta^{2}H_i}$ is similar across concurrently collected samples of faeces and blood within individuals, and (ii) derived measurements of DEE for pied babblers are similar when using water from concurrently collected faecal and blood samples within individuals. To ensure that a non-invasive technique is both practically feasible and sufficiently sensitive to detect relationships of biological

interest, I field tested oral dosing and faecal sampling with a habituated, free-living population of pied babblers in the southern Kalahari Desert. As a demonstration, I used data collected in the field to test a third prediction (iii) that measurements derived from faecal samples will detect an inverse relationship between DEE and maximum daily air temperature, expected as both endotherm resting metabolic rates (Scholander, Hock, Walters, & Johnson, 1950; Tomlinson, 2016) and activity levels in free-living birds (Smit & McKechnie, 2015) decline as temperatures rise.

2.3 Materials and methods

2.3.1 Study site and system

Pied babblers (60-90 g) are cooperative breeders endemic to the Kalahari (see Chapter 1). I compared derived measurements from blood and faeces after oral dosing with DLW using birds captured from a wild population near the town of Askham in the southern Kalahari, South Africa (26°58'S 20°46'E). Field-testing of the non-invasive technique took place on and around the 33 km^2 Kuruman River Reserve (KRR) (26°58'S, 21°49'E), approximately 120 km east of Askham (see Chapter 1). Due to the importance of maintaining habituation to human observers for the purposes of long-term study in the study population of pied babblers, repeated capture and confinement of the KRR birds is undesirable. This is why a separate population near Askham was used for the captive component of the study. Fieldwork was undertaken over the two austral summers between September 2016 and February 2018).

2.3.2 Non-invasive dosing and sampling

The DLW solution used contained one part 99.9 atom. % deuterium oxide to five parts 97 atom. % ^{18}O (Sigma-Aldrich, Kempton Park, SA, USA), a dosage based on desired initial enrichments of approximately 1,000 ‰ Vienna Standard Mean Ocean Water (VSMOW) for δ^2H and approximately

400 ‰ VSMOW for $\delta^{18}O$. One batch of DLW was used for all captive individuals and for field study individuals in austral summer 2016/2017, and a second batch was used for all field study individuals in austral summer 2017/2018. A standard dose of ~50 μL was administered to each bird.

Total body water was measured in six pied babblers caught for a separate study at Radnor Farm (26°06'S 22°53'E) in June 2018. An initial 100 μL blood sample was obtained from each bird to establish background isotope ratios, after which 45 μL of DLW was injected into the pectoralis muscle. After 64.4 min (SD = 3.0), a second sample was taken to determine initial enrichment levels. These data were used to calculate total body water from the hydrogen isotope dilution space (Speakman, 1997), which averaged 69.3% (SD = 4.3) of body mass. At an average body mass of 78 g, the 50 μL dose was thus diluted in ~54 ml of body water.

All DLW doses were injected into partially dehydrated darkling beetle larvae *Zophobus morio* and fed to a target bird within one minute of injection, following Anava et al. (2000). Partial dehydration of the larvae prior to injection was required to prevent loss of DLW as a result of hydrostatic pressure within the exoskeleton. Non-fasted captive birds were dosed by force-feeding while in the hand, whereas during the field test doses were presented to habituated individuals on the ground and consumed naturally within one minute of being offered. In all cases, a background faecal sample was collected prior to dosing, an initial enriched faecal sample at least 1 h after dosing, and a final enriched faecal sample as close as possible to 24 h after dosing (captive birds: mean = 23.6 h, SD = 0.5, n = 5; field test: mean = 24.5 h, SD = 2, n = 31). To avoid disrupting active breeding attempts, some captive birds could be held for only short periods and their final samples were collected after approximately 12 h (mean = 11, SD = 0.9, n=3). Between the initial and final samples, I collected many additional faecal samples (described below), all of which were stored in labelled 2 ml plastic vials with silicon O-rings, double-sealed with Parafilm (Bemis NA, Neenah, USA), and refrigerated at 4°C.

2.3.3 Comparing blood and faeces using captive individuals

Eight birds were trapped using a combination of mist-netting off roost at dawn (n = 3) and spring-traps baited with *Z. morio* larvae (n = 5). Birds were transported in drawstring cotton pouches, no more than 20 km from the sites of capture. Although the first two individuals captured were housed in an outdoor aviary, I was able to get much more information relevant to this study by confining individuals in smaller cages. All subsequent birds were therefore housed under shade and exposed to a natural light:dark cycle in purpose-built 40x20x20 cm black shadecloth holding cages with removable Perspex floors. Cages were checked for fresh faeces every 15 minutes, faecal samples collected from the removeable floor, and the floor cleaned and dried thoroughly after the collection of each sample. All individuals were provided with perches and food (mealworms *Tenebrio molitor* larvae) *ad libitum*. Pied babblers are arid-zone insectivores that obtain the majority of their free water from their food (Hockey et al., 2005), and the birds were thus not specifically provided with drinking water.

Initial faecal samples were collected from five birds after a 1 h equilibration period (Speakman, 1997; Butler et al., 2004) and from the remaining three after allowing 2 h in case equilibration was slowed by the oral administration of the dose and/or slow emptying of the stomach into the intestine (Levey & Karasov, 1994). Blood samples were obtained by brachial venipuncture using a sterile 26-gauge needle. Background, initial, and final blood samples (< 100 μL per sample) were collected concurrently with faecal samples (mean = 11 min apart, max = 21 min apart), to allow for direct comparison between the two types of sample. All individuals were weighed after blood sampling. At the end of the study all the birds were released without incident at the sites of capture and reintegrated naturally into their groups and territories. No active nests were abandoned during the study.

2.3.4 Field study with free-living individuals

The field study was designed to test the practicality of the non-invasive method with completely free-living birds of the same species, and to generate data with which to address prediction (iii), that the method is sensitive enough to detect a predicted relationship between DEE and air temperature. Baseline faecal samples were collected between 05h28 and 08h48 on the morning of dosing when excreted naturally by the focal bird. DLW doses were administered between 06h30 and 09h30, after collection of the baseline faecal sample. Target individuals were weighed within 20 minutes of first light on both the dosing day and final sampling day (consecutive) to ensure pre-foraging body mass measurements were obtained. Breeding stage was standardised to the incubation period to ensure that birds could be easily located around nests and to avoid the dose being provisioned to young, which are confined to inaccessible nests. Dosed individuals were observed from close range in their natural habitat for all daylight hours between background and final sampling and all observed faeces excreted during this time were collected. I analysed data from 31 birds that were successfully dosed and from which I collected a series of faecal samples over periods of 24 - 36 h. The birds were not handled at any time during the field study.

Air temperature (T_{air}) data were collected from an onsite weather station (Vantage Pro2, Davis Instruments, Hayward, California, USA), logged at ten-minute intervals. Daily maximum T_{air} (T_{max}) were calculated from these data for each observation day. Based on previous research on critical temperatures affecting behaviour in pied babblers (du Plessis et al., 2012; Wiley & Ridley, 2016), I have defined hot days as those on which $T_{max} \geq 35.5°C$.

2.3.5 Laboratory extractions

To extract water from faeces I adapted a technique used for plant material (Priyadarshini et al., 2016) and sediments (S. Woodborne, unpublished data). Faecal samples ($n_{captive}$ = 79, n_{field} = 335) were transferred to glass test tubes and connected to a vacuum extraction line via a cold finger configured to trap water vapour on the outer wall. A circular vacuum manifold with 10 ports allowed simultaneous extraction of multiple samples. The cold finger traps were cooled using liquid nitrogen and subjected to a downstream vacuum of < 10^{-1} mbar. Once samples were completely dehydrated (~2 h), the cold finger traps were removed and rapidly warmed. Thawed samples were transferred to sampling vials for isotopic analysis using glass Pasteur pipettes fitted with a micro bulb assembly. Water was distilled from blood samples (n = 24) by cryogenic vacuum distillation as described by Speakman (1997).

2.3.6 Sample analysis

Serial aliquots of each water sample were analysed using a DLT-100 liquid water isotope analyser (Los Gatos Research, Mountain View, CA, USA) following the procedure described by Smit & McKechnie (2015) with an additional rinse cycle of distilled water before working standards (water samples with known $\delta^{18}O$ and $\delta^{2}H$ values). All data were corrected against working standards and by removing measured baseline values for each individual from all subsequent sample values of $\delta 1^{8}O$ and $\delta^{2}H$.

The physiological basis of the DLW approach is the differential between elimination rates (k, in units of time d^{-1}) of both ^{18}O (k_O) and ^{2}H (k_H), and measurements typically compare the enrichments of initial and final body water samples (Lifson & McClintock, 1966; Speakman, 1997). Because the ^{18}O label is lost via both CO_2 production and water turnover, whereas ^{2}H declines due to only the latter, the rate of CO_2 production (rCO_2) is a function of the difference $k_O - k_H$ in units of time d^{-1}. The calculation of rCO_2 also requires, at a minimum, some knowledge of pool size (N, in mol) into

which the isotopes distribute, most of which is body water: 18.02 g H_2O/mol (Nagy, 1980; Speakman, 1997). Oral dosing can affect the precise dose of isotope solution administered in wild animals, and therefore precludes measurement of *N* by isotope dilution. Thus, for the purposes of this study, total body water as a percentage of mass was measured in a separate control group of pied babblers ($n = 6$) and the average $N = 69.3\%$ used as a constant throughout. This is standard practice in SS DLW methods (Webster & Weathers, 1989; Speakman, 1997; Lynn et al., 2000).

CO_2 production can be calculated from the body water pool and the rate of decline of the natural log of the ratio of $\frac{\delta^{18}O}{\delta^{2}H}$ (Nagy & Costa, 1980; Speakman, 1997). Here I used a measured initial value, $\ln(\frac{\delta^{18}O_i}{\delta^{2}H_i})$, along with each animal's measured log ratio of final enrichments, $\ln(\frac{\delta^{18}O_f}{\delta^{2}H_f})$, and a mass-specific estimate of N, to calculate rCO_2. When the same dosing solution is used on all animals, the initial log ratio, $\ln(\frac{\delta^{18}O_i}{\delta^{2}H_i})$, is independent of body mass and of the exact dose administered across study individuals (Speakman, 1997). Although I collected multiple faecal samples from each individual (Fig. 2.1), and the multiple-sample DLW method (Speakman, 1997; Speakman et al., 2001) could be applied, I used the TS method to calculate turnover, as recommended by Speakman and Racey (1986), and the single-pool model recommended for animals smaller than 4 kg (Speakman, 1997). I used Speakman's (1997) Equation 17.7 (see eq. 2.1 below) for calculations of rCO_2 in mol d^{-1} because empirical testing has shown this equation to be the most accurate (Visser, Boon, & Meijer, 2000) and based on the most realistic assumptions of fractionation during evaporation (Butler et al., 2004; Speakman & Hambly, 2016):

$$rCO_2 = \left(\frac{N}{2.078}\right)(k_O - k_H) - 0.0062 * k_H * N \qquad \text{(eq. 2.1)}$$

where N is moles of body water and values of k represent turnover of an isotope identified by the subscript. The divisor of N (2.078) accounts for the fact that each molecule of CO_2 expired removes two molecules of oxygen from the pool and, with the inclusion of the last term ($0.0062 \bullet k_H \bullet N$), reflects a correction for fractionation. Omitting this correction causes an overestimate of rCO_2 of ~ 3% in pied babblers (see also Anava et al. 2000). I calculated k_H in the final term of eq. 2.1 based on change in $\ln(\delta^2H)$ between maximally enriched faecal samples collected at early time points and final samples, where t is time (in days) elapsed between early and final samples:

$$k_H = \frac{\ln[\delta^2 H_{1-max}] - \ln[\delta^2 H_f]}{t} \qquad \text{(eq. 2.2)}$$

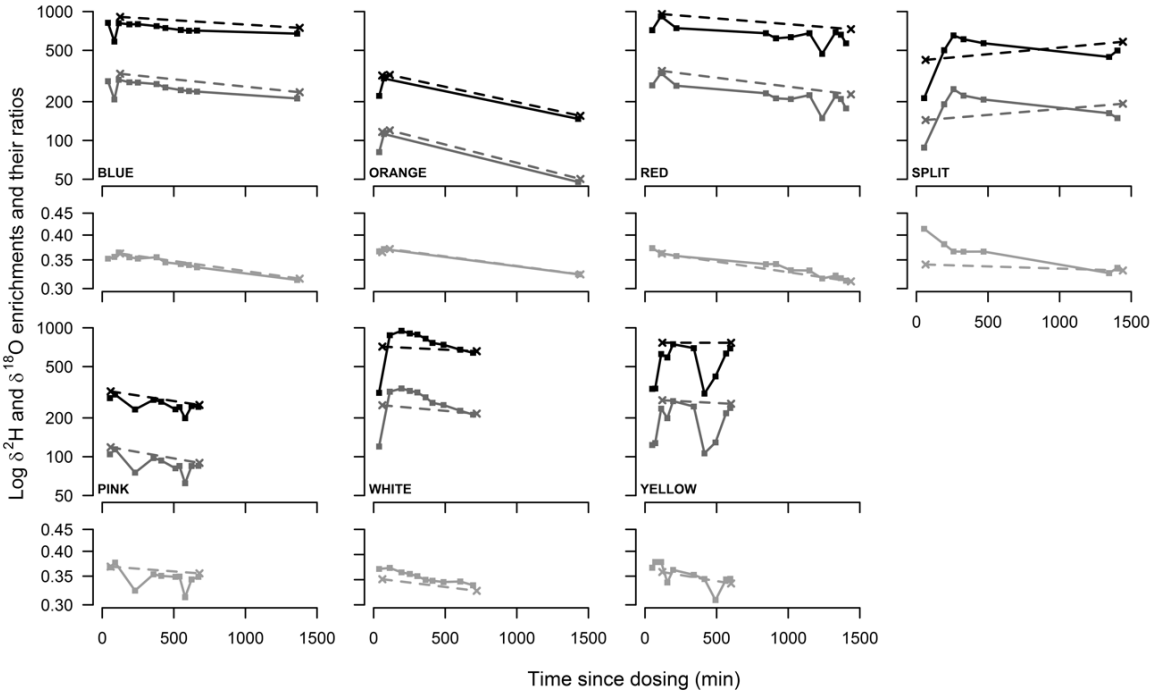


Figure 2.1: Values for δ^2H and $\delta^{18}O$ enrichment levels, and the values of $\delta^{18}O/\delta^2H$, in seven captive southern pied babblers Turdoides bicolor. *Although I only collected three blood samples per individual (of which two are shown – initial enriched and final enriched samples; crosses connected by dashed lines), I collected multiple faecal samples for each bird (filled squares connected by solid lines). Labels (e.g. "PINK", "WHITE") refer to the colour ring given to the individual bird. There were unexpected instances in which faecal water enrichment showed transient declines in both $\delta^{18}O$ and δ^2H (examples in most individuals but see birds "RED" and "YELLOW" particularly).*

Values of $(k_O - k_H)$ can be calculated from the rate of decline of $\ln(\frac{\delta^{18}O_i}{\delta^2H_i})$, (Nagy & Costa, 1980; Speakman, 1997):

$$(k_O - k_H) = \left(ln\left[\frac{\delta^{18}O_i}{\delta^2H_i}\right] - ln\left[\frac{\delta^{18}O_f}{\delta^2H_f}\right]\right) * \left(\frac{1}{t}\right) \qquad \text{(eq. 2.3)}$$

where $\delta^{18}O_i$ and δ^2H_i are the initial $\delta^{18}O$ and δ^2H values in faeces or blood, and $\delta^{18}O_f$ and δ^2H_f are the final $\delta^{18}O$ and δ^2H values. Using this format, ($k_O - k_H$) can be calculated even if dosing has been inconsistent among individuals, because all animals dosed with the same labelled water solution will share a similar initial $\ln(\frac{\delta^{18}O_i}{\delta^2H_i})$. Any minor variation among individuals in $\frac{\delta^{18}O_i}{\delta^2H_i}$ will result from interindividual variation in the distribution space for the two isotopes (Speakman, 1997). The most reliable measurements of ($k_O - k_H$) are made between one and two biological half-lives ($t_{1/2}$) of the isotopes (Nagy, 1980).

For both captive and free-living birds, $\dot{r}CO_2$ was converted from mol d^{-1} to L d^{-1} using the conversion factor 22.4 L of ideal gas per mol at standard temperature and pressure, and L CO_2 d^{-1} was converted to kJ d^{-1} using the relationship 27.4 kJ L^{-1} CO_2 for an insectivorous bird (Gessaman & Nagy, 1988). The metabolic rate calculated from $\dot{r}CO_2$ is subsequently referred to as daily energy expenditure (DEE).

All measurements of DEE were normalised to 24 h and corrected for body mass changes during the measurement period (Speakman, 1997). Derived measurements were compared with estimated basal metabolic rate (BMR) for a 70 g bird using the phylogenetically-independent regression equation presented by McKechnie & Wolf (2004). I expected biologically reasonable estimates of DEE to approximate 2-3 x BMR – see Drent and Daan (1980) and Nagy (2005) – and not fall below BMR or exceed 5 x BMR (Hammond & Diamond, 1997). I compared derived measurements with

estimates of DEE for a congeneric arid-zone species, *T. squamiceps* (Anava et al., 2000), to confirm that measurements fell within the range expected on the basis of comparable studies.

2.3.7 Statistical analyses

All statistical analyses were conducted in R v 3.4.1 (R Core Team, 2017). To check agreement across measurements of DEE from the two sample types, I used the Bland-Altman mean-difference method (Bland & Altman, 1987; Lehnert, 2015), taking the average of measurements per individual by each sample type against the difference between the two measurements. In exploring the relationship between DEE and T_{max}, I used both simple linear regression and one-way ANOVA in order to demonstrate that the data can be applied to questions around the effect of a predictor variable of interest.

The initial value of $\frac{\delta^{18}O_i}{\delta^2H_i}$ for one individual (out of 7), and the DEE measurement for another individual (out of 7), were excluded from statistical analyses of captive birds because of an evident analytical error (based on close inspection of multiple samples per individual) and an amplification of error associated with a short measurement duration (DEE below predicted BMR), respectively. Unlikely initial ratios were also identified for three field study birds (out of 31). In these cases, the average initial $\frac{\delta^{18}O_i}{\delta^2H_i}$ for other birds sampled close together in time was used to calculate DEE. Uncertainty around final $\frac{\delta^{18}O_f}{\delta^2H_f}$ values was detected in four individuals (out of 31) in the field study (again based on close inspection of multiple final samples per individual). In these four cases, an average of the measured final $\frac{\delta^{18}O_f}{\delta^2H_f}$ values for that individual was used.

2.4 Results

2.4.1 Comparing blood and faeces using captive individuals

In the captive birds, values of $\frac{\delta^{18}O}{\delta^{2}H}$ in water from faeces closely matched those in water from blood from the first to the last blood sample (n=6; Fig. 2.2A). The mean difference for six time-matched initial values of $\frac{\delta^{18}O}{\delta^{2}H}$ measured in blood and faeces was -0.007 ± 0.009 (paired t-test: t_5 = -1.495, p = 0.195), with a corresponding mean difference of -0.001 ± 0.005 for seven final values (paired t-test: t_6 = -0.698, p = 0.511), see Fig. 2.2C. Also, as expected, initial values of $\frac{\delta^{18}O_i}{\delta^{2}H_i}$ were very similar across individuals (coefficient of variation, CV [=S.D./mean] < 0.02 in both blood and faecal samples; Fig. 2,2B), and the initial values of $\frac{\delta^{18}O_i}{\delta^{2}H_i}$ in body water approximated the measured value for the injectate (mean = 0.3613, CV = 0.01, n = 4). The average measured initial $\frac{\delta^{18}O_i}{\delta^{2}H_i}$ values for both faeces (mean = 0.3676, CV = 0.01, n = 6) and blood (mean = 0.3628, CV = 0.02, n = 6), all of which were collected between 1 and ~ 2 h of dosing, fall within the 99% confidence interval of the injectate mean (Fig. 2.2A and 2.2B). The constancy of the initial values of $\frac{\delta^{18}O_i}{\delta^{2}H_i}$ across individuals was striking, particularly considering that three of the seven individuals received less than 75% of the intended dose, as indicated by lower initial than expected initial values of $\delta^{18}O$ and $\delta^{2}H$. This result is consistent with theory that the initial ratio $\frac{\delta^{18}O_i}{\delta^{2}H_i}$ is robust to variation in equilibration time and total dose, and approximates the $\frac{\delta^{18}O_i}{\delta^{2}H_i}$ value of the injectate solution (Speakman, 1997).

Most values for faecal samples collected between the initial and final samples fell along an expected general log-linear decline of the $\frac{\delta^{18}O}{\delta^{2}H}$ against time since dosing (Fig. 2.2A). Four values (out

of 62, see pink and yellow lines on Fig. 2.2A) fell well below the general pattern, but without replicated measures I was not able to determine whether these reflected analytical errors or some other factor. These deviations ('transient declines') occurred between initial and final sampling and did not affect my calculations using the TS method. It is theoretically consistent and methodologically confirming that fitting the log-linear decline of $\frac{\delta^{18}O}{\delta^{2}H}$ against time for each individual using all available faecal samples and estimating $\frac{\delta^{18}O}{\delta^{2}H}$ at 2 h after dosing produces an average estimated $\frac{\delta^{18}O}{\delta^{2}H}$ at 2 h of 0.3568 ± 0.0111 (n = 7; mean = 0.3591 if the four deviant points are omitted). Again, these linear regression estimates of $\frac{\delta^{18}O}{\delta^{2}H}$ at 2 h are similar to each other, to those calculated directly from initial samples, and to the measured $\frac{\delta^{18}O}{\delta^{2}H}$ in four dilutions of the injectate solution.

The use of $\frac{\delta^{18}O}{\delta^{2}H}$ values proved a powerful diagnostic tool and I was able to identify likely analytical errors on the basis of clearly unusual $\frac{\delta^{18}O}{\delta^{2}H}$ values. For example, visual inspection of Fig. 2.2B reveals likely analytical errors in the initial samples for the individual coded in green. Excluding this individual, 92% of initial $\frac{\delta^{18}O_i}{\delta^{2}H_i}$ values fall within the 99% confidence interval for the injectate.

Estimates of DEE averaged 1.51 ± 0.31 kJ g^{-1} d^{-1} for captive babblers, equivalent to ~2.7 x BMR and within ~2% of Anava et al.'s (2000) estimates for the congeneric *T. squamiceps* (Fig. 2.3A). Within-individual estimates of DEE derived from blood samples differed from those derived from faecal samples in the captive birds by ~ 4.6 ± 3.6% (n = 6, range = 0.5% to 10%), a small and nonsignificant difference (paired t-test: t_5 = 0.425, p = 0.688), see Fig. 2.3A. The mean difference between measurements derived from blood and from faeces was 0.017 kJ g^{-1} d^{-1} (95% CI -0.086 - 0.120), and the limits of agreement are small enough (-0.175 and 0.209 kJ g^{-1} d^{-1}) to be confident that the two sample types can be used interchangeably to calculate DEE (Fig. 2.3B). After 12 h, 20 ± 10%

of $\delta^{18}O$ had been eliminated (n = 3, range 9% to 27%). After 24 h, 41 ± 12% of $\delta^{18}O$ had been eliminated (n = 4, range = 27% to 57%). Precision would be further improved by extending the duration to 48 h, at which time all study animals would have eliminated more than 50% $\delta^{18}O$.

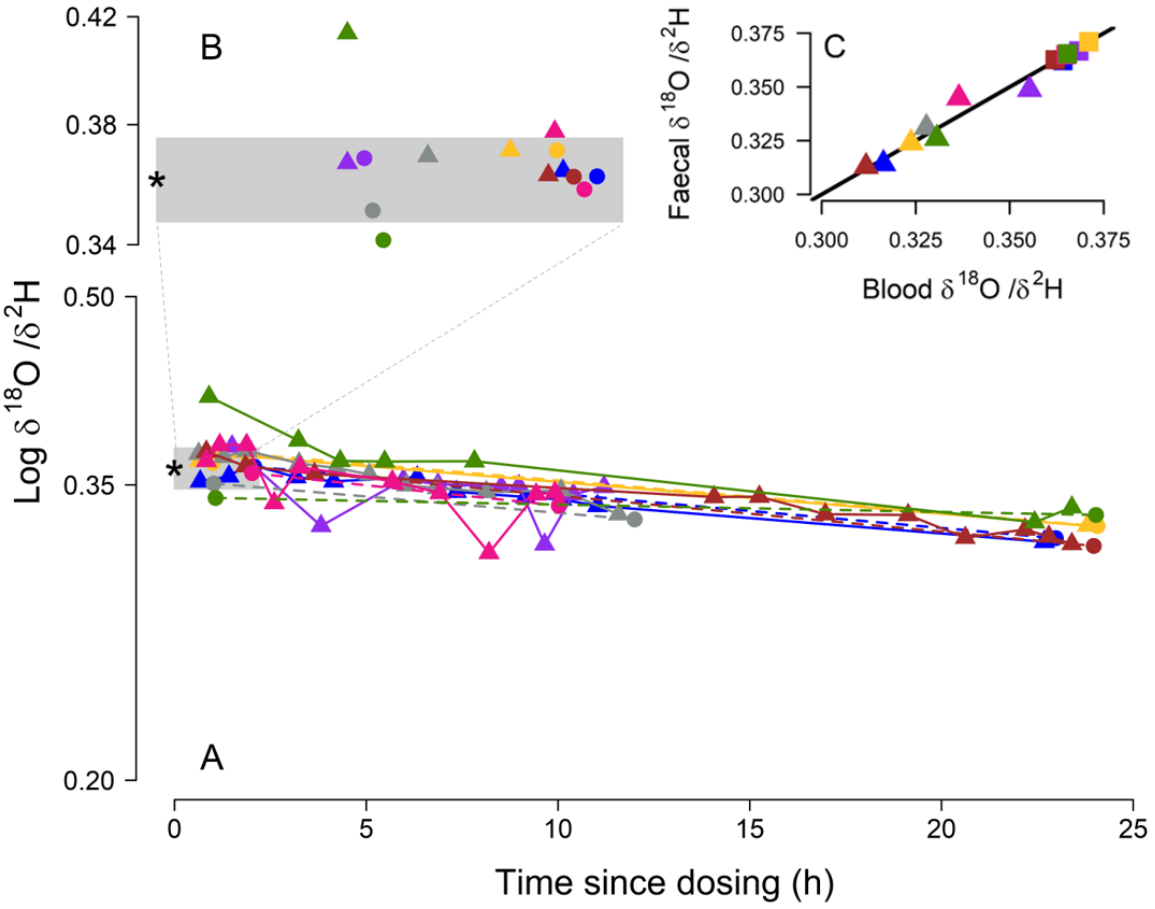


Figure 2.2: Values of $\frac{\delta^{18}O}{\delta^{2}H}$ as a function of time since dosing tracked each other very closely for each of seven captive southern pied babblers Turdoides bicolor *(each individual coded with a unique colour) when sampled from blood (filled circles connected by dashed lines) and faeces (filled triangles connected by solid lines). Values on the y-axes of panel A and B are the ratios $ln(\frac{\delta^{18}O}{\delta^{2}H})$, and in panel C both axes are measured values of $\frac{\delta^{18}O}{\delta^{2}H}$, all of which are unitless. Black stars show the mean value for the labelled water injectate solution, and the lower and upper bounds of the grey rectangles correspond to the 99% confidence interval based on four measurements of the injectate. The left boundary of the grey rectangle is at time = 0 and the right boundary is at time = 2 h, when isotopes are presumed to be fully equilibrated with body water. The upper left inset (B) shows the selection of the data from the first 2 h which, unless otherwise indicated in the text, were used as initial values for calculations of DEE. The upper right inset (C) shows the correlation of blood values with time-matched faecal values for early time points (n = 6, filled squares) and final time points (n = 7, filled triangles). The black line represents the y=x line. Both initial and final samples lie along this line of equivalence, indicating not only high correlation but good agreement between the two sample types.*

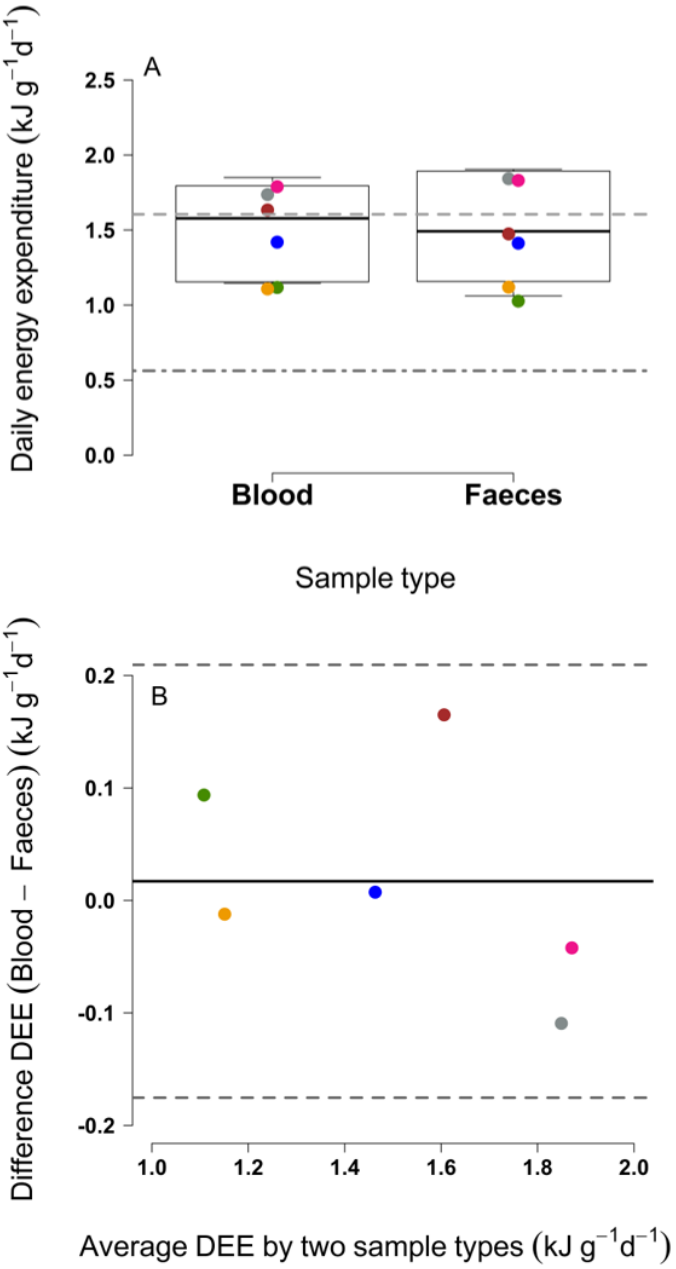


Figure 2.3: Daily energy expenditure (DEE) in kJ g^{-1} d^{-1} averaged 2-3 x basal metabolic rate in six captive southern pied babblers Turdoides bicolor *(each individual coded with a unique colour), irrespective of whether this was calculated using blood or faecal samples (Panel A). The lower dashed and dotted line represents predicted basal metabolic rate for a 70 g bird* (McKechnie & Wolf, 2004) *and the upper dashed line represents mean field metabolic rate in congeneric T. squamiceps* (Anava et al., 2000).*Points have been jittered to improve visibility. Measurements of DEE, derived from concurrent blood and faecal samples from captive birds, were very similar within individuals (Panel B). Differences averaged .0.016 kJ g^{-1} d^{-1} (solid black line, Panel B) and fell well within two standard deviations of the mean (upper and lower grey dashed lines in Panel B). Disagreement between measurements derived from faeces and from blood did not exceed 10%.*

2.4.2 Field study with free-living individuals

In the field it was not possible to control the timing of sampling, and faecal samples were collected as they were naturally excreted by the birds. Initial samples were collected from 31 birds 2.3 h (±1.8 h) after dosing. Seven of the 31 individuals analysed here did not receive the full intended dose, indicated by lower than expected initial values of $\delta^{18}O$ and $\delta^{2}H$. As with captive individuals (demonstrated above), initial values of $\frac{\delta^{18}O}{\delta^{2}H}$ in faecal samples from the free-living birds approximated the injectate solution and were not affected by equilibration times or dose volumes. Isotopic enrichment data for each individual bird in the field study revealed very similar patterns to those in the captive birds, with $\frac{\delta^{18}O}{\delta^{2}H}$ values showing the expected log-linear declines over time between initial and final samples (Table 2.1). Consecutive samples for most individuals included instances where $\delta^{18}O$ and $\delta^{2}H$ enrichment levels declined transiently.

Estimates of DEE for free-living pied babblers averaged 1.62 ± 0.57 kJ g^{-1} d^{-1} (n = 31), equivalent to ~2.8 x BMR and within ~3% of Anava et al.'s (2000) estimates for free-living, congeneric *T. squamiceps* (Fig. 2.4). I found no evidence that estimates of DEE derived using this non-invasive technique in the field differed from those derived using faecal samples from captive individuals (difference between means = 6%, Mann-Whitney-Wilcoxon U = 85, $n_{captive}$ = 6, n_{field} = 31, p = 0.763), or blood samples from captive individuals (difference between means = 7%, Mann-Whitney-Wilcoxon U = 86, $n_{captive}$ = 6, n_{field} = 31, p = 0.794).

Table 2.2: Measurements of DEE from faecal samples in the field study birds

Bird	Mass	Deuterium		Oxygen		Ratio		DEE	x BMR
	(g)	$\delta^2H_{i\text{-}max}$	δ^2H_f	$\delta^{18}O_{i\text{-}max}$	$\delta^{18}O_f$	$\delta^{18}O_i/\delta^2H_i$	$\delta^{18}O_f/\delta^2H_f$	kJ g^{-1} d^{-1}	kJ g^{-1} d^{-1}
1	82.8	755.578	392.755	245.713	113.956	0.325	0.290	1.299	2.312
2	77.5	603.398	387.039	182.605	108.241	0.319	0.279	1.509	2.685
3	75.3	413.859	291.112	161.700	113.675	0.435	0.390	1.205	2.143
4	78.8	598.684	485.294	161.607	110.898	0.269	0.229	2.068	3.678
5	76.5	360.771	310.675	124.681	100.226	0.346	0.323	0.747	1.328
6	80.5	776.617	596.737	281.552	193.387	0.356	0.324	1.016	1.808
7	76.8	624.989	510.088	221.364	169.438	0.354	0.332	0.660	1.175
8	73.4	696.874	506.615	257.315	160.585	0.369	0.317	1.744	3.103
9	80.4	285.499	195.114	112.759	68.9301	0.395	0.353	1.276	2.270
10	88.6	302.934	205.970	119.905	73.5549	0.396	0.357	1.110	1.975
11	80.2	294.797	207.892	109.147	72.3528	0.400	0.348	1.539	2.738
12	83.7	647.444	480.305	235.440	157.112	0.370	0.327	1.381	2.457
13	75.4	811.874	604.305	228.646	139.456	0.269	0.231	1.396	2.482
14	80.2	941.559	552.909	263.122	117.746	0.279	0.213	2.951	5.249
15	82.9	1201.291	823.414	333.670	186.344	0.278	0.226	2.199	3.912
16	76.6	743.718	585.792	191.924	122.118	0.272	0.208	2.754	4.899
17	86.8	824.191	521.355	217.820	119.959	0.278	0.230	1.963	3.491
18	82.2	747.755	540.810	200.560	121.736	0.268	0.225	2.035	3.621
19	74.9	973.344	624.802	258.942	132.857	0.273	0.213	2.774	4.934
20	73.9	1198.200	823.963	324.005	199.251	0.270	0.242	1.183	2.103
21	68.5	796.020	495.543	227.763	117.332	0.299	0.237	2.503	4.452
22	75.1	835.367	514.426	231.414	123.048	0.277	0.248	1.333	2.371
23	74.6	1082.639	511.375	319.689	122.376	0.293	0.246	1.579	2.808
24	70.8	947.788	507.398	273.586	120.719	0.289	0.238	1.893	3.367
25	76.6	897.914	542.205	264.669	138.588	0.289	0.256	1.352	2.406
26	81.3	964.749	577.970	274.847	143.122	0.285	0.248	1.591	2.831
27	65.9	591.442	385.561	155.878	100.935	0.294	0.262	0.912	1.621
28	76.2	865.283	414.918	256.616	98.176	0.297	0.249	1.711	3.044
29	59.7	1212.348	547.597	357.152	121.105	0.295	0.245	1.854	3.298
30	77.7	920.614	532.292	258.664	139.415	0.295	0.262	1.367	2.432
31	70.4	935.574	653.559	275.643	166.960	0.295	0.255	1.271	2.261

I obtained DEE measurements for days varying in T_{max} from 20.7°C to 38.8°C. I found that DEE was significantly negatively related to T_{max} (Est = - 0.07, $F_{1,29}$ = 14.72, $p < 0.001$, conditional R^2 = 0.553; Fig. 2.4). With the data categorised according to the known critical temperature for pied

babblers (du Plessis et al., 2012; Wiley & Ridley, 2016), average DEE was 0.56 kJ g^{-1} d^{-1} lower on hot days ($T_{max} \geq 35.5°C$; mean = 1.36 ± 0.36 kJ g^{-1} d^{-1}, $n = 17$) than on cool days ($T_{max} < 35.5°C$; mean = 1.94 ± 0.65 kJ g^{-1} d^{-1}, $n = 14$; One-way ANOVA, $F_{1,29} = 9.333$, $p = 0.005$). This represents a ~30% reduction in mean DEE on hot days. After 24 h, 42 ± 7% of $\delta^{18}O$ had been eliminated ($n = 31$, range 20% to 66%). In two individuals re-sampled at 72 h, 88% of $\delta^{18}O$ had been eliminated. Ideally, final sampling would occur after 48 h, by which time the majority of study animals would have eliminated more than 50% $\delta^{18}O$.

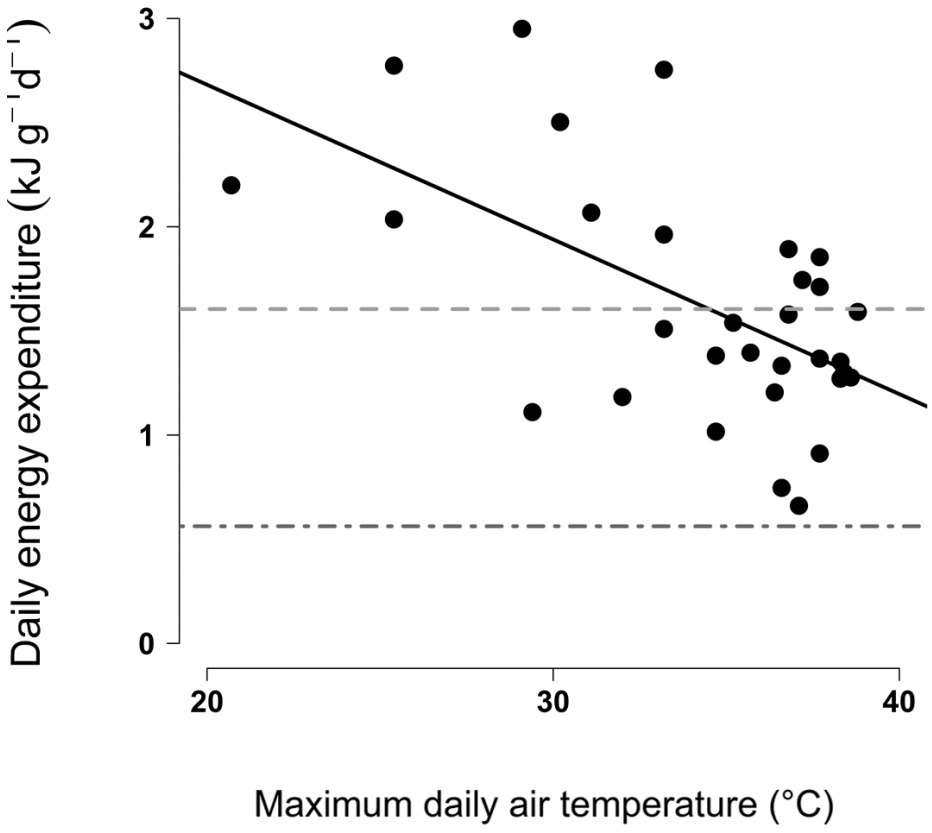


Figure 2.4: Daily energy expenditure (DEE) of southern pied babbler Turdoides bicolor *individuals as a function of T_{max} (maximum daily air temperature) for all data collected in the field (n=31), showing a linear regression (solid black line). The lower, dark grey, dashed and dotted line represents predicted basal metabolic rate for a 70 g bird* (McKechnie & Wolf, 2004) *and the upper, light grey dashed line represents mean field metabolic rate in congeneric* T. squamiceps (Anava et al., 2000).

2.5 Discussion

2.5.1 Non-invasive doubly labelled water method

By directly comparing isotopic enrichment, elimination rates, and derived measurements of DEE from concurrently-collected faecal and blood samples within individual birds, I have demonstrated that a non-invasive DLW technique using oral dosing and faecal sampling can produce measurements of $\ln(\frac{\delta^{18}O}{\delta^{2}H})$ and of DEE that 1) substantially agree between blood and faeces, and 2) are sufficiently sensitive to detect meaningful patterns in DEE. These results support my predictions, that (i) $\frac{\delta^{18}O}{\delta^{2}H}$ is constant across samples of both faeces and blood within individuals (Fig. 2.2B) and (ii) measurements of DEE, derived from concurrent blood and faecal samples from captive birds, agree within individuals (Fig. 2.3A). These findings address the issue raised by Speakman and Hambly (2016), that the extent to which derived measurements from faecal samples diverge from more traditional applications of the method using blood samples was not known.

My finding that $\frac{\delta^{18}O}{\delta^{2}H}$ values in blood and faecal water are so similar to each other and, in initial samples, to the injectate solution, is an empirical finding of high practical importance for effectively using oral dosing and faecal sampling in the field for non-invasive measurements of energy expenditure by isotopic turnover. This is because a core element of the calculation of CO_2 production is the difference between turnover rates of $\delta^{18}O$ and $\delta^{2}H$ (k_O-k_H), which can be calculated from the slope of the decline of $\ln(\frac{\delta^{18}O}{\delta^{2}H})$ against time since dosing (see eq. 2.3). Calculating CO_2 production using these ratios is useful for field applications of non-invasive DLW, which can indeed be somewhat 'hit and miss' in terms of optimal dosing and sampling (Speakman & Hambly, 2016). The ratios are robust to individual variation in equilibration times and total dose consumed, factors over which

researchers have limited control in the field. Administration of a DLW dose establishes an initial value of $\frac{\delta^{18}O}{\delta^{2}H}$ that will approximate that of the injectate solution because naturally occurring background levels of both isotopes are negligible. This value of $\frac{\delta^{18}O}{\delta^{2}H}$ in the body water pool declines over time, providing a measure of the quantity (k_O-k_H) irrespective of differences in individual equilibration times or dose volumes.

Comparing estimates of DEE in pied babblers with both the BMR expected for a 70 g bird and estimated DEE in a congener (Fig. 2.4), revealed that measurements were within the expected range. In combination with within-individual comparisons of measurements derived from blood and faeces, field application measured the effect of daily T_{max} on DEE. A negative relationship between DEE and T_{max} is expected on the basis of both the decreases in endotherm resting metabolic rates with increasing ambient temperatures (Scholander et al., 1950; Tomlinson, 2016), and reductions in activity during hot weather (Smit & McKechnie, 2015). Both foraging efficiency (du Plessis et al., 2012) and provisioning rates to nestlings (Wiley & Ridley, 2016) decline in pied babblers at daily $T_{max} \geq$ 35.5°C, suggesting reduced activity levels at higher temperatures. I therefore predicted an inverse relationship between T_{max} and DEE in pied babblers (prediction iii, expressed in the introduction to this chapter) and found that DEE was inversely associated with daily maximum temperature, as expected based on other studies using traditional DLW methods (Anderson & Jetz, 2005; Smit & McKechnie, 2015; Cooper et al., 2019). Thus, field application of the non-invasive technique is certainly sensitive enough to detect relationships between DEE and predictor variables that might be expected to influence energy expenditure in animals, such as environmental variables (Klein & Fairall, 1986; Jan-Åke Nilsson, Molokwu, & Olsson, 2016), and to detect differences in DEE between cohorts of individuals. This result strongly suggests that a non-invasive technique involving oral dosing and

faecal sampling provides measurements of CO_2 production that reflect real biological variation in DEE.

Field-testing the technique with habituated study animals was useful for demonstrating that many of the practical challenges associated with applying the non-invasive method in the field referred to by Speakman and Hambly (2016) can be overcome. Because the birds in the KRR study population are individually marked and habituated (Ridley & Raihani, 2007b; Ridley, 2016), a specific bird can be targeted for feeding a food item, its body mass can be obtained without handling it, and faecal samples can be collected within one minute of excretion. The arid environment meant that collecting faecal samples unaffected by environmental water was possible most of the time, as the faeces were excreted onto dry sand. The fact that pied babblers are primarily terrestrial foragers in open savanna (Ridley, 2016) enabled the relatively straightforward collection of faeces from the ground. Due to the nature of the study system, I was able to implement a particularly data-rich version of the technique. I collected multiple initial and final samples and used these to identify maximally enriched samples, analytical errors, and final samples with confidence (Fig. 2.2A).

A duplication of the methods presented here is probably feasible only with another habituated study population in a relatively open habitat. However, a truncated version of the same approach has potential application in other types of study systems. The minimum requirements for the technique are that researchers should be able to target a particular individual for dosing, dose fairly quickly to minimise the risk of fractionation, and find the same individual again to collect a final faecal sample. Multiple samples are not necessarily required. I have demonstrated that the TS method will suffice in most cases. A SS method could even be used to calculate DEE, estimating initial $\frac{\delta^{18}O}{\delta^{2}H}$values from other individuals or even from the injectate solution if it is only possible to collect a single final sample. In systems where the study animals are not habituated, but researchers would still like to reduce

disturbance while measuring DEE, the dose could be administered to the study animal in a bait, feeder, or dart and a faecal sample collected some time later, after one or two $t_{1/2}$ of the isotope. If observing the dosing is impossible, cameras could be placed at bait sites to record which individuals ingested the dose. Ingestion of the dose from bait will work (Scantlebury et al., 2014) even if the whole dose is not consumed (provided there is a reasonable chance that the targeted study animal will consume it quickly) because (k_O-k_H) can be calculated and compared even if dosing has been inconsistent among individuals - all individuals dosed with the same labelled water solution will share a very similar initial $\frac{\delta^{18}O}{\delta^{2}H}$ value, related to the $\frac{\delta^{18}O}{\delta^{2}H}$ value of the injectate, regardless of the volume of their particular dose.

2.5.2 Limitations of the technique

Oral dosing is not ideal for ensuring that known, or intended, quantities of isotope enter the study animal, and this was apparent here as substantial variation among individuals in initial, equilibrated enrichments of $\delta^{18}O$ and $\delta^{2}H$ (see Table 2.1). These were lower than expected in several of the study animals in both the captive and field studies. In the SS method, initial enrichments are typically measured from a separate sample of additional individuals. As I have shown above, one could also estimate initial enrichments based on known quantities of the injectate solution if absolutely necessary. Values of $\frac{\delta^{18}O}{\delta^{2}H}$ are insensitive to volumes of isotope ingested, as they reflect the relationship between the two isotopic tracers regardless of volume. Absolute certainty about the initial dose is, therefore, not a prerequisite for calculations of metabolic rate.

However, some certainty about the initial dose is required for the measurement of the body water pool (N) by isotope dilution. Due to uncertainty about initial doses, I was unable to calculate N based on dilution spaces for each individual. I therefore had to apply an estimate of N as a constant in calculations using measurements of body water as a percentage of body mass collected from a

separate control group of individuals injected with DLW. This will have affected the magnitude, and therefore accuracy, of my DEE measurements. For example, scrutiny of eq. 2.1 indicates that if mean body water were 3% lower or higher in an individual than the average I used, then mean DEE would have been about 3% lower or higher than calculated. Note, however, that this follows standard practice in the SS method, where percentage body water by mass is typically measured in a sample of other individuals (Speakman, 1997; Niizuma & Shirai, 2015) and applied as a constant to the study population.

In this study, equilibration time, important for determination of k_H in the fractionation correction in eq.2, was variable, taking between 0.5 h and 4 h. In the field, it was difficult to optimally time collection of initial and final samples because it was necessary to wait for the animal to excrete naturally, resulting in reduced precision. However, varying sample collection times led to small variation in $\frac{\delta^{18}O}{\delta^{2}H}$ values at early time points in the captive birds. Robust calculations of DEE were still possible as long as the interval between the early sample and final sample was long enough (i.e.at least 24 h) for sufficient elimination of the isotopes and hence a decline in $\frac{\delta^{18}O}{\delta^{2}H}$ that is large relative to routine analytical error.

Together, these limitations mean that non-invasive dosing and sampling in the field is best suited for research questions that explore relative differences in energy expenditure between cohorts, for example between sexes (Anava et al., 2000) or sites (Smit & McKechnie, 2015), or that investigate variation in relation to a predictor variable of interest, for example temperature (Cresswell et al., 2004). The method is less appropriate for studies that focus on the precise quantification of energy expenditure for a population or individual animals. The technique is also not suitable for applications in marine and aquatic environments.

The choice of study species and of a 24 h sampling duration was based on my broader research questions seeking to correlate DEE with behaviour patterns in pied babblers over 24 h periods. Whereas I clearly demonstrate that measurements from blood and faeces agree within individuals, and that the method is sufficiently sensitive to detect differences between cohorts, even at 24 h, the precision of measurements of DEE could be improved by extending the time between initial and final sampling. Where measurement durations were substantially shorter than 24 h (in three captive birds), a larger likelihood of error was introduced. The most reliable estimates would be made between one and two $t_{1/2}$ of the isotopes (Nagy, 1980), and this would occur in pied babblers by approximately 48 h after dosing. Due to habituation in the study population, and therefore limitations on my ability to capture and handle the birds, I was not able to compare the non-invasive with the traditional DLW technique in the same individuals in the field. This also resulted in a relatively small sample size for the captive birds.

It is important to note that measurements may be affected by slow equilibration times and/or sampling during a transient decline (see individual "RED", Fig. 2.1). Several initial enrichment and final enrichment samples should be collected and analysed to avoid spurious results caused by sampling during a transient decline.

2.6 Conclusion

The approach described here is likely to be suitable for research questions in which relative measures enable comparison across cohorts of animals, and for research contexts where measuring physiological costs of behavioural activities under natural conditions, avoiding disturbance, and/or maintaining habituation are important. Field applications are limited by constraints on the ability to optimally dose and time sample collection, and the technique is thus not suitable for studies aiming to precisely quantify DEE for an individual or species. The data strongly suggest that measurements of DEE using

a non-invasive technique are feasible, within the limitations that I have identified. The non-invasive technique builds on the benefits of the SS method by measuring energy expenditure in a way that reduces handling and minimises the potential contribution of handling stress to resulting estimates of DEE. It also retains the power of the TS method when both initial and final samples from which to calculate DEE can be collected, and initial values do not need to be estimated. The finding that measurements of $\frac{\delta^{18}O}{\delta^{2}H}$ and DEE agree between blood and faecal samples collected concurrently, particularly for final values $\frac{\delta^{18}O}{\delta^{2}H}$, is potentially very useful to behavioural ecologists who wish to explore physiological correlates of behavioural strategies without disrupting the behaviour of their study organisms to collect these data. DEE can be correlated directly with observed natural behaviour and environmental variables, and I have demonstrated that a DLW technique based on oral dosing and faecal sampling, applied in the field with 31 birds, is sufficiently sensitive to detect the expected inverse relationship between DEE and temperature. Wider application of this technique could open new avenues for assessing behavioural and physiological responses concurrently in wild animals under natural conditions.

CHAPTER 3: High temperatures drive offspring mortality in a cooperatively breeding bird

Preamble

In this chapter, I present an analysis of nest life history and fledgling survival data using the 15-year Pied Babbler Research Project dataset. I show that, while different combinations of weather and social factors influence survival probabilities during each early developmental stage (egg -> nestling, nestling -> fledgling, fledgling -> independent juvenile), exposure to high temperatures reduced survival probabilities during all of these developmental stages. The data from this chapter are published.

Bourne AR, Cunningham SJ, Spottiswoode C, Ridley AR. 2020. High temperatures drive offspring mortality in a cooperatively breeding bird. *Proceedings of the Royal Society B 287: 20201140*

3.1 Abstract

An improved understanding of life history responses to current environmental variability is required to predict species-specific responses to anthropogenic climate change. Previous research has suggested that cooperation in social groups may buffer individuals against some of the negative effects of unpredictable climates. In this chapter, I use a 15-year dataset on a cooperatively-breeding arid-zone bird, the southern pied babbler *Turdoides bicolor*, to test i) whether temperature, rainfall and group size correlate with survival of young during three developmental stages (egg, nestling, fledgling), and ii) whether group size mitigates the impacts of adverse environmental conditions on reproductive success. I found that exposure to high temperatures during early development was associated with reduced survival probabilities of young in all three developmental stages. Impacts of high temperatures were not moderated by group size, a somewhat unexpected result given the predictions of prevailing theory on the evolution of cooperation. Reduced reproductive success at high temperatures has broad implications for recruitment and population persistence in avian communities given the rapid pace of advancing climate change.

3.2 Introduction

Anthropogenic climate change has altered weather patterns in every ecosystem on Earth (Scheffers et al., 2016; Stillman, 2019), with far-reaching consequences for population dynamics across taxa (Spooner et al., 2018). An improved understanding of life history responses to current environmental variability is required to predict species-specific responses to climate change (Conradie et al., 2019). While cooperative breeders occur in diverse habitats (Shen et al., 2017; Lin et al., 2019), comparative research has demonstrated that both cooperatively-breeding birds (Jetz & Rubenstein, 2011) and mammals (Lukas & Clutton-Brock, 2017) occur with disproportionate frequency in regions characterised by high spatial and temporal variability in environmental conditions. This implies that

group living enhances a species' ability to persist in challenging environments (Rubenstein & Lovette, 2007). To date, however, there are few empirical studies that explicitly test the extent to which group living mitigates the effects of climate variability on reproduction (Covas et al., 2008; Langmore et al., 2016; Guindre-Parker & Rubenstein, 2018; van de Ven, Fuller, et al., 2020). None of these studies explore impacts of temperature alongside rainfall and group size, despite evidence of thermoregulatory benefits of group living (Paquet et al., 2016; Mares et al., 2017), and only Covas et al. (2008) consider offspring survival across more than one developmental stage, important because the specific factors influencing survival can differ substantially between early developmental stages (Meade et al., 2010; Mumme et al., 2015; DuRant, Willson, & Carroll, 2019).

Temperature and rainfall patterns are important measures of environmental variability, playing a critical role in the variation in reproductive success observed in vertebrates (Wingfield & Sapolsky, 2003), and recent changes in temperature and rainfall patterns have resulted in adjustments to the timing and success of reproduction in some bird species (Stevenson & Bryant, 2000; McDermott & Degroote, 2016; Wingfield et al., 2017). For birds in arid environments, higher rainfall is often associated with improved reproductive success (Skagen & Yackel Adams, 2012; Hidalgo Aranzamendi, Hall, Kingma, van de Pol, & Peters, 2019), while droughts are usually associated with reduced reproductive success (Conrey et al., 2016; Cruz-McDonnell & Wolf, 2016) and periods of very hot weather are typically associated with lower nest survival rates (van de Ven, 2017; DuRant et al., 2019) and nestling growth rates (Cunningham et al., 2013; Salaberria, Celis, López-Rull, & Gil, 2014). Therefore, it is reasonable to expect that reproductive success and population persistence of birds in arid environments will be impacted as regions become hotter and drier under climate change (Ji, Huang, Xie, & Liu, 2015; Huang et al., 2017).

Cooperative breeding, where more than two individuals rear a single brood (Cockburn, 2002), occurs in ~9% of bird species (Cockburn, 2006). Benefits of cooperation for reproduction include earlier fledging age and more broods raised per season than non-cooperatively breeding species (Ridley & van den Heuvel, 2012); reduced costs of breeding for females (Cockburn et al., 2008; Langmore et al., 2016); enhanced egg investment (Valencia et al., 2016); increased fledging success and fledgling recruitment (Hatchwell, 1999; Canestrari, Marcos, et al., 2008; Meade et al., 2010); and the ability to raise overlapping broods (Ridley & Raihani, 2008; Guindre-Parker & Rubenstein, 2018). Global comparative studies suggest that cooperative breeding evolved in unpredictable environments (Rubenstein, 2011), facilitated the colonisation of such environments (Cornwallis et al., 2017), or prevented extinction under increasingly harsh conditions (Griesser et al., 2017). Specifically, the temporal variability hypothesis suggests that cooperative breeding is adaptive in highly variable environments (Jetz & Rubenstein, 2011) by reducing interannual variation in reproductive success (Rubenstein & Lovette, 2007). This implies that cooperation might buffer breeding attempts from failure during adverse environmental conditions (Covas et al., 2008; Koenig & Walters, 2018). Previous studies have focused on the buffering effect of group size when rainfall is low, and I further hypothesise that temperature may be an important factor underlying cooperative breeding as a reproductive strategy (also see van de Ven, Fuller & Clutton-Brock 2019). Nest attendance (Clauser & McRae, 2017) and provisioning rates to young (Cunningham et al., 2013; Wiley & Ridley, 2016; van de Ven et al., 2019) often decline in response to increasing temperature, with implications for reproductive success (J. M. Carroll, Davis, Elmore, Fuhlendorf, & Thacker, 2015; van de Ven, Fuller, et al., 2020). In larger groups, there are more individuals available to assist with breeding attempts, which can lead to load-sharing amongst individual group members (Ridley & Raihani, 2008; Langmore

et al., 2016) and / or cumulatively greater investment in young (Canestrari, Marcos, et al., 2008; Pike et al., 2019), a potential benefit of group living given unfavourable rainfall or temperature conditions.

In this chapter, I have used a comprehensive 15-year dataset on southern pied babblers *Turdoides bicolor* (hereafter 'pied babblers'), a cooperatively-breeding passerine endemic to the Kalahari in southern Africa, to explore the impacts of temperature, rainfall, and group size on nest success and fledgling survival. Specifically, I have tested for influences of these parameters on survival of 1) eggs, 2) nestlings, and 3) fledglings from 1) initiation of incubation to hatching; 2) hatching to fledging (leaving the nest); and 3) fledging to nutritional independence at 90 days of age (Ridley & Raihani, 2007b). I expected high temperatures to reduce survival, and high rainfall and larger group sizes to enhance survival during each developmental stage. If the presence of helpers buffers the effect of environmental variation on reproduction, as proposed by the temporal variability hypothesis (Rubenstein & Lovette, 2007), then I would also expect an interaction between environmental factors and group size such that weaker impacts of adverse climatic conditions on reproduction would be observed in larger groups.

3.3 Materials and methods

3.3.1 Study site and system

Fieldwork was conducted with a habituated population of individually marked pied babblers at the Kuruman River Reserve (33 km^2, KRR; 26°58'S, 21°49'E) in the southern Kalahari. See Chapter 1 for a detailed description of the study site and study species.

3.3.2 Data collection

Data were collected for each austral summer breeding season from September 2005–February 2019 (14 breeding seasons in total), of which I collected all the data from September 2016 onwards. Each

breeding season was coded with a letter of the modern Latin alphabet e.g. Season C = Sept 2005 – March 2006.

Nest monitoring followed Ridley & van den Heuvel (2012): nests were located by observing nest-building; incubation start, hatch and fledge dates were determined by checking nests every two to three days; breeding attempts were considered to have failed when nests were no longer attended or dependent fledglings were not seen on two consecutive visits; failure dates were calculated as the midpoint between the date of the last pre-fail nest/group check and the date when the nest was no longer attended or the fledgling was missing. In most cases, it was not possible to determine the proximate cause of nest failure or fledgling death (some plausible causes are predation, abandonment, or starvation). Group size (number of adults present in the group, including the breeding pair; range: 2–10, mean = 4.2 ± 1.5) was recorded for each nest incubated. Brood size refers to the number of nestlings in the brood as recorded 11 days post-hatch, when nestlings were ringed. I define early development as the period between initiation of incubation and nutritional independence at 90 days of age (Ridley & Raihani, 2007b). Average time from initiation of incubation to hatching is 14 ± 1.2 days. Average time between hatching and fledging is 15.4 ± 1.7 days.

Nestlings were sexed and weighed to 0.1g at 11 days of age ($Mass_{11}$) and on-site weather data collected as described in Chapter 1. Daily maximum air temperatures were averaged for each developmental stage: incubation (mean T_{maxInc}), nestling (mean $T_{maxBrood}$), and fledgling (mean T_{max90}); and also for the whole early development period from initiation of incubation until independence (mean $T_{maxTotal}$). Rainfall was summed for the 60 days prior to initiation of incubation ($Rain_{60}$), and for the periods between fledging and independence ($Rain_{90}$) and initiation of incubation and independence ($Rain_{Total}$).

3.3.3 Statistical analyses

Statistical analyses were conducted in R v 3.6.0 (R Core Team, 2017). Analyses exclude groups of > 8 individuals due to small sample sizes for groups of 9 (n = 5) and 10 (n = 1) over the 15 years of records. Sensitivity power analyses (Cohen, 1988; Greenland et al., 2016), using the R package *pwr* (Champely et al., 2018), confirmed sufficient sample size to detect a range of effect sizes, from small to large, in all analyses including main effects (all Cohen's $f^2 < 0.03$) and two-way interactions (all $f^2 < 0.12$) – see Table 3.1 below. I tested for temporal trends in environmental (temperature and rainfall) and reproductive (nest success, fledgling survival) parameters using univariate linear models with breeding season as the only predictor.

Table 3.1: Power analyses for the interactions: multiple regression power calculations

Developmental stage	*u*	*v*	*α*	*power*	f^2
Egg					
Main effects	3	492	0.05	0.8	0.019
Interactions	3	123	0.05	0.8	0.080
Nestling					
Main effects	3	341	0.05	0.8	0.029
Interactions	3	85	0.05	0.8	0.118
Fledgling					
Main effects	3	378	0.05	0.8	0.026
Interactions	3	95	0.05	0.8	0.105

*u = model degrees of freedom; v = sample size, α = the significance level, and power (p) = probability of finding an effect that is there; f^2 = measure of determinable effect size (values of ~0.02, ~0.15, and ~0.35 represent small, moderate, and large determinable effect sizes respectively).

Risk of mortality during early development

I conducted an exploratory Cox proportional hazards model (D. R. Cox, 1972) to assess the relationship between overall risk of mortality over time (Austin, 2017) during early development and the following explanatory parameters: mean $T_{maxTotal}$, a quadratic term for mean $T_{maxTotal}$, $Rain_{Total}$, group size, and the interactions between these parameters. Pair tenure (the number of consecutive breeding seasons in which the same dominant breeding pair were present in a group) was also included in the

Cox model. Pairs that stay together longer have higher breeding success (Wiley, 2017) and so it is reasonable to expect that pair tenure may influence mortality risk of young during early development. In order to account for non-independence of data, group identity and year were included as random effects. The Cox analysis expresses mortality risk at each time step as a hazard ratio (HR), where HR > 1 indicates a higher risk of mortality and HR < 1 indicates a lower risk of mortality. Model terms with HR confidence intervals not intersecting one were considered to explain significant patterns within the data.

The Cox analysis was computed in the R package *survival* (Therneau & Lumley, 2009), visualised using the R package *survminer* (Kassambara, Kosinski, Biecek, & Scheipl, 2017), and used to identify general patterns of mortality risk during early development overall for further exploration. I calculated 95% confidence intervals for survival probabilities using the Clopper-Pearson interval (Puza & O'Neill, 2006) which calculates a confidence interval for a proportion that keeps within the limits of (0,1).

Survival probabilities during each developmental stage

Pied babbler survival probabilities are not constant across time during early development (Ridley, 2016), and explanatory variables are unlikely to have precisely the same relationship with survival during all three developmental stages considered here. Therefore, to identify the relative importance of each of the above predictors on survival during each discrete developmental stage, I conducted separate generalised linear mixed effects models (GLMMs) with a binomial distribution (binary response; survived = 1, died = 0) and a logit link function in the R package *lme4* (Bates, Maechler, Bolker, & Walker, 2015). Model selection using Akaike's information criterion corrected for small sample size (AICc) with maximum likelihood estimation was used to test a series of models, each representing a biological hypothesis, and to determine which model/s best explained patterns of

variation in the data. Lower AICc values were taken to represent more parsimonious models, following Harrison et al (2018a). Where several models were within 5 AICc of the top model (Symonds & Moussalli, 2011), top model sets were averaged using the R package *MuMIn* (Barton, 2015). Model terms with confidence intervals not intersecting zero were considered to explain significant patterns in the data (Grueber, Nakagawa, Laws, & Jamieson, 2011).

I tested survival probabilities during incubation and up until fledging at the scale of the clutch or brood, because nestlings were only individually marked at 11 days of age, by which time many nests had already failed. Specifically, I considered the influence of the following parameters on (a) the probability of at least one egg per clutch surviving to hatch, and (b) the probability of at least one nestling per brood surviving to fledge: for (a) group size, $Rain_{60}$, mean T_{maxInc} and all two-way interactions between these variables for (b) group size, $Rain_{60}$, mean $T_{maxBrood}$, and mean $T_{maxBrood}^2$ and all two-way interactions between these variables. I tested survival probabilities between fledging and nutritional independence at the scale of the individual fledgling, including only known individuals with known $Mass_{11}$. Specifically, I considered the influence of group size, $Rain_{90}$, mean T_{max90}, $Mass_{11}$ and all two-way interactions between these variables on the probability of surviving to nutritional independence per individual fledgling. Pair tenure was excluded as it did not significantly influence the response in the above Cox hazards model, which was run first. Clutch/brood size was not considered for inclusion as it was determined 11 days after hatching, and thus not available for the majority of breeding attempts. Group identity and year were included as random effects in all three analyses. Significant interactions were visualised using the R package *interplot* (Solt & Hu, 2018).

Understanding the influence of nestling mass on fledgling survival

Prior research has shown that pied babbler nestling mass is influenced by environmental factors (Wiley & Ridley, 2016) and larger nestling mass is associated with higher survival probability in other bird

species (Kruuk, Osmond, & Cockburn, 2015; Mumme et al., 2015). My GLMM analysis of fledgling survival (described above) indicated that nestling mass was important for predicting fledgling survival. I therefore undertook a confirmatory path analysis (Shipley, 2009; Larson, Sheley, Hardegree, Doescher, & James, 2015) in order to test for indirect effects of environmental factors and group size on survival to nutritional independence via nestling mass, using the R package *piecewiseSEM* (Lefcheck, 2016) which can accommodate multiple error structures and calculates standardised effects sizes across component models. In this analysis I considered survival probabilities of known individuals from fledge to nutritional independence in a single model testing the relative importance of direct effects of environmental and group size factors vs. effects mediated via nestling mass. Path analysis allowed me to specify and simultaneously quantify all hypothesised relationships, including the indirect effects of weather and group size on survival via nestling mass. Path coefficients are partial regression coefficients and can be interpreted similary to simple and multiple regression outputs. While model selection processes can be applied to multiple path analyses (Shipley & Douma, 2019), I was not using path analysis to choose between competing hypotheses and but rather to test a single model. Statistical significance was taken as $p < 0.05$.

I used the path analyses to test the following statistical hypotheses:

Survival would be negatively affected by a) high mean daily maximum temperatures during the nestling and dependent fledgling stages, b) low rainfall between fledging and independence, c) smaller group size, and d) low nestling body mass (logit).

Nestling body mass would be negatively affected by a) high mean daily maximum temperatures during the nestling period, b) low rainfall prior to the nestling period, and c) smaller group size (Gaussian).

Identifying threshold temperatures

It is useful to identify specific temperature thresholds for biological data (such as reproductive success) because these can be used for predictive population or species viability models (*sensu* Conradie et al 2019), providing valuable and actionable information for conservation planning and management. I therefore supplemented the above GLMM and path analyses with a series of segmented linear regressions fit to survival data per breeding attempt, indicating the length of time a breeding attempt persisted during each developmental stage [i.e. the number of days between initiation of incubation and hatch of at least one egg, or failure (age at hatch/fail), the number of days between hatch and fledge of at least one chick, or failure (age at fledge/fail)], and per individual [i.e. the number of days between fledge and survival to nutritional independence or death per fledgling (age at survival/death)]. I used the R package *segmented* (Muggeo, 2008) to identify temperature thresholds ('breakpoints') above which survival was compromised for each developmental stage, fitting simple linear regressions with temperature (mean $T_{maxInc,}$ mean $T_{maxBrood,}$ and mean T_{max90} as appropriate) as the ony predictor for the data above and below the identified breakpoints.

3.4 Results

The total number of days (October–March) exceeding 35.5°C, identified as a critical temperature threshold in pied babblers (du Plessis et al., 2012; Wiley & Ridley, 2016), has increased significantly at the study site since 2005 ($F_{1,12}$ = 7.448, p = 0.018, R^2 = 0.383; Fig. 3.1a). Total summer rainfall (October–March) over the same time period was highly variable and showed a non-statistically significant declining trend ($F_{1,12}$ = 1.616, p = 0.228, R^2 = 0.119; Fig. 3.1b). Both the number of nests fledged per breeding season ($F_{1,12}$ = 3.747, p = 0.077, R^2 = 0.238; Fig. 3.1c) and the number of surviving young produced per breeding season ($F_{1,12}$ = 5.285, p = 0.040, R^2 = 0.108; Fig. 3.1d) have declined at the study site since 2005, despite the number of groups monitored remaining relatively

constant between years (coefficient of variation = 0.17). Most rain falls between December and February (72%), when temperatures are high (Fig. 1e). Most pied babbler breeding activity occurs between October and December (68%), when conditions are generally drier and cooler than later in the season, and breeding after December only occurred in response to rain (Fig. 3.1e).

3.4.1 Risk of mortality during early development

The Cox proportional hazards model showed that mortality risk was a) influenced by a combination of group size, temperature, and rainfall, and b) not consistent for all developmental stages. Risk of mortality was higher for clutches and broods (i.e. while young were still in the nest) than for fledglings (n = 488 breeding attempts over 14 seasons; Fig. 3.2a). High temperatures (HR = 1.145, 95% CI: 1.011 - 1.296, z = 2.139; including the quadratic term for temperature HR = 1.349, 95% CI: 1.275 - 1.426, z = 10.472) were associated with an increased risk of failure (Fig. 3.2b). At mean daily temperatures ≥ 38°C (n = 17), 100% of breeding attempts failed. At the 17 coolest nests, where mean daily temperatures ≤ 28°C, ~ 80% of nests failed. This compares to an optimum temperature of ~34°C (n = 84) at which only 52% of breeding attempts failed. Breeding attempts undertaken by larger groups (HR = 0.699, 95% CI: 0.585 - 0.834, z = -3.980) and during wetter periods (HR = 0.297, 95% CI: 0.236 - 0.373, z = -10.372; Fig. 3.2b) were less likely to fail. When rainfall > 189 mm over the development period (n = 44), 0% of nests failed. Pair tenure (HR = 0.975, 95% CI: 0.859 - 1.107, z = -0.385) and the interactions between temperature and group size (HR = 0.975, 95% CI: 0.891 - 1.066, z = -0.562) and between rainfall and temperature (HR = 0.966, 95% CI: 0.827- 1.129, z = -0.434) were not important for predicting risk of failure of breeding attempts (Fig. 3.2b). From the Cox proportional hazards model, it was not possible to evaluate the relative influence of each significant predictor during each developmental stage, or to determine whether predictors influenced variation in mortality risk in the same way during each developmental stage.

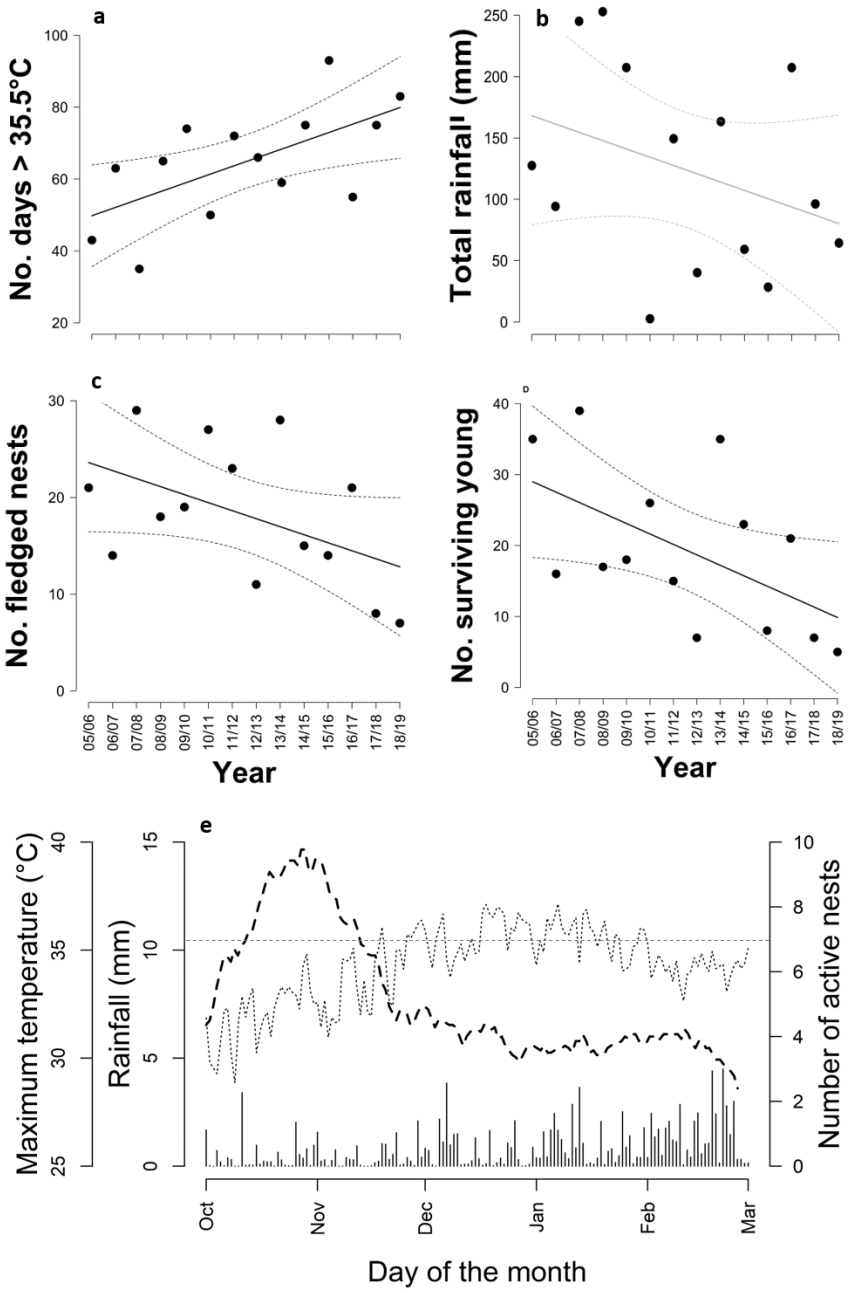


Figure 3.1: (a) the number of days > 35.5°C at the study site (b) total summer rainfall, (c) number of southern pied babbler Turdoides bicolor *nests fledged in the study population, and (d) number of surviving young produced in the study population per breeding season per year (austral summer: 1 Oct to 1 Mar) since 2005 . Black lines represent predictions from the models, and dashed lines the 95% CIs. (e) breeding activity between Oct and Mar (average number of active nests per day: dashed line), relative to temperature (average daily maximum temperature (°C) per day: dotted line) and rainfall (average rainfall (mm) per day: vertical bars). The regression line in (b) is greyed out as the trend shown was not statistically significant. The horizontal gray dotted line in (e) represents the critical threshold temperature of 35.5°C above which pied babblers do not maintain body mass overnight and reduce provisioning effort to nestlings* (du Plessis et al., 2012; Wiley & Ridley, 2016).

Overall, 33.3% of breeding attempts produced at least one fledgling that survived to nutritional independence (95% CI = 31.9 – 34.6%). Mean survival probabilities of young differed between developmental stages (Fig. 3.2c). On average, survival during early development was lower (69.4% of incubated clutches hatched with 95% CI = 67.9 – 70.5%; 61.1% of hatched nests fledged with 95% CI = 59.2 – 62.5%) than after fledging (89.5% of broods that fledged produced at least one fledgling that survived one week with 95% CI = 87.9 – 90.6%; 84.6% of broods that produced at least one week-old fledgling produced at least one independent juvenile with 95% CI = 82.6 – 85.9%).

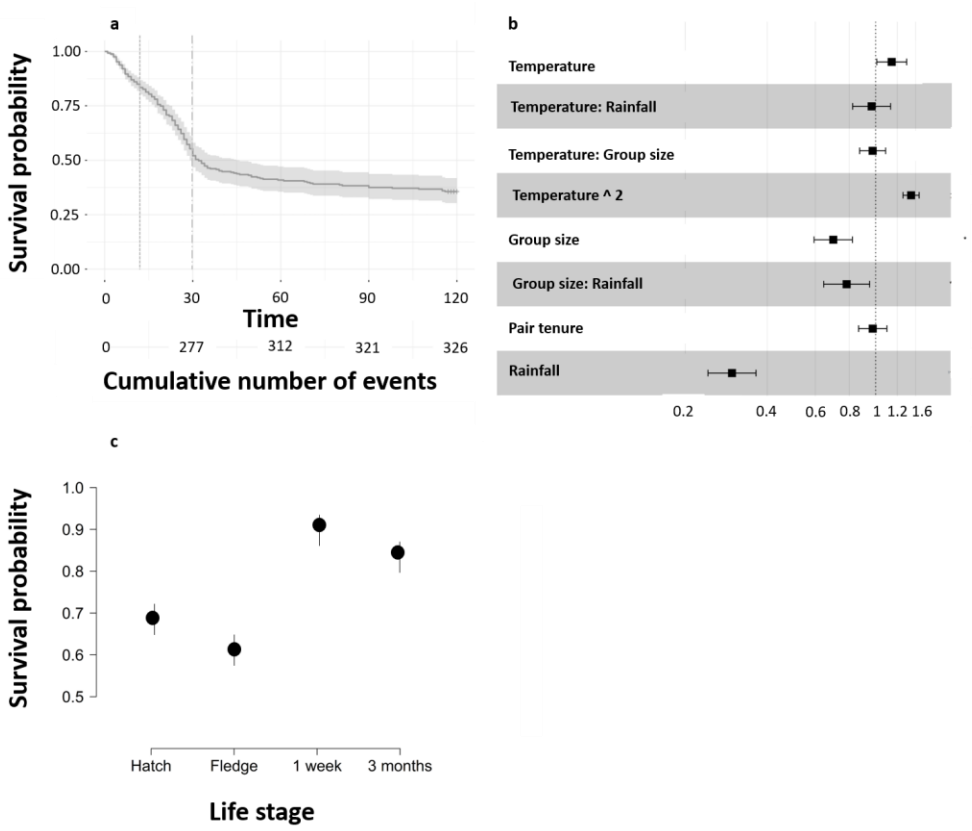


Figure 3.2: (a) the estimated survival probability curve of southern pied babbler Turdoides bicolor *breeding attempts at the mean values of all covariates in the full Cox proportional hazards model between initiation of incubation and hatching (dotted vertical line) and between hatching and fledging (dashed vertical line; n = 488 nests). (b) forest plot showing the hazard ratio and 95% confidence interval for each covariate in the full Cox regression. Covariates with confidence intervals not crossing 1 are considered to explain significant patterns in the data. Hazard ratios above 1 indicate a positive association with probability of dying. (c) mean ± se survival probabilities for each life stage transition: from start of incubation to hatch, from hatch to fledge, from fledge to 7 days of age, and from 1 week of age to nutritional independence at 3 months of age.*

While a significant interaction between rainfall and group size was detected in the Cox proportional hazards model (HR = 0.782, 95% CI: 0.643 - 0.952, z = -2.453), further investigation indicated that this interaction was not robust. Visualisation of the data (Fig. 3.3) suggests that the slopes are similar across group sizes . The observed relationship, that larger groups required less rain than smaller groups in order to breed successfully, is driven primarily by the higher survival of young in very large groups (8 individuals) at low rainfall, and their shallower increase in survival of young as rainfall increased, relative to all other group sizes. Groups with as many as eight adults are unusual, and therefore seldom relevant, in this particular study population. In the dataset used for this chapter, I only found records for eight nests where group size = 8. At group sizes < 8, group size did not appear to influence the relationship between rainfall and survival of young. I therefore concluded that I would need substantial further evidence for an interaction between group size and rainfall in the finer-scale analyses that follow in order to view the observed interaction as providing strong evidence in support of a buffering effect of larger group size.

3.4.2 Survival probabilities during each developmental stage

Of 492 breeding attempts by 50 groups over 14 breeding seasons, 341 hatched. The probability of incubated eggs surviving to hatch decreased as mean daily maximum temperatures during the incubation period increased (Table 3.2, Fig. 3.4a; see Appendix Table 3.1 for full model output). I found no evidence that rainfall or group size, or any interactions between group size and climatic factors, influenced the probability of hatching (Appendix Table 3.1).

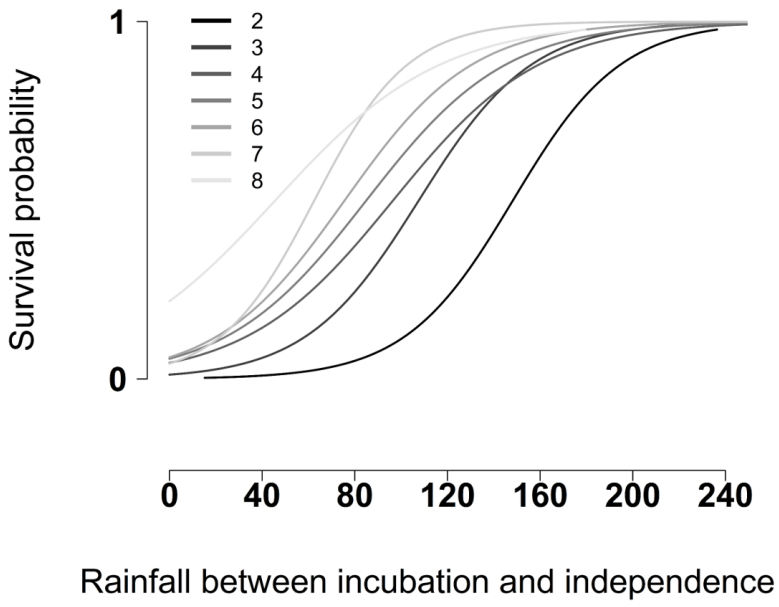


Figure 3.3: There is a main effect of rainfall, with higher survival rates of southern pied babbler Turdoides bicolor *breeding attempts at higher values of rainfall, and a main effect of group size, with higher survival rates of breeding attempts in larger groups, but the interaction effect detected in the Cox proportional hazards model is likely an artifact of the higher survival of breeding attempts in very large groups (8 individuals) at low rainfall, and their shallower increase in survival of breeding attempts as rainfall increased, relative to all other group sizes. Group sizes this large are seldom relevant in this study population (n = 8 over 15 years of monitoring).*

Of 341 hatched nests by 46 groups over 14 seasons, 210 fledged at least one chick. Larger groups were more likely to fledge a chick (Table 3.3, Fig. 3.4b), and the probability of at least one chick fledging increased with increasing mean temperature until ~33.1°C, after which survival probability decreased (Table 3.3). At mean maximum temperatures > 38°C (n=12), no nests fledged. Temperatures reached or exceeded 38°C on 13% of days at my study site in 2005 and 24% of days at my study site in 2018. I found no evidence that probability of fledging was influenced by rainfall or interactions between group size and climatic factors (see Appendix Table 3.2 for full model output).

Table 3.3: Top GLMM model set for factors influencing survival from initiation of incubation to hatching (n = 492 clutches by 50 different groups over 14 breeding season). Model averaging was implemented for models with ΔAICc < 5 of the 'best-fit' model. Significant terms after model averaging are shown in bold. Null models shown for comparison with top model sets.

Model	***AICc***	***ΔAICc***	***ωí***
Null model	606.80	4.96	0.00
Top model set:			
Mean T_{maxInc}	601.84	0.00	0.54
Mean T_{maxInc} * $Rain_{60}$	603.51	1.66	0.23
Mean T_{maxInc} * Natal group size	603.58	1.73	0.23
Effect size of explanatory terms after model averaging	*Estimate*	*SE*	*95% CI*
Intercept	0.861	0.119	0.626/1.096
Mean T_{maxInc}	**-0.270**	**0.101**	**-0.469/-0.072**
$Rain_{60}$	0.003	0.049	-0.095/0.101
Natal group size	0.036	0.084	-0.129/0.201
Mean T_{maxInc} * $Rain_{60}$	0.039	0.087	-0.132/0.210
Mean T_{maxInc} * Natal group size	0.006	0.049	-0.091/0.104
*Residual deviance: 579.716 on 489 degrees of freedom (ratio: 1.186)			

Table 3.3: Top GLMM model set for factors influencing survival from hatching to fledging (n = 341). Model averaging was implemented for models with ΔAICc < 5 of the 'best-fit' model. Significant terms after model averaging are shown in bold. Null models shown for comparison with top model sets.

Model	***AICc***	***ΔAICc***	***ωí***
Null model	456.50	19.90	0.00
Top model set:			
Mean $T_{maxBrood}$ + Mean $T_{maxBrood}$ ^2	439.39	2.60	0.21
Mean $T_{maxBrood}$ + Mean $T_{maxBrood}$ ^2 + Natal group size	436.80	0.00	0.79
Effect size of explanatory terms after model averaging	*Effect*	*SE*	*95% CI*
Intercept	0.861	0.158	0.548/1.173
Mean $T_{maxBrood}$	-0.069	0.120	-0.307/0.167
Mean $T_{maxBrood}$ ^2	**-0.391**	**0.095**	**-0.577/-0.205**
Natal group size	**0.264**	**0.124**	**0.019/0.509**
*Residual deviance: 418.789 on 336 degrees of freedom (ratio: 1.246)			

Of 372 fledglings from 34 groups over 14 seasons, 256 survived to independence. The likelihood of a fledgling surviving to independence increased as rainfall (Table 3.4, Fig. 3.5a) and nestling body mass (Table 3.4, Fig. 3.5b) increased. There was an interaction between average

maximum temperature and rainfall, whereby rainfall was a better predictor of survival to independence at higher mean temperatures than at low mean temperatures (Table 3.4, Fig. 3.5c; see Appendix Table 3.3 for full model output). At mean temperatures > 38°C (n = 8), no fledglings survived to independence. I found no evidence that interactions between group size and climatic factors influenced the probability of surviving to independence (see Appendix Table 3.3 for full model output).

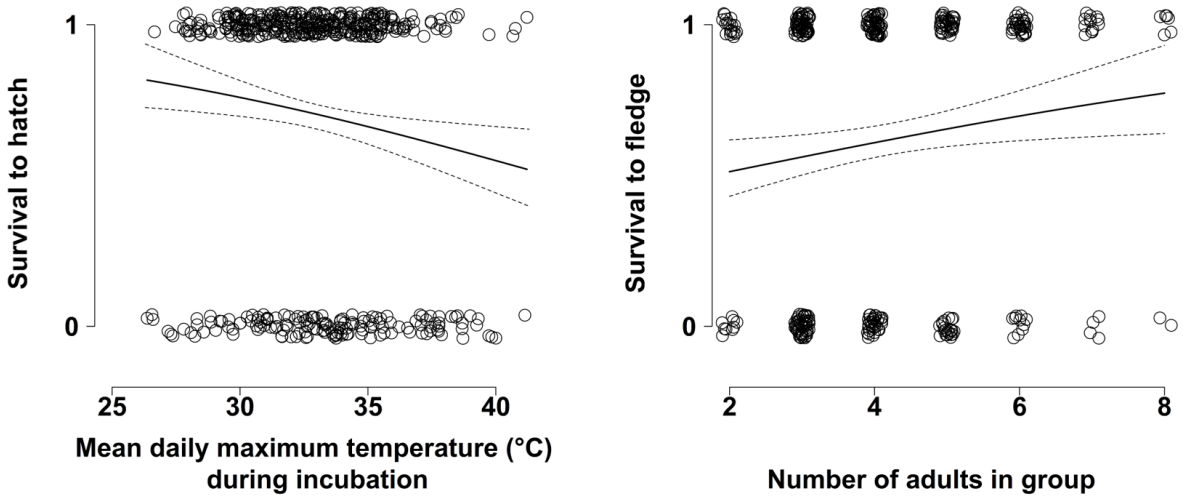


Figure 3.4: (a) survival from initiation of incubation to hatching in southern pied babblers Turdoides bicolor *in relation to mean daily maximum temperatures during incubation (°C); and (b) survival from hatching to fledging in relation to natal group size. Data points are integers (where 1 = survived), jittered for improved visibility.*

Table 3.4: Top GLMM model set for factors influencing survival from fledging to nutritional independence in southern pied babblers Turdoides bicolor *(n = 372). Model averaging was implemented for models with ΔAICc < 5 of the 'best-fit' model. Significant terms after model averaging are shown in bold. Null models shown for comparison with top model sets.*

Model	***AICc***	***ΔAICc***	***ωí***
Null model	460.20	139.50	0.00
Top model set:			
Mean T_{max90} * $Rain_{90}$	320.96	2.54	0.22
Mean T_{max90} * $Rain_{90}$ + $Mass_{11}$	323.49	0.00	0.78
Effect size of explanatory terms after model averaging	*Effect*	*SE*	*95% CI*
Intercept	1.919	0.303	1.324/2.514
Mean T_{max90}	0.302	0.208	-0.107/0.711
$Rain_{90}$	**2.516**	**0.362**	**1.797/3.234**
$Mass_{11}$	**0.324**	**0.151**	**0.028/0.620**
Mean T_{max90} * $Rain_{90}$	**0.854**	**0.270**	**0.323/1.385**
*Residual deviance: 287.779 on 366 degrees of freedom (ratio: 0.786)			

3.4.3 Understanding the influence of nestling mass on fledgling survival

The path analysis model explained 47% of the variation in survival from fledging to independence ($X^2 = 0.689, p = 0.708$; Fig. 3.6). Path analysis showed that high temperatures were associated with reduced survival both directly (high temperatures were associated with reduced survival) and indirectly (high temperatures were associated with reduced nestling mass, which was in turn associated with reduced survival). Higher $Rain_{90}$ was directly associated with increased survival, and larger group sizes were indirectly associated with increased survival via the effect of larger group size on increased nestling mass.

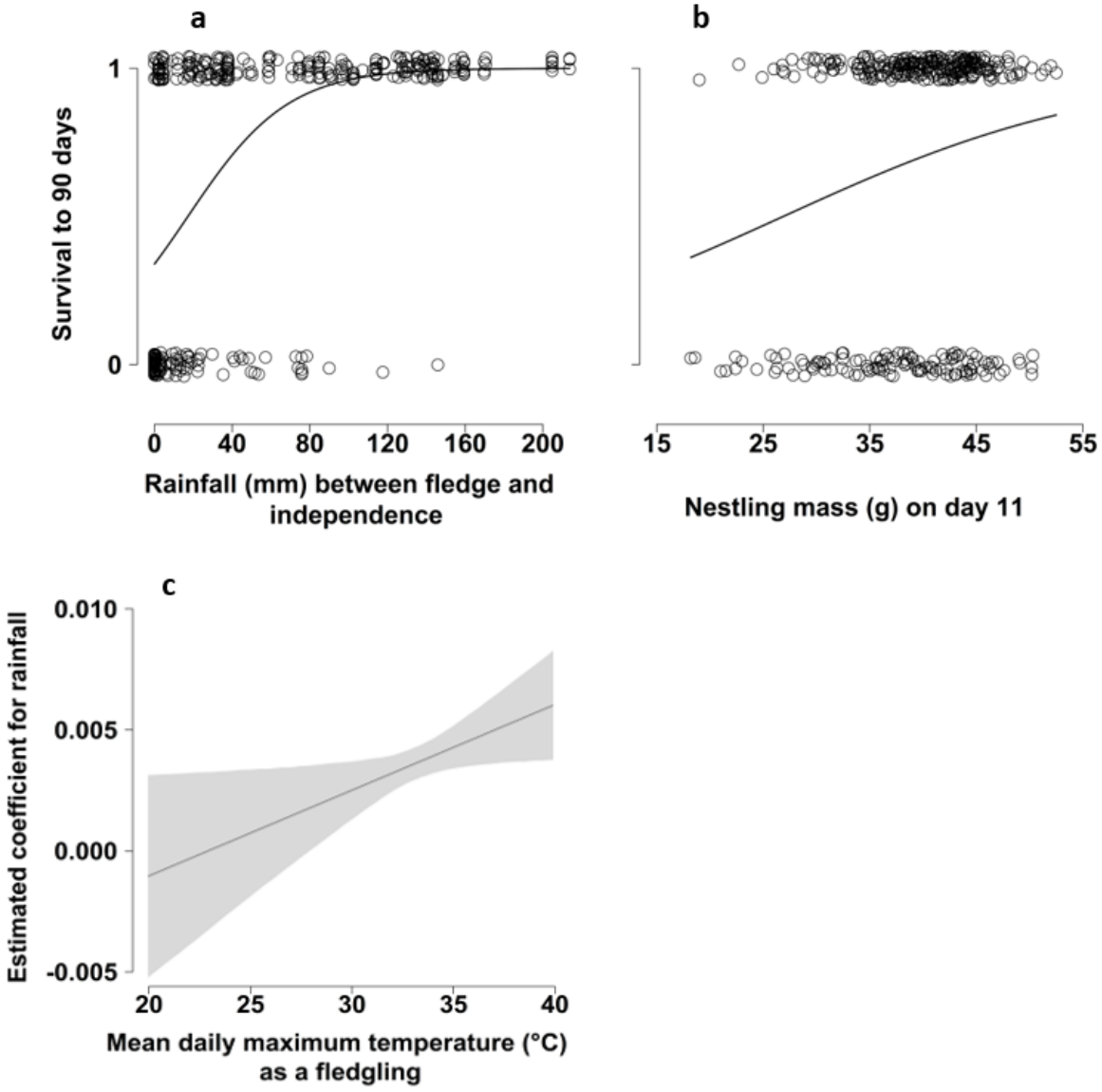


Figure 3.5: (a) survival from fledging to nutritional independence at 90 days of age in southern pied babblers Turdoides bicolor *in relation to rainfall (mm) between fledging and independence, (b) nestling mass (g) measured on 11 days post-hatching, and (c) the interaction between rainfall and temperature. Data points (a, b) are integers (where 1 = survived), jittered for improved visibility. (c) is a marginal effects plot with the coefficient estimates for rainfall on survival on the y-axis, conditional on the values of meanT_{max90} on the x-axis, showing that the effect of rainfall on survival is more strongly positive at higher temperatures.*

Specifically, larger nestlings were more likely to survive to independence (Est = 0.116, p = 0.019), as were fledglings that experienced higher $Rain_{90}$ (Est = 0.750, $p < 0.001$). However, fledglings were less likely to survive (Est = -0.169, p = 0.003) when they had experienced higher mean temperatures during the nestling period (mean $T_{maxBrood}$). Nestlings were heavier when raised by larger groups (Est = 0.118, p = 0.021) and lighter when they experienced high temperatures during the nestling period (Est = -0.224, $p < 0.001$). There was an indirect negative effect of mean $T_{maxBrood}$ on survival via nestling mass [Est = -0.026 (calculated by multiplying standarised estimates for each component of the indirect path: -0.244 × 0.116)]. The combined direct and indirect effect of mean $T_{maxBrood}$ (via nestling mass) on survival was negative [-0.195, calculated by summing standardised estimates for direct and indirect paths: -0.169 + (-0.026)]. The direct effect of mean $T_{maxBrood}$ was more prominent (~87% of the combined effect) than the indirect effect via nestling mass (~13% of the combined effect). Natal group size had an indirect positive effect on survival via nestling mass [Est = 0.014 (= 0.118 x 0.116)], with an overall effect of natal group size = 0.132 (0.059+0.014). There was no evidence for a direct effect of either mean T_{max90} or natal group size on survival to independence, or an effect of rainfall prior to the breeding attempt on nestling mass.

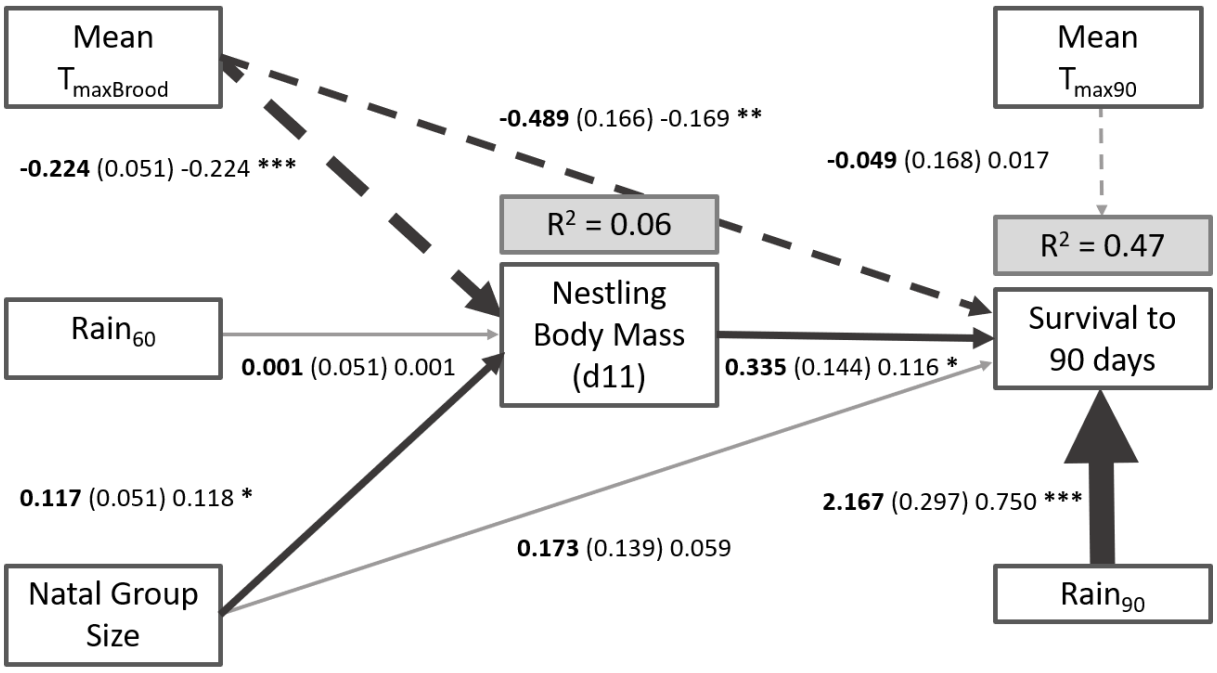


Figure 3.6: Confirmatory path analysis exploring the effects of environmental factors (temperature and rainfall) and group size on nestling body mass and survival to nutritional independence (90 days) in southern pied babblers Turdoides bicolor. *Boxes represent measured variables. Arrows represent hypothesised unidirectional relationships among variables. Solid arrows denote positive relationships, dashed arrows negative relationships. Unstandardised path coefficients are shown in bold, followed by standard errors in parentheses, standardised estimates, and an indicator of statistical significance of the effect (*). Non-significant paths are grey. The thickness of significant paths has been scaled relative to the absolute magnitude of the standardised estimates, such that stronger effects have thicker arrows. R^2 for component models are given in the grey boxes above response variables.*

3.4.4 Identifying temperature thresholds

For the period between initiation of incubation and hatching, a breakpoint was detected at 35.5°C. There was no effect of temperature on age of the breeding attempt at hatch/fail below 35.5°C (95% CI: 33.9 - 36.9; $F_{1,403} = 0.016$, $p = 0.899$), and age at hatch/fail declined with increasing temperature above 35.5°C ($F_{1,81} = 8.893$, $p = 0.004$; Fig. 3.7a). For the period between hatching and fledging a breakpoint was detected at 37.3°C. Age of the breeding attempt at fledge/fail tended to increase with increasing temperature until 37.3°C (95% CI: 36.5 - 38.0; $F_{1,317} = 3.239$, $p = 0.073$), above which age at fledge/fail declined with increasing temperature ($F_{1,20} = 13.370$, $p = 0.002$; Fig. 3.7b). For the period between fledging and independence a breakpoint was detected at 36.6°C. There was no effect of temperature on age of individual fledglings at independence/death below 36.6°C (95% CI: 35.9 - 37.2;

$F_{1,335}$ = 1.942, p = 0.164), and age at independence/death declined with temperature above 36.6°C ($F_{1,33}$ = 15.170, p < 0.001; Fig. 3.7c).

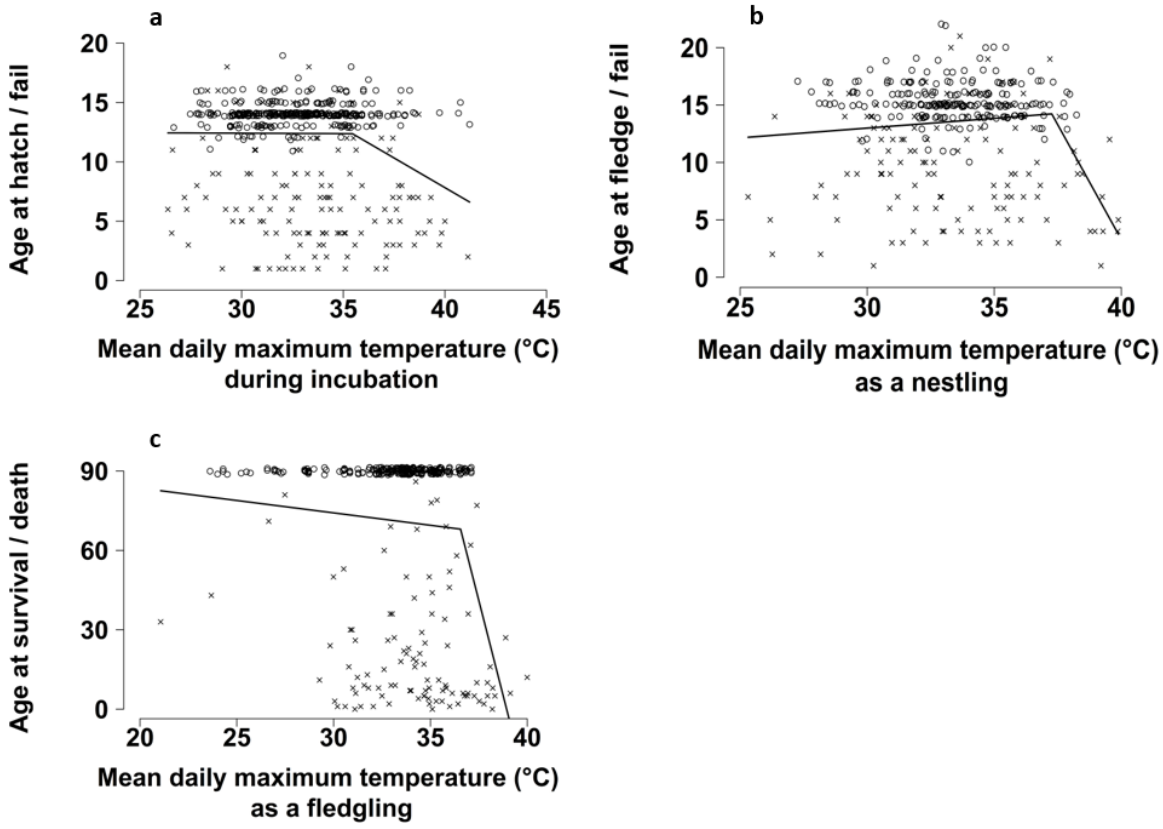


Figure 3.7: Survival in southern pied babblers Turdoides bicolor *from (a) initiation of incubation to hatch per breeding attempt, (b) hatch to fledge per breeding attempt, and (c) fledge to nutritional independence at 90 days per individual fledgling as a function of mean daily maximum air temperature during the corresponding time period. Lines represent segmented linear regressions for the relationship between survival age and air temperature above and below the detected temperature thresholds. Open circles indicate that the nest (a, b) or fledgling (c) transitioned to the next life stage; crosses indicate that the nest failed (a, b) or the fledgling died (c).*

3.5 Discussion

In this chapter I investigated the potential for group living to buffer a cooperatively-breeding bird against the impacts of unfavourable environmental conditions on egg, nestling, and fledgling survival. I present three main findings. First, as in other recent studies of vertebrates (Cunningham et al., 2013;

Cruz-McDonnell & Wolf, 2016; Paniw, Maag, Cozzi, Clutton-Brock, & Ozgul, 2019), exposure to high temperatures during early development was associated with significant reductions in survival probabilities across all three developmental stages. Second, different combinations of climatic and social factors were important for predicting survival during different stages of early development. Third, contrary to my expectations given a prominent theory on the evolution of cooperative breeding in highly variable regions (Jetz & Rubenstein, 2011; Shen & Rubenstein, 2019), I did not find strong evidence that climatic effects on reproduction were moderated by group size, despite considerable statistical power to detect such interactions.

3.5.1 Impacts of high temperatures during early development

In pied babblers, high mean temperatures during early development were associated with a significantly increased risk of mortality across all developmental stages. Adverse weather is known to impair egg (Ospina, Merrill, & Benson, 2018) and nestling development (Mainwaring & Hartley, 2016). For example, survival to fledging can be compromised both by sub-optimally cool (Vafidis et al., 2016) and sub-optimally hot conditions (Cunningham et al., 2013; Marrot, Garant, & Charmantier, 2017), often via effects on provisioning rates (Wiley & Ridley, 2016; van de Ven, 2017). For each early developmental stage, I identified temperature thresholds in the mid- to high-30s (35.5°C during incubation, 37.3°C for nestlings, and 36.6°C for dependent fledglings) above which survival of eggs and young became significantly less likely. These temperature values are within ~2°C of an apparent thermal upper limit of average daily maximum temperature = 38°C, above which I found no records of successful breeding in this species over 15 years of research. Declines in survival probabilities above identified temperature thresholds were progressively steeper as young moved through developmental stages and relied more on their own thermoregulation - i.e. the decline in survival probability with

higher temperatures was steeper for dependent fledglings, which thermoregulate themselves, than for eggs, which are thermoregulated by incubating adults.

While the effect of high temperatures on post-fledging mortality was reduced during periods of moderate to high rainfall, suggesting that the greater availability of food resources following rain (Cumming & Bernard, 1997) could at least partially buffer impacts of heat exposure on fledgling survival (Naef-Daenzer & Grüebler, 2016), the presence of a thermal limit at 38°C highlights a very narrow margin for successful breeding at high temperatures in this species. With temperatures increasing rapidly in the Kalahari (van Wilgen et al., 2016, Fig. 1A), pied babblers may increasingly experience conditions that inhibit successful breeding. This could undermine population growth and ultimately lead to localised extinctions for this species.

3.5.2 Different factors influence survival during each early developmental stage

The primary climatic (temperature and rainfall) and social (group size) factors that influence survival probability were different across the three developmental stages. Mean daily maximum temperature was the strongest predictor of survival probability during incubation - at high temperatures over prolonged periods, incubating birds may not be able to sustain nest attendance to regulate egg temperature (Carroll et al., 2018), leaving eggs vulnerable to overheating and becoming unviable (Ospina et al., 2018; DuRant et al., 2019) or experiencing other problems such as increased hatching asynchrony (Griffith, Mainwaring, Sorato, & Beckmann, 2016) and an increased risk of nest predation (DeGregorio, Westervelt, Weatherhead, & Sperry, 2015), see Chapter 4.

Temperature and group size were the strongest predictors of survival probability during the nestling stage. In cooperative breeders, survival of young often improves with increasing group size (Russell et al., 2002; Canestrari, Marcos, et al., 2008; Ridley, 2016). Larger groups may be able to

provision more regularly (Meade et al., 2010) although see MacLeod & Brouwer 2018 and Wiley & Ridley 2016, better detect and repel predators (Raihani & Ridley, 2007b), or access higher quality territories or nest sites (Mumme et al., 2015), see Chapter 5.

Rainfall and nestling mass were the strongest predictors of survival probability during the dependent fledgling stage. Higher rainfall periods are associated with greater food availability (Hidalgo Aranzamendi et al., 2019), which likely enhanced both provisioning rates to fledglings (Russell et al., 2002) and their ability to find food for themselves (Wheelwright & Templeton, 2003). Path analysis (Fig. 3.6) indicated that group size and temperature influenced fledgling survival probabilities indirectly, via respective positive and negative effects on nestling mass, itself a well-established positive predictor of post-fledging survival in cooperative breeders (Kruuk et al., 2015; Mumme et al., 2015). The direct effect of temperatures experienced in the nest on survival from 11-day-old nestling to independent juvenile, as revealed in the path analysis, suggests that carryover effects of high temperatures during early development continued to impact on the survival probabilities of individuals for weeks to months after they had fledged (Blomberg, Sedinger, Gibson, Coates, & Casazza, 2014; Jones, Ward, Benson, & Brawn, 2017), see Chapter 6.

3.5.3 Buffering effect of group size

I found no evidence that group size buffered the effects of high temperatures on breeding outcomes. While I found large and persistent negative effects of high temperatures on survival across all developmental stages, and positive effects of larger group size on survival from hatching to fledging, and from fledging to independence, I found no evidence that group size interacted with temperature to buffer effects of high temperatures on survival from one early developmental stage to the next. High temperatures negatively affected breeding outcomes across all group sizes. This suggests that physiological tolerance limits (Smit et al., 2018) and resource constraints (Nowakowski, Frishkoff,

Agha, Todd, & Scheffers, 2018) at high temperatures may exceed any potential buffering effect of group size in cooperative breeders (van de Ven, Fuller, et al., 2020).

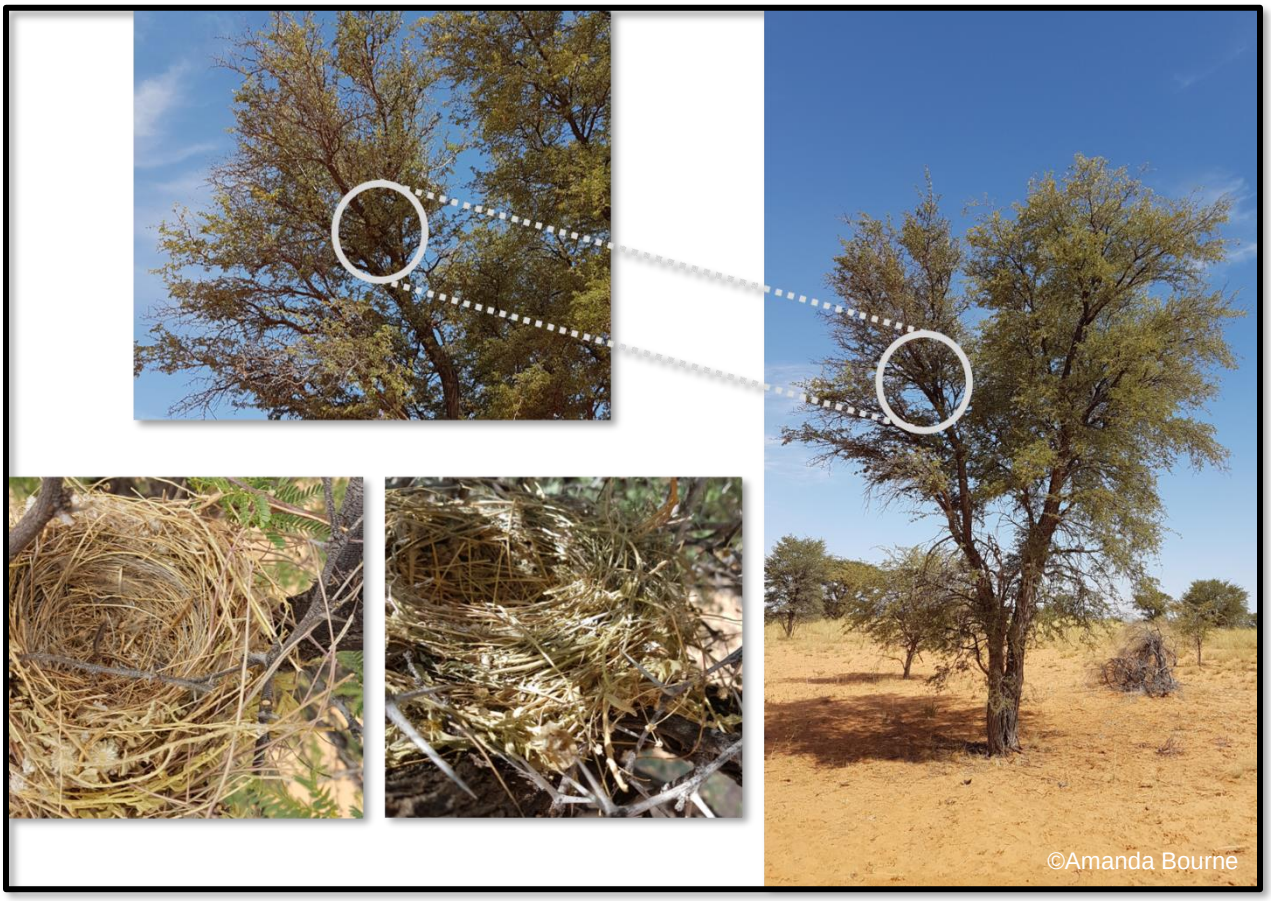
Alternatively, it is possible that group size does not adequately capture the benefits of sociality in pied babblers, or that group size in this study population does not vary enough to allow small buffering effects to be detected. It is also possible that the benefits of larger group sizes and the presence of helpers may have previously helped to mitigate the effects of adverse environmental conditions (Jetz & Rubenstein, 2011; Russell, 2016; Cornwallis et al., 2017), and that any such advantage is no longer detectible given current extreme conditions and a rapidly changing climate. Given that some cooperatively breeding species occur in temporally stable environments (Gonzalez et al., 2013; Dey et al., 2017), and there are many different potential benefits of cooperation that might explain why it evolved in a particular species, pied babblers simply may not be amongst those species that evolved cooperative breeding as a response to a fluctuating environment with highly variable rainfall. (Jetz & Rubenstein, 2011; Lukas & Clutton-Brock, 2018).

3.6 Conclusion

In this chapter, I showed that the negative effects of adverse weather conditions on breeding success in a cooperative breeder were not moderated by group size, suggesting that reproduction in pied babblers is constrained by available resources and physiology at high temperatures and low rainfall, regardless of any potential for load sharing between group members in larger groups. These results have broad implications for avian communities, particularly resident species in arid and semi-arid regions already affected by both decreased precipitation and increased warming, and where daily maximum temperatures already approach physiological tolerance limits. Climate change has been recognised globally as one of the defining challenges of our time, posing a serious threat to biodiversity (Pacifici et al., 2015; Spooner et al., 2018) and society (Winkler, Boyd, Torres Gunfaus,

& Raubenheimer, 2015; Scheffers et al., 2016). The Intergovernmental Panel on Climate Change now predicts with virtual certainty that the incidence of hot extremes will continue to become more frequent and the length, frequency, and intensity of heatwaves will continue to increase over most land masses (IPCC, 2013). At higher average and extreme temperatures, dryland bird species may increasingly experience temperatures that do not permit successful breeding. Despite the intuitive appeal of the hypothesis that the presence of helpers should buffer cooperative breeders against some of these effects, I found no evidence this will be the case in pied babblers. Over time, negative effects of high temperatures on offspring survival could undermine population recruitment and lead to localised extinctions. Taken together, the findings presented here raise concerns for the long-term persistence of arid zone species in the face of rapidly changing environmental conditions, and suggest that cooperative strategies are unlikely to confer an advantage over alternative strategies as species respond to advancing climate change.

CHAPTER 4: Dehydration limits nest attendance and may affect hatching success in a cooperatively breeding bird



Preamble

In this chapter, I present an integrated analysis of behaviour, physiology, and nest temperature data collected from incubating pied babbler groups over three austral summers between Sept 2016 and Feb 2019. I explore the mechanisms behind the relationship between hatching failure and high temperature identified in Chapter 3. To collect the physiology data, I used the non-invasive DLW technique described in Chapter 2. I show that high temperatures likely drive hatching failure via water costs incurred by incubating birds attending the nest for long periods of time on hot days. High water costs may explain extended incubation recesses observed at high temperatures, which leave eggs exposed to nest operative temperatures approaching or exceeding lethal limits for avian embryos. The data from this chapter have been included in a manuscript submitted to, and currently in revision for, *Conservation Physiology*.

4.1 Abstract

High air temperatures have measurable negative impacts on reproduction in wild animal populations, including during incubation in birds. Understanding the mechanisms driving these impacts requires comprehensive knowledge of animal physiology and behaviour under natural conditions. I used a novel combination of a non-invasive doubly-labelled water technique, nest temperature data, and field-based behaviour observations to test effects of temperature, rainfall, and group size on physiology and behaviour during incubation in southern pied babblers *Turdoides bicolor*, a cooperatively-breeding passerine endemic to the arid savanna regions of southern Africa. The proportion of time that clutches were incubated declined as air temperatures increased, traditionally interpreted as a benefit of ambient incubation. However, I show that a) clutches of eggs had a less than 50% chance of hatching when exposed to daily maximum air temperatures > 35.3°C; b) pied babbler groups incubated their nests almost constantly (95% of daylight hours) except on hot days; c) operative temperatures in unattended nests were substantially higher than air temperatures and frequently exceeded 40.5°C, above which bird embryos are at risk of death; d) pied babblers incubating for long periods of time failed to maintain water balance on hot days but not cool days; and e) pied babblers from incubating groups lost mass on hot days. These results suggest that, rather than taking advantage of opportunities for ambient incubation, pied babblers leave the nests during hot periods to avoid dehydration as a consequence of incubating at high operative temperatures. The impacts of high air temperatures during incubation were consistent across all group sizes, suggesting that cooperative breeding does not buffer the thermoregulatory costs of incubation by allowing individual birds to invest less in incubation while ensuring the same level of nest attendance overall. As mean air temperatures increase and extreme heat events become more frequent under climate change, cooperatively-breeding and non-

cooperatively breeding birds alike will incur ever greater thermoregulatory costs of incubation, leading to compromised nest attendance and increased potential for eggs to overheat, with implications for hatching success and, ultimately, population persistence.

4.2 Introduction

Anthropogenic climate change is driving declines in bird populations globally (Thomas et al., 2004; Saino et al., 2011; Iknayan & Beissinger, 2018; Spooner et al., 2018; Rosenberg et al., 2019), often via negative impacts on reproduction (Stevenson & Bryant, 2000; Cahill et al., 2013; Cunningham et al., 2013). For example, hatching failure in birds is particularly common during hot weather (Wada et al., 2015; Clauser & McRae, 2017; Sharpe et al., 2019), and droughts (Conrey et al., 2016), see Chapter 3, both of which are becoming more frequent under climate warming (Ripple et al., 2019). A sound understanding of the behavioural and physiological mechanisms driving such patterns *in situ* in wild populations is required to accurately predict species-specific responses to climate change (Conradie et al., 2019; Stillman, 2019). Few studies to date have combined behaviour and physiology in the wild to explore mechanistic determinants of responses to climate change (Breuner & Hahn, 2003; Stillman, 2019).

Incubation is energetically costly in temperate environments where eggs need to be kept warm (Ardia, Pérez, & Clotfelter, 2010; Nord, Sandell, & Nilsson, 2010; Nord & Williams, 2015; Vaugoyeau, Meylan, & Biard, 2017; Nord & Cooper, 2020), but also extremely challenging in warm environments (Amat & Masero, 2004; Coe, Beck, Chin, Jachowski, & Hopkins, 2015; Nwaogu, Dietz, Tieleman, & Cresswell, 2017), where incubating birds must prevent eggs from overheating (G. S. Grant, 1982; Webb, 1987; Conway & Martin, 2000; J. M. Carroll, Davis, Elmore, & Fuhlendorf, 2015; S. McDonald & Schwanz, 2018) while also thermoregulating themselves (O'Connor, Brigham, & McKechnie, 2018; DuRant et al., 2019; McKechnie, 2019). Birds initially respond to high temperatures by increasing

incubation constancy (AlRashidi, Kosztolányi, Shobrak, Küpper, & Székely, 2011; Mougeot, Benítez-López, Casas, Garcia, & Viñuela, 2014; Mortensen & Reed, 2018) or engaging in shading behaviour (G. S. Grant, 1982; Downs & Ward, 1997; Brown & Downs, 2003; Clauser & McRae, 2017) in order to regulate nest temperatures. As incubating birds reach limits in their ability to tolerate high temperatures over long periods, they undertake more frequent (Clauser & McRae, 2017) or longer incubation recesses (Bueno-Enciso, Barrientos, Ferrer, & Sanz, 2017), and may ultimately abandon their nests (Clauser & McRae, 2017; Sharpe et al., 2019).

Cooperative species may respond differently to environmental variability than pair-breeding or solitary species, because reproductive success can be influenced by the presence of helpers (Wiley & Ridley, 2016; van de Ven, Fuller, et al., 2020). Comparative research has demonstrated that both cooperatively-breeding birds (Jetz & Rubenstein, 2011) and mammals (Lukas & Clutton-Brock, 2017) occur with disproportionate frequency in regions characterised by high spatial and temporal variability in environmental conditions, a finding that implies group living enhances a species' ability to persist in variable environments (Rubenstein & Lovette, 2007). To date, however, there are few empirical studies exploring the extent to which responses to climate variability might be mitigated by cooperative breeding strategies (Langmore et al., 2016; van de Ven, Fuller, et al., 2020), and none exploring behavioural and physiological responses to environmental conditions during incubation simultaneously in the same individuals under natural conditions.

In Chapter 3, I showed that hatching probabilities are influenced by temperature in a population of cooperatively-breeding southern pied babblers *Turdoides bicolor* (hereafter 'pied babblers'). Here, I go further to investigate the effects of weather and social factors on the behaviour and physiology of incubating adults in pied babblers in order to explore the hypothesis that poor hatching success at high temperatures may be associated with physiological pressures on incubating

adults at high temperatures. While there are a growing number of studies that consider both behaviour and physiology in avian reproduction (Andreasson, Nord, & Nilsson, 2018; Cooper et al., 2019), I present the first study to combine direct observations of incubation behaviour in the wild, under natural conditions, with physiological measurements from the same individuals simultaneously.

I expected that high air temperatures would reduce hatching rates via reduced nest attendance as a result of thermoregulatory costs on incubating adults, thus increasing the risk of lethal heat exposure for developing embryos. I addressed this expectation by testing predictions related to 1) nest outcomes (lower probability of hatching at high air temperatures); 2) incubation behaviour (reduction in the proportion of time nests are attended at high air temperatures); 3) the temperatures to which unattended nests would be exposed at high air temperatures (exceeding lethal limits for avian embryos in some species, explaining why hot nests are less likely to hatch); and 4) physiological costs of incubation (higher costs of incubation at higher temperatures evident in patterns of body mass maintenance, energy expenditure, and water balance). I tested the latter prediction using the novel, non-invasive doubly-labelled water technique presented in Chapter 2 of this thesis (Bourne et al., 2019). I expected higher rainfall and larger group sizes to be associated with reduced costs and improved nest outcomes. Additionally, if the presence of helpers does buffer the effect of environmental variation on reproduction (Rubenstein & Lovette, 2007) by, for example, allowing each individual bird to attend the nest for shorter periods of time during hot weather without compromising overall rates of nest attendance, then I expected weaker impacts of higher temperatures during nest attendance for individuals in larger groups, i.e. an interaction between group size and temperature.

4.3 Materials and Methods

4.3.1 Study site and system

Fieldwork was conducted with a habituated population of individually marked pied babblers at the Kuruman River Reserve (33 km^2, KRR; 26°58'S, 21°49'E) in the southern Kalahari. Pied babblers lay a clutch of ~3 eggs during each breeding attempt. As indicated in Chapter 3, clutches are incubated for 14 ± 1.2 days (see also Ridley & Raihani 2008 who show that clutches are incubated for 13-15 days). While only the dominant female incubates overnight (Ridley, 2016), during the day all adult group members (individuals > 1 year old), including subordinates, take turns to incubate (Ridley & Raihani, 2007b; Ridley & van den Heuvel, 2012) and the nest is rarely left unattended for more than a few minutes at a time (Ridley & Thompson, 2011). See Chapter 1 for a detailed description of the study site and study species.

4.3.2 Data collection

Data were collected for each austral summer breeding season between September 2016 and February 2019 (three breeding seasons in total). I noted group size (number of adults; mean = 4 ± 1, range: 3–6) during each breeding attempt, daily maximum air temperature (T_{max}; mean = 34.1 ± 4.46°C, range: 20.7°C–40.8°C) for each observation day, and total rainfall in the two months prior to the initiation of incubation ($Rain_{60}$; mean = 21.3 ± 33.0 mm, range: 0–140.2 mm) for each breeding attempt. For analyses of nest outcomes, I additionally calculated average T_{max} between initiation of incubation and hatching or nest failure (Mean T_{maxInc}).

Nest outcomes

Monitoring of nest outcomes (*n* = 99 breeding attempts over three breeding seasons) followed Ridley and van den Heuvel (2012): breeding attempts were defined as discrete clutches laid and incubated;

nests were located by observing nest-building visits during weekly monitoring visits; once located, nests were checked approximately every two days to identify incubation start and hatch dates; and nest fates were categorised as hatched when adult group members were observed carrying small food items to the nest, and as failed when nests were left unattended for longer than 90 min on two consecutive monitoring visits or the group was observed building a new nest.

Incubation behaviour

Incubation bout and recess data were collected by waiting near the nest at dawn, observing the first bird to replace the dominant female in the morning, and subsequently walking with the group all day until 19h00, noting the details of each incubation bout or recess. Data on proportion of time per day that clutches were incubated (total incubation time / observation time) were collected by recording the start and end time of each incubation bout, and the duration of any time periods during which the nest was left unattended (recesses), between the dominant female first leaving the nest in the morning (usually at dawn: 05h00–06h48, with one leaving later, at 09h45) until 19h00 (n = 45 observation days at 35 nests). Total incubation time was calculated as the sum of all incubation bouts per nest per day. Both members of the dominant pair incubated on every observation day, with the help of at least one subordinate group member on most (91%) days. In over 90% of cases, the incubating bird did not leave the nest until it was replaced by another, therefore making it unlikely that many incubation recesses were missed.

Nest temperatures

To investigate the thermal environment of pied babbler nests, I measured operative temperature [T_e: a measure of thermal load experienced by the bird (Bakken, Santee, & Erskine, 1985)] using black bulbs placed in 23 nests after fledge/fail. Black bulbs were constructed according to Bakken et al.'s

(1985) 'rugged model' method. T_e can be used to describe the environmental temperature experienced by individual animals in a single metric incorporating ambient temperature, solar radiation, and convection (Bakken, Boysen, Korschgen, Kenow, & Lima, 2001; J. M. Carroll, Davis, Elmore, & Fuhlendorf, 2015). Black bulbs comprised two copper half-spheres (42 mm diameter – approximating pied babbler thoracic cavity dimensions – and 0.8 mm thick), sealed together using cryanoacrylate adhesive and painted matt black (J. M. Carroll, Davis, Elmore, & Fuhlendorf, 2015; van de Ven et al., 2019). Black bulbs were equipped with internally mounted temperature loggers (Thermocron iButton, DS1923, Maxim, Sunnyvale, CA, USA, resolution 0.0625°C) suspended in the center and logging temperature at 10-minute intervals (*sensu* Cunningham, Martin, & Hockey, 2015; van de Ven, McKechnie, et al., 2019). The advantage of using T_e rather than ambient temperature derived from weather stations is that T_e describes heat load more accurately by including some aspects of thermal properties specific to particular microsites, as well as thermally relevant parameters of the animal itself such as shape and size (Camacho, Trefaut Rodrigues, & Navas, 2015). Black bulbs do not provide a complete representation of thermal conditions experienced by incubating pied babblers, because they neither mimic feather arrangement or colour (J. M. Carroll, Davis, Elmore, & Fuhlendorf, 2017) nor take humidity and evaporative heat loss into account (Bakken et al., 1985). Nonetheless, they provide a relative measure of differences in temperature across nest microsites which cannot be approximated by air temperature alone (Cunningham et al., 2015).

Black bulbs were placed in nests within 5 days after they had been vacated by the birds (Griffith et al., 2016), and were left in the nest recording T_e continously for approximately two weeks (13 ± 3 days, range: 10–21 days; n = 21,872 records of daytime T_e in total). To compare nest-specific T_e with simulteously occurring air temperature, I recorded air temperatures at synchronised 10-minute intervals at the on-site weather station.

Energy expenditure and water balance

During observation days on which total incubation time for the clutch was recorded, I also obtained detailed physiology [daily energy expenditure (DEE) and water balance] and behaviour (incubation effort) data for a subset of adult birds within the group. I collected physiology data from up to four individuals per observation day (mean = 1.6 ± 0.9, range: 1–4; n = 70 individuals in total). I targeted a range of T_{max} values, group sizes, sex, and rank, and obtained physiology data from individuals belonging to groups ranging in size from three to six adults, both sexes (n = 38 females , 31 males, 1 unknown sex) and ranks (n = 40 dominant birds, 30 subordinate birds), and measured on hot [n = 35 at $T_{max} \geq 35.5°C$, identified as a critical temperature threshold in pied babblers (du Plessis et al., 2012; Wiley & Ridley, 2016)] and cool (n = 35 at $T_{max} < 35.5°C$) days.

Physiology data were collected using a non-invasive doubly-labelled water (DLW) technique validated by Bourne et al. (2019), using the methods described in detail in Chapter 2. DLW is a non-toxic isotopic solution enriched with oxygen-18 (measured as $\delta^{18}O$) and deuterium (measured as $\delta^{2}H$). In brief, selected individuals were dosed with ~50 μL of DLW injected into darkling beetle *Zophobias morio* larvae and fed to the birds between 06h00 and 09h00 on the observation day. Body water samples were then obtained during all daylight hours over a 24 hr observation period by collecting faeces from dosed individuals as they were excreted naturally onto the ground. Water samples were extracted from faeces by cryogenic distillation, using a technique adapted from Priyadarshni et al. (2016), and analysed in a PAL autosampler and DLT-100 liquid water isotope analyser (Los Gatos Research, Mountain View, CA, USA) following the procedures described by Smit & McKechnie (2015) and Bourne et al. (2019). I calculated CO_2 production (rCO_2) from the body water pool and the rate of decline of the natural log of the ratio of $\delta^{18}O/\delta^{2}H$ (Nagy & Costa, 1980; Speakman, 1997). CO_2 production was converted to kJ day^{-1} using the relationship 27.42 kJ l^{-1} CO_2 for an insectivorous bird (Gessaman &

Nagy, 1988) and used to estimate DEE (kJ g^{-1} day^{-1}). Water balance was calculated by dividing water influx by water efflux, where values > 1 indicate positive water balance (a hydrated status) and values < 1 indicate negative water balance (a dehydrated status). I used Nagy and Costa's (1980) Equation 4 (see Equation 4.1 below) and Equation 6 (see Equation 4.2 below) to calculate water efflux and water influx (ml H_2O $kg^{-1}d^{-1}$) respectively:

$$(1)\ \frac{mlH_2O\ efflux}{kg\ day} = \frac{2{,}000(W_2 - W_1)\log[(H_1 \times W_1) \div (H_2 \times W_2)]}{(M_1 + M_2)[1 - (W_2 \div W_1)]t} \qquad \text{(eq. 4.1)}$$

$$(2)\ \frac{mlH_2O\ influx}{kg\ day} = \frac{mlH_2O\ efflux}{kg\ day} + \frac{2{,}000(W_2 - W_1)}{t(M_1 + M_2)} \qquad \text{(eq. 4.2)}$$

where the subscripts 1 and 2 represent initial and final values respectively, H = measured deuterium enrichment levels, M = body mass in grams, W = the body water pool, and t = time in days between initial and final sampling of deuterium enrichment levels. The body water pool was estimated as 69.3% of body mass (see Chapter 2), as per measured total body water in pied babblers (Bourne et al., 2019).

Because continuous attention is required to collect faecal samples from wild, free-living birds, it was generally only possible to collect detailed behaviour data from one bird per observation day. To construct time budgets and to identify the proportion of time adult birds which had been dosed with DLW allocated to incubation, I collected detailed behaviour data during ~ 4 x 20-minute continuous time-activity focal behaviour observations (Altmann, 1974) within each of 6 focal sessions per day (mean = 23 focals per bird per day, range: 15–27; n = 48 focal days; data were collected from two birds on the same day on 5 occasions, i.e. 10 of the focal days). Focal sessions lasted two hours each, with the first starting at 07h00 and the last starting at 17h00. I captured the data on an Android smartphone (Mobicel Trendy), using Prim8 software (McDonald & Johnson, 2014) in which the duration of each observed behaviour is recorded to the nearest second.

Body mass

To determine effects of weather and social factors on body mass maintenance of adults from groups incubating clutches, body mass data were collected from as many adult group members as possible on observation days (mean = 2.6 ± 1.4 measurements per observation day, range: 1–5). Body mass measurements were obtained by enticing individuals to stand on a top pan balance in exchange for a small food reward (Ridley, 2016), and were taken at dawn on the morning of each observation day ($Mass_1$) and again at dawn the following morning ($Mass_2$). Body mass change (ΔM_b) was calculated in grams as $Mass_2$ - $Mass_1$.

4.3.4 Statistical analyses

Statistical analyses were conducted in R v 3.6.0 (R Core Team, 2017), primarily using mixed-effects models in the package *lme4* (Bates et al., 2015). Rainfall in the two months prior to initiation of incubation was correlated with breeding season ($F_{2,67}$ = 10.994, $p < 0.001$); I chose the categorical variable 'breeding season' for all analyses due to the fact that rainfall ≥ 30.2 mm occurred in only one breeding season (2016/2017). Sensitivity power analyses (Cohen, 1988; Greenland et al., 2016), using the R package *pwr* (Champely et al., 2018), indicated that two-way interaction effects would have to be very large for me to be able to detect them in this dataset (all Cohen's $f^2 > 0.36$). I have sufficient sample size to detect a range of main effect sizes, from small to large, in all analyses (range f^2: 0.07 – 0.18) – see Table 4.1 below.

Model selection using the Akaike's information criterion corrected for small sample size (AICc) with maximum likelihood estimation was used to determine which of a series of models, each representing a biological hypothesis, best explained patterns of variation in the data. Lower AICc values were taken to represent more parsimonious models, following Harrison et al (2018a). Where

there were several models within 2 AICc of the top model, top model sets were averaged using the package *MuMIn* (Barton, 2015). Model estimates with confidence intervals that did not intersect zero were considered to explain significant patterns in the data (Grueber et al., 2011).

Table 4.1: Power analyses for the interactions; multiple regression power calculations

Analysis	*u*	*v*	*α*	*power*	f^2
Nest outcomes					
Main effects	2	99	0.05	0.8	0.081
Interactions	3	25	0.05	0.8	0.443
Nest attendance					
Main effects	2	46	0.05	0.8	0.178
Interactions	3	12	0.05	0.8	1.142
Energy expenditure and water balance					
Main effects	2	70	0.05	0.8	0.115
Interactions	3	17	0.05	0.8	0.658
Mass change					
Main effects	2	120	0.05	0.8	0.066
Interactions	3	30	0.05	0.8	0.359

*u = model degrees of freedom; v = sample size, α = the significance level, and power (p) = probability of finding an effect that is there; f^2 = measure of determinable effect size (values of ~ 0.02, ~0.15, and ~0.35 represent small, moderate, and large determinable effect sizes respectively).

To determine which variables predicted a) nest outcomes and b) the overall proportion of time clutches were incubated per day, I used generalised linear mixed-effects models (GLMM) with binomial error structure and logit link function. I considered the influence of breeding season, temperature [for a) MeanT_{maxInc}; for b) T_{max} on observation day], group size, group size^2, and the interactions between breeding season and group size and T_{max} and group size. To account for repeated measures and thus for nonindependence of data, I included nest identity as a random factor. For b), I further included an observation level random factor to address overdispersion in the data (Harrison, 2014).

To determine which variables predicted DEE (n = 68) and water balance (n = 69), I used maximum likelihood linear mixed-effects models (LMMs) considering the influence of breeding season, T_{max}, group size, sex, rank, and the interactions between breeding season and group size and

T_{max} and group size, with bird identity included as a random factor. For a subset of individuals for which I had collected both behaviour and physiology data from the same birds on the same day (n = 26), I further considered the influence of proportion of time spent incubating on DEE (n = 38) and water balance (n = 39), fitting separate linear regressions for hot (≥ 35.5°C) and cool (< 35.5°C) days. Bird identity was included as a random factor for all DEE and water balance analyses.

To determine which variables predicted ΔM_b, I used the R package *segmented* (Muggeo, 2008) to identify the temperature threshold ('breakpoint') above which ability to maintain body mass between days was compromised, and followed this with separate LMMs for the data above and below the identified breakpoint. For each model segment, I considered the influence of breeding season, T_{max}, group size, sex, rank, and the interactions between breeding season and group size and T_{max} and group size, with nest identity included as a random factor.

4.4 Results

4.4.1 Nest outcomes

Of 99 nests monitored over three breeding seasons, 61 hatched and 38 failed. Mean T_{maxInc} was the most parsimonious predictor of variation in hatching success in pied babblers (the single best-fit model had a model weight of 0.817), and pied babbler nests were less likely to hatch as mean daily maximum temperatures experienced during incubation increased (Est = -0.303 ± 0.079, 95% CI: -0.467 - -0.157, z = -3.853; Fig. 4.1; see Appendix Table 4.1 for full model ouputs). When average daily maximum air temperatures exceeded 35.3°C during incubation, the likelihood of pied babbler nests hatching dropped below 50% (Fig. 4.1).

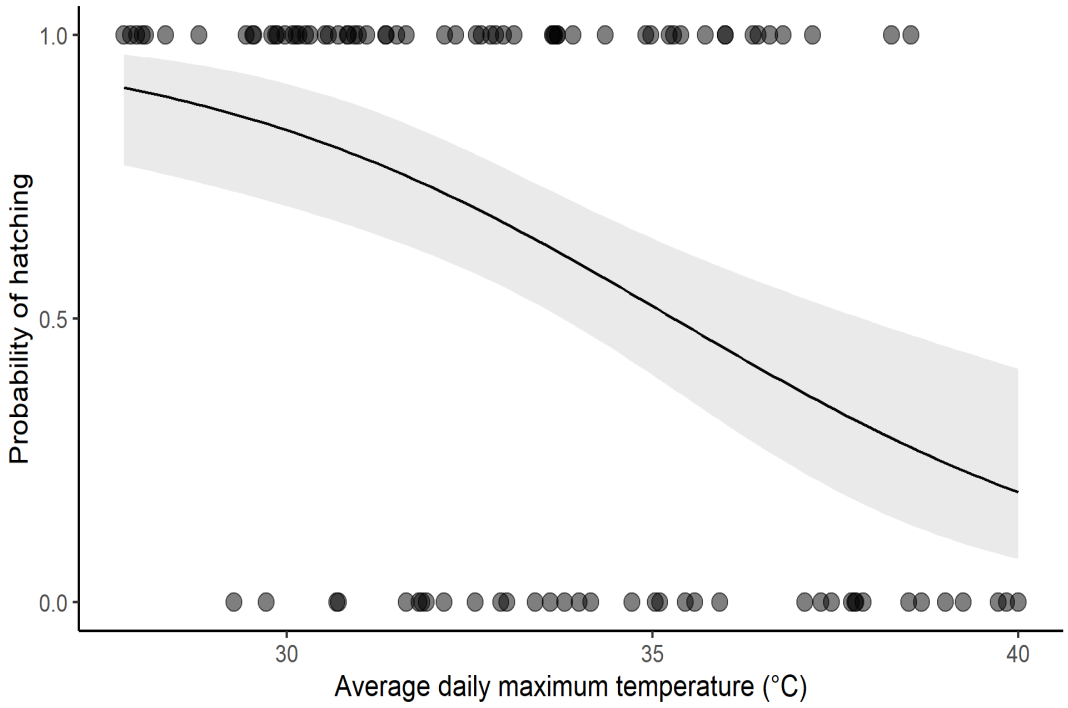


Figure 4.1: Nest outcomes as a function of mean daily maximum temperatures during incubation. Data from 99 nests by 23 southern pied babbler Turdoides bicolor *groups over 3 breeding seasons. Figure is generated from the data presented in Appendix Table 4.1.*

4.4.2 Nest attendance

The percentage of time between dawn and 19h00 that clutches were incubated ranged from 57.3 to 100% (mean = 95.1%). Only three nests were incubated for < 80% of daylight hours, all of which were observed on days with T_{max} > 37°C. T_{max} was the most parsimonious predictor of variation in the proportion of time that clutches were incubated (of two competing top models, the best-fit model had T_{max} as the only predictor and a model weight of 0.498), and the proportion time incubated declined as temperatures increased (Table 4.2, Fig. 4.2; see Appendix Table 4.2 for full model ouputs; also see Appendix Fig. 4.1-4.3 and Appendix Table 4.3-4.5 for details on the frequency, duration, and probability of incubation recesses in relation to temperature).

Table 4.2: Top GLMM model set for factors influencing the proportion of time that clutches were incubated (n = 46 observation days at 35 nests by 15 different groups over 3 breeding seasons). *Model averaging was implemented for models with ΔAICc < 2 of the 'best-fit' model. Significant terms after model averaging are shown in bold. Null models shown for comparison with top model sets.*

Model	***AICc***	***ΔAICc***	***ωí***
Null model	376.6	12.13	0.00
Top models:			
T_{max}	364.47	0.00	0.520
T_{max} + Group size + Group size^2	364.64	0.17	0.480
Effect size of explanatory terms after model averaging	Estimate	SE	95% CI
Intercept	6.084	0.855	4.379/7.788
T_{max}	**-1.588**	**0.466**	**-2.528/-0.648**
Group size	0.259	0.419	-0.576/1.095
Group size ^ 2	-0.633	0.771	-2.156/0.889
*Residual deviance: 9.324 on 42 degrees of freedom (ratio: 0.222)			

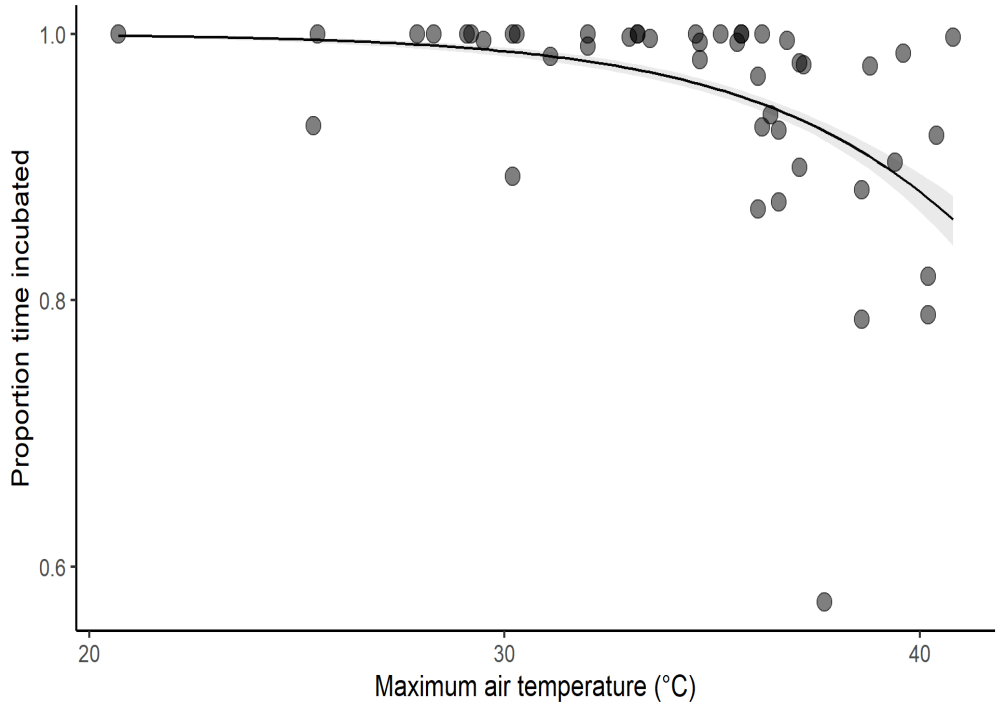


Figure 4.2: Proportion of time that the clutch was incubated as a function of maximum air temperature on the observation day. Data from 46 observation days at 35 southern pied babbler Turdoides bicolor *nests by 15 different groups over 3 breeding seasons. Figure is generated from the data presented in Table 4.2.*

4.4.3 Nest temperatures

Nest T_e during the day always exceeded air temperatures (06h00–19h00; mean difference = 7.9 ± 11.2°C, range: 0.01–31.8°C; Fig. 4.3a; Appendix Table 4.6). At the coolest daily air temperature recorded (~8°C, n = 2 days), nest T_e averaged 10.1 ± 0.7°C (range: 8.8–11.6°C; n = 5 nests), and at the warmest daily air temperature recorded (~41°C, n = 1 day), T_e averaged 44.4 ± 2.8°C (range: 40.9–49.1°C; n = 1 nest). I found that individual nests could be up 25°C hotter than other nests for same air temperatures of 35.5°C, identified as a critical temperature threshold for body mass maintenance and parental care behaviour in pied babblers (du Plessis et al., 2012; Wiley & Ridley, 2016).

Nest T_e increased significantly with increasing air temperatures (linear regression; Est = 1.207 ± 0.005, 95% CI: 1.196 - 1.217, t = 229.2; Fig. 4.3b). The highest nest T_e recorded was 65°C and T_e > 60°C were recorded at two nests for a range of air temperatures between ~30 and ~37°C. I recorded 2,379 instances of T_e in unattended nests > 41°C (10.8% of all T_e records; 22 of 23 nests; mean = 108.1 ± 84.6 instances per nest, range: 30–295), identified as a potentially lethal temperature for avian embryos in many temperate species (Webb, 1987; DuRant, Hopkins, Hepp, & Walters, 2013). I further recorded 487 instances of T_e in unattended nests > 50°C (2.2% of all T_e records; 17 of 23 nests; mean = 28.6 ± 41.4 instances per nest, range: 1-163), known to be lethal for the embryos of many arid zones bird species (Grant, 1982; Reyna & Burggren, 2012; Griffith et al., 2016).

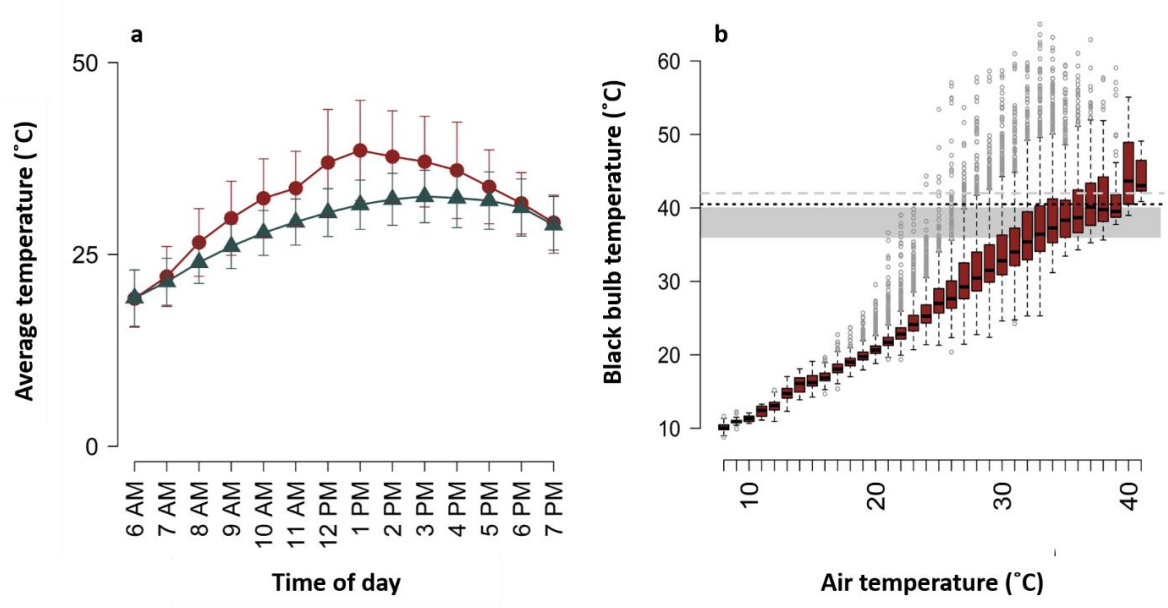


Figure 4.3: (a) Comparison of average temperatures recorded per hour between 6AM and 7PM (mean ± sd) by an onsite weather station (blue triangles) and black bulbs placed in vacated southern pied babbler Turdoides bicolor *nests (red circles); (b) black bulb temperature as a function of air temperature. Boxplots show the median and interquartile range (IQR) of operative temperature for each air temperature value rounded to the nearest digit. Dashed whiskers indicate the lowest and highest value datapoints with 1.5 IQR. Points plotted beyond the whiskers represent a relatively small number of extreme values in this large dataset,* n *= 21,872 temperature records. The optimal temperature range for avian embryo development (36–40˚C, shaded area), lethal temperature for avian embryos given prolonged exposure (40.5˚C, black dotted line), and the average upper critical limit for thermoneutrality in passerines (41˚C, grey dashed line) are indicated on (b).*

4.4.4 Energy expenditure and water balance

I quantified DEE (n = 68; mean = 1.613 ± 0.463 $kJ^{-1}g^{-1}d$, range: 0.639 – 2.855 $kJ^{-1}g^{-1}d$) and water balance (n = 69; mean = 1.034 ± 0.116, range: 0.869 – 1.691; where 1 = neutral water balance) in 45 different birds from groups incubating clutches. T_{max} was the most parsimonious predictor of variation in DEE (of two competing top models, the best-fit model had T_{max} as the only predictor and a model weight of 0.553), and DEE declined with increasing temperature (Est = -0.223 ± 0.046, 95% CI: -0.315 - -0.131, χ = 4.762; Table 4.3, Fig. 4.4; see Appendix Table 4.7 for full model ouput). My within-individual physiology and behaviour data showed no evidence that DEE was predicted by the proportion of time spent incubating on either hot or cool days (n = 38; Table 4.4, Fig. 4.5a).

Table 4.3: Top LMM model set for factors influencing variation in daily energy expenditure (n = 68 measurements from 45 different birds at 33 nests by 15 different groups over 3 breeding seasons). *Model averaging was implemented for models with ΔAICc < 2 of the 'best-fit' model. Significant terms after model averaging are shown in bold. Null models shown for comparison with top model sets.*

Model	***AICc***	***ΔAICc***	***ωí***
Null model	92.5	14.08	0.00
Top models:			
T_{max}	78.42	0.00	0.69
T_{max} + Season	80.00	1.58	0.31
Effect size of explanatory terms	Estimate	SE	95% CI
Intercept	1.117	0.754	-0.361/2.595
T_{max}	**-0.223**	**0.046**	**-0.315/-0.131**
Season (2016-17)	0.428	0.638	-0.823/1.679
Season (2017-18)	0.550	0.818	-1.054/2.155
Season (2018-19)	0.508	0.755	-0.971/1.987

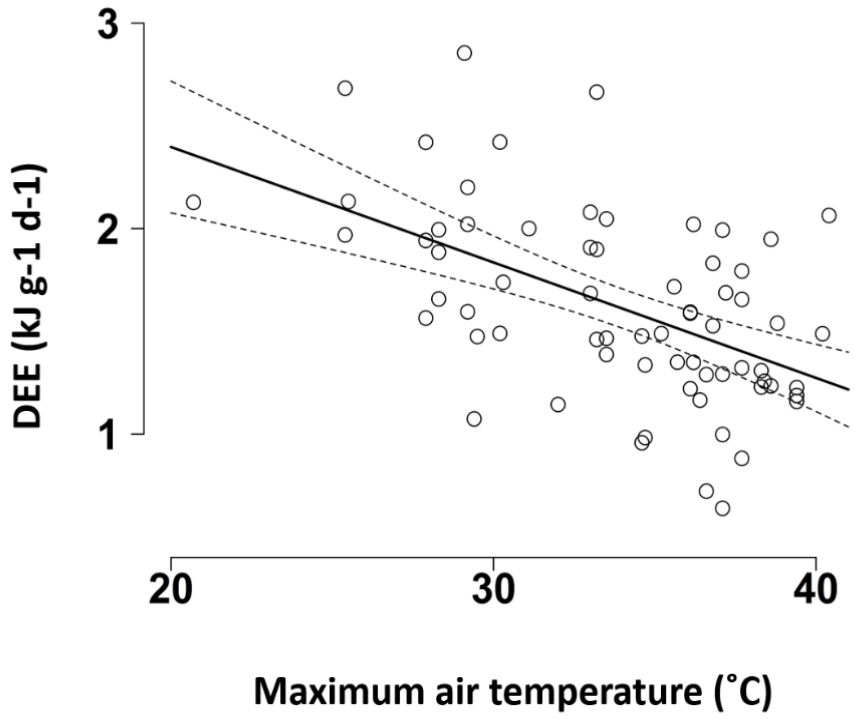


Figure 4.4: Variation in daily energy expenditure by maximum air temperature (°C) on the measurement day in southern pied babblers Turdoides bicolor. *Figure is generated from the data presented in Table 4.3.*

Variation in water balance was not predicted by breeding season, T_{max}, group size, sex, rank, or the interactions between breeding season and group size and T_{max} and group size (Appendix Table 4.8). My within-individual physiology and behaviour data showed that pied babblers' ability to maintain neutral or positive water balance declined with an increasing proportion of time spent incubating on hot days, but not on cool days (n = 39; Table 4.4, Fig. 4.5b).

Table 4.4: Daily energy expenditure and water balance as a function of proportion of time spent incubating, analysed separately for cool (T_{max} < 35.5˚C) and hot (T_{max} ≥ 35.5˚C) days. Significant relationships are shown in bold.

Response	*n*	Temperature	Estimate	Std error	95% CI	*t* value	*p* value
Daily energy expenditure	22	Cool	0.360	0.871	-1.456/2.177	*0.414*	0.684
	16	Hot	0.258	0.662	-1.162/1.678	*0.390*	0.703
Water balance	22	Cool	0.089	0.117	-0.155/0.332	*0.758*	0.457
	17	**Hot**	**-0.369**	**0.149**	**-0.687/-0.052**	***-2.480***	**0.026**

4.4.5 Body mass

Mass change over 24 h averaged 0.29 ± 2.26 g (range: -4.3-6.3 g, or -9.1-8.5% of body mass; n = 120 individuals). Using a segmented regression analysis, I detected a breakpoint in the data at 36.2°C (95% CI: 34.1 - 38.2°C). At temperatures < 36.2°C (n = 72), ΔM_b was not influenced by any of the predictor terms (Appendix Table 4.9). At temperatures ≥ 36.2°C (n = 48), T_{max} was the only predictor that significantly influenced body mass change (model weight = 0.633), with mass loss becoming more likely as temperatures increased (Est = -0.926 ± 0.318, 95% CI: -1.609 - -0.303, t = -2.908; Fig. 4.6; Appendix Table 4.10).

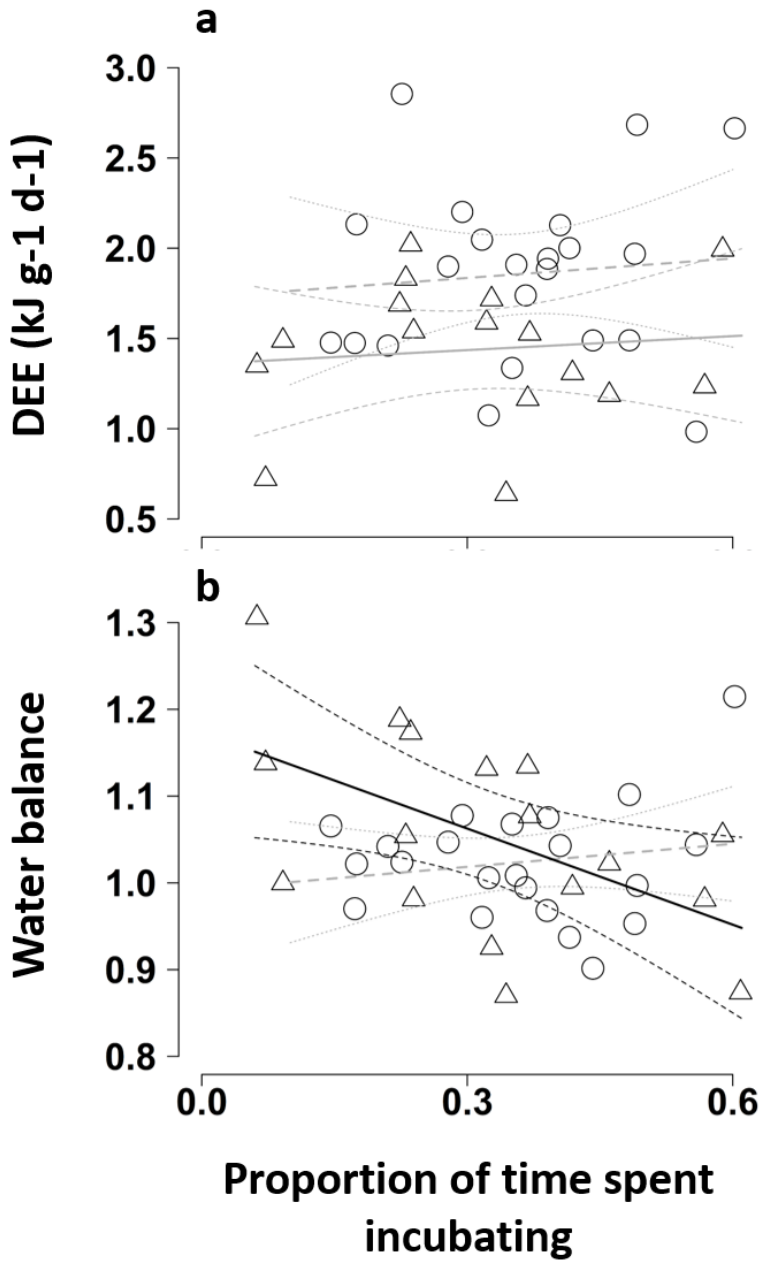


Figure 4.5: Influence of proportion of time southern pied babblers Turdoides bicolor *spent incubating on cool (T_{max} < 35.5 ˚C, open circles, dashed lines, dotted 95% CIs) and hot (T_{max} ≥ 35.5 ˚C, open triangles, solid lines, dashed 95% CIs) days on the (a) daily energy expenditure and (b) water balance of incubating birds. Model fit lines for non-significant relationships are faded. In order to construct this figure models were fitted separately to data collected on cool and hot days – this was only done in order to clearly visualise the direction of interaction between temperature and proportion of time spent incubating. Model outputs reported in the text and in Table 4.4 included temperature as a continuous variable.*

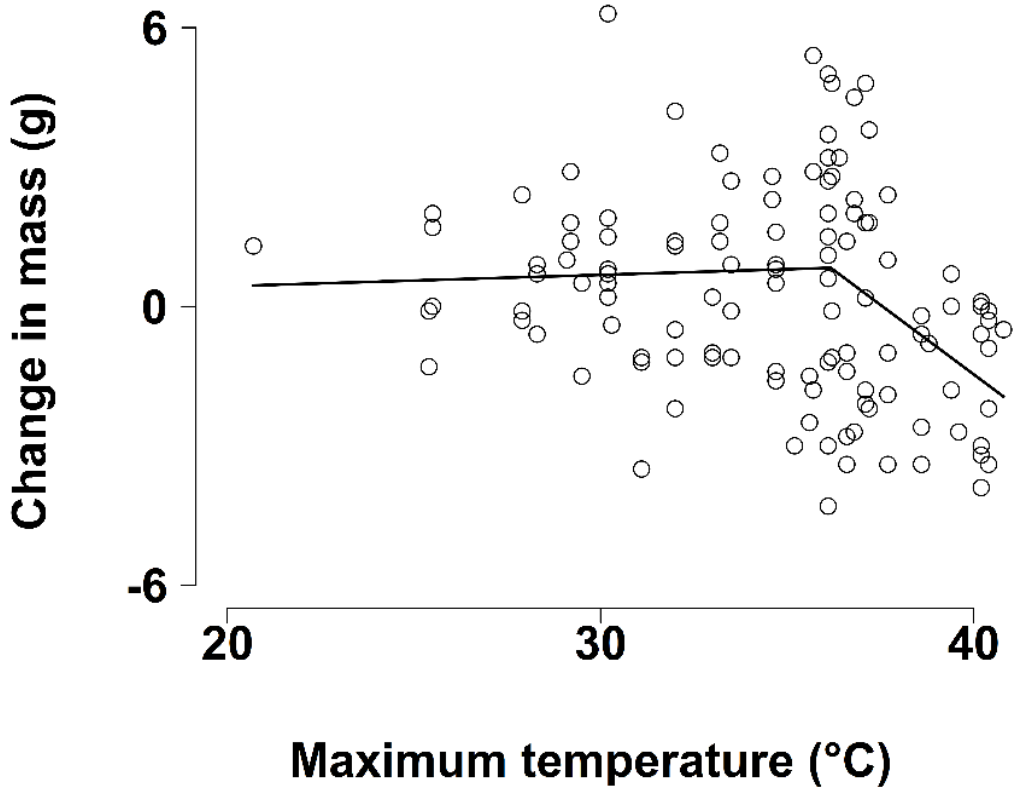


Figure 4.6: Change in southern pied babbler Turdoides bicolor *body mass (g) from one morning to the next as a function of maximum air temperature (°C) on the observation day. Line represents the segmented linear regressions for the relationship between mass change and temperature above and below the detected temperature threshold (36°C), i.e. no relationship below the threshold temperature and a significant negative relationship above the temperature threshold. Figure is generated from the data presented in Appendix Table 4.10 and Appendix Table 4.11.*

4.5 Discussion

Pied babblers exhibited poor hatching success at high temperatures, as I also showed in Chapter 3 using a larger, long-term dataset. In order to explore the mechanisms behind this relationship further, I collected behavioural and physiological data simultaneously from the same individuals in the wild. Employing a novel combination of non-invasive DLW, nest temperature data, and field-based behaviour observations, I have demonstrated that 1) pied babblers generally incubated their nests

almost constantly (95% of daylight hours), but the proportion of time that nests were attended declined with increasing air temperature (Bueno-Enciso et al., 2017; Clauser & McRae, 2017); 2) operative temperatures in unattended nests were substantially higher than air temperatures and frequently exceeded widely reported lethal limits for avian embryos (Webb, 1987; Conway & Martin, 2000; Birkhead, Hall, Schut, & Hemmings, 2008; DuRant et al., 2013; Wada et al., 2015) and the inflection air temperature values above which passerine birds rapidly increase rates of evaporative water loss via panting (McKechnie et al., 2017; Smith, O'Neill, Gerson, McKechnie, & Wolf, 2017); 3) pied babblers incurred water costs, but not energy costs, of incubation at high temperatures (Smit & McKechnie, 2015; Cooper et al., 2019); and 4) pied babblers from incubating groups lost mass during very hot weather (du Plessis et al., 2012; Sharpe et al., 2019; van de Ven et al., 2019). Multiple lines of evidence therefore suggest that, during very hot periods, incubating pied babblers leave nests unattended to avoid dehydration (Downs & Ward, 1997; Clauser & McRae, 2017), rather than to take advantage of ambient incubation (De Marchi, Chiozzi, Fasola, De Marchi, & Chiozzi, 2008; Londoño, Levey, & Robinson, 2008; Boulton, Richard, & Armstrong, 2010; Shibuya, Braga, & Roper, 2015; Bambini, Schlicht, & Kempenaers, 2019). With operative temperatures in unattended nests regularly exceeding lethal limits for avian embryos, reduced nest attendance at high air temperatures may contribute to reduced hatching success during hot incubation periods.

Impacts of high air temperatures during incubation were consistently more important than group size effects in this cooperatively breeding bird. In fact, air temperature was the single most important factor for predicting hatching probabilities, nest attendance during incubation, and ΔM_b in pied babblers from incubating groups. High air temperatures were associated with significant declines in each case, consistent with well-established relationships between high air temperatures and reduced hatching success (Birkhead et al., 2008; Wada et al., 2015; Clauser & McRae, 2017), reduced nest

attendance (Bueno-Enciso et al., 2017), and body mass loss (du Plessis et al., 2012; Sharpe et al., 2019; van de Ven et al., 2019) in the literature. That DEE declined with T_{max} was unsurprising, given that a) cooler periods pose a greater energetic challenge for incubating birds than hot periods, on account of the increased thermoregulatory cost of maintaining a high body temperature and warming eggs against a thermal gradient (Bryan & Bryant, 1999; Nord et al., 2010; D. T. C. Cox & Cresswell, 2014), b) incubating birds are less physically active (Ardia, Pérez, Chad, Voss, & Clotfelter, 2009; Nwaogu et al., 2017), and c) animals can exhibit signs of stress, such as high levels of oxidative stress, alongside low energy metabolism (Bury, Cichoń, Bauchinger, & Sadowska, 2018). The finding is consistent with several other recent studies showing declining DEE with increasing T_{max} (De Heij, Ubels, Visser, & Tinbergen, 2008; Smit & McKechnie, 2015; Cooper et al., 2019).

However, my finding that incubating pied babblers did not maintain water balance when incubating for long periods of time on hot days, but not on cool days, is of crucial importance. This finding strongly suggests that birds incubating at high temperatures may leave the nest as a result of the water costs incurred. Incubating birds cannot fully engage in normal behavioural thermoregulation activities, such as retreating to the shade (Wolf, 2000), or adjusting foraging and drinking behaviours (Smit et al., 2016; Abdu, McKechnie, Lee, & Cunningham, 2018; Cooper et al., 2019). Foraging and drinking time is constrained during incubation (Bueno-Enciso et al., 2017), and incubating birds need to be relieved regularly (Clauser & McRae, 2017). They rely on evaporative cooling to maintain body temperature below lethal levels while incubating (G. S. Grant, 1982; Downs & Ward, 1997; Brown & Downs, 2003; O'Connor et al., 2018), presumably at high water cost to themselves given high nest operative temperatures relative to air temperatures (see Appendix for three examples where I observed physical signs of water stress and dehydration in incubating birds). Lethal dehydration has resulted in mass mortality of birds (reviewed by McKechnie, Hockey, & Wolf, 2012; McKechnie & Wolf, 2010)

and mammals (Welbergen, Klose, Markus, & Eby, 2008; Ratnayake, Kearney, Govekar, Karoly, & Welbergen, 2019) and the water turnover habits of birds in arid environments tend to be frugal (Cooper et al., 2019). That temperature did not affect water balance (also see Cooper et al., 2019; Williams, 2001), except in interaction with the proportion of time spent incubating, provides an indication of just how important it is for birds to maintain water balance in hot and dry environments, even over short timescales.

Pied babblers build open cup nests in sparse vegetation (Ridley, 2016) and the operative temperatures I recorded in unattended pied babbler nests regularly exceeded a) temperatures at which evaporative water loss increases rapidly in passerine birds (4°C, McKechnie et al., 2017; Smith et al., 2017), b) optimal temperatures for embryo development in passerine birds (36–40°C, DuRant et al., 2013), and c) lethal temperature limits for developing avian embryos (40.5°C-51°C, DuRant et al., 2013; Grant, 1982; Griffith et al., 2016; Stoleson & Beissinger, 1999; Webb, 1987). Such high nest temperatures have been recorded in several bird species nesting in exposed sites (Brown & Downs, 2003; Tieleman, van Noordwijk, & Williams, 2008; AlRashidi et al., 2011; Clauser & McRae, 2017), and some arid zone species exhibit quite high heat tolerance in developing embryos (Grant, 1982; Reyna & Burggren, 2012; Griffith et al., 2016). Nonetheless, leaving nests unattended for long periods of time during the heat of the day risks exposing developing avian embryos to high temperatures (Mayer et al., 2009; J. M. Carroll, Davis, Elmore, & Fuhlendorf, 2015; DuRant et al., 2019), potentially exceeding lethal limits (Webb, 1987) and risking embryo death (Birkhead et al., 2008; Wada et al., 2015; Clauser & McRae, 2017) or leading to other problems such as increased hatching asynchrony (Griffith et al., 2016) and an increased risk of nest predation (DeGregorio et al., 2015). It is therefore likely that near-constant nest attendance is both highly desirable (G. S. Grant, 1982), in order to limit exposure of embryos to excessive heat via incubation and shading, and difficult to sustain at high temperatures,

because birds prevent body temperature exceeding lethal limits by engaging in costly evaporative cooling (Albright et al., 2017; O'Connor, Wolf, Brigham, & McKechnie, 2017; McKechnie & Wolf, 2019). The reduced nest attendance I observed at high temperatures is, therefore, likely to indicate that parental investment in incubation is constrained by the water costs of heat exposure (Amat & Masero, 2004; Coe et al., 2015), and may suggest progress towards eventual nest abandonment (Stoleson & Beissinger, 1999; Sharpe et al., 2019).

I found no evidence that negative effects of high temperatures on hatching probabilities, nest attendance, DEE, water balance, or mass change were moderated by group size. Although I did not have strong statistical power to detect such an interaction in this dataset and the effect would have had to be very large, this result is consistent with my conclusion in Chapter 3. Given that cooperative breeding strategies are associated with highly variable environments (Jetz & Rubenstein, 2011; Lukas & Clutton-Brock, 2018), helpers may play a role in buffering breeding against adverse weather conditions. In cooperative breeders, most group members contribute to caring for young (Koenig & Dickinson, 2004), and consequently nests are rarely left unattended for more than a few minutes (Canestrari et al., 2009; Ridley & Thompson, 2011). In this case, I did not find evidence of a buffering effect of group size on the thermoregulatory costs of incubation, since temperature affected individuals and nests in the same way across all group sizes. This may be because pied babblers share incubation effort unequally between group members (Ridley & Raihani, 2008), with some individuals carrying higher costs of breeding than others (Canestrari, Chiarati, et al., 2008; Wiley & Ridley, 2016), an area of inquiry that would benefit from further research (see Appendix Table 4.11 and Fig. 4.4 – Fig. 4.7 for some exploratory data analyses on variation in individual incubation effort).

4.6 Conclusions

Given that a) pied babblers incubate their eggs almost constantly during the day, b) instances where lower than normal incubation constancy was observed all occurred on hot days, and c) unusually low incubation constancy was followed by nest abandonment or failure, I suggest that reduced incubation constancy at high temperatures contributes to hatching failure by increasing the risk of exposure of embryos to lethal temperatures. I could not directly test for causal relationships between effects of temperature on the behaviour and physiology of incubating pied babblers and hatching success, which would require an experimental approach or at least observations over multiple days within the same breeding attempts. However, I present multiple lines of evidence suggesting that pied babblers should closely attend nests at high temperatures, to prevent embryos from overheating, but may be constrained from doing so by the thermoregulatory costs of incubation at high temperatures. Birds incubating for long periods of time on hotter days did not maintain neutral/positive water balance, and birds in incubating groups lost mass on hotter days. I therefore suggest that, rather than strategically leaving the nest to take advantage of opportunities for ambient incubation, pied babblers leave their nests on hot days due to the water costs incurred as a result of incubating at high temperatures. Considering both behaviour and physiology simultaneously in the same individuals, at the same time, under natural conditions, provided invaluable insights into the thermal constraints incubating birds were operating under. Finally, as I found no effect of group size on the responses I measured, either alone or in interaction with environmental factors, I conclude that cooperative breeding may not confer an advantage over non-cooperative breeding strategies during the incubation phase in terms of buffering the thermoregulatory costs of incubation.

Although parental care strategies are flexible in response to both weather and social conditions (Russell et al., 2002; Clutton-Brock et al., 2004; Langmore et al., 2016), these strategies have limits

(Clauser & McRae, 2017; Sharpe et al., 2019). Given that both mean temperatures and hot extremes are increasing in frequency under global climate change (IPCC, 2013), the incubation period could become a major bottleneck for reproduction across species with different reproductive strategies. Birds will likely incur ever greater thermoregulatory costs of incubation as temperatures rise, leading to reduced nest attendance, potential overheating of eggs, and ultimately, compromised population replacement and persistence.

CHAPTER 5: High temperatures are associated with poor nestling growth and altered parental care and may limit fledging rates in a cooperatively breeding bird

Preamble

In this chapter, I present an analysis of nestling size and daily growth rates, and parental care behaviour data, collected from breeding pied babbler groups over three austral summers between Sept 2016 and Feb 2019. I explore the mechanisms behind the relationship between fledging failure and high temperature identified in Chapter 3. I show that high temperatures likely drive fledging failure via compromised nestling mass, size and nestling daily growth rates on hot days. I also found that high temperatures were associated with fewer provisioning visits by adults. Even though the number of visits to the nest was reduced, provisioning adults delivered comparable biomass to nestlings between hot and cool days, but this was not sufficient to mitigate the negative effects of high temperatures on nestling mass, size and growth.

5.1 Abstract

Determining the mechanisms by which climatic factors influence survival and reproduction is critical for predicting how climate change will influence population persistence. In Chapter 3, I showed that that groups of all sizes were less likely to produce surviving young during hot weather. In this chapter, I use detailed nest life history, nestling growth, and adult behaviour datasets collected from cooperatively breeding southern pied babblers *Turdoides bicolor* over three breeding seasons to explore the mechanisms by which weather (temperature, rainfall) and social (group size) factors affect nest outcomes during the nestling developmental stage. Temperature had a quadratic effect on fledging probability (negative effect of temperature above 33°C, positive effect below), with an upper limit of 38°C, above which no nests fledged. High temperatures led to lower provisioning rates by adults and were associated with lower nestling body mass, smaller size, and reduced growth of nestlings. Path analysis showed that higher rainfall and larger group sizes positively affected adult investment in nestlings but did not directly influence nestling mass or size. Adult birds in larger groups invested less per individual in raising young than adult birds in smaller groups, while nestlings received consistent care across group sizes and temperatures, suggesting a 'load-lightening' benefit of larger group size accruing to all adult group members. Adult group members adjusted their provisioning strategy at higher temperatures, provisioning larger quantities of food per visit to the nest, but at less frequent intervals. Adjustments to adult provisioning strategies did not compensate for the direct negative effects of high air temperatures on nestling mass, size and daily growth rates, which likely explain low fledging success rates at high temperatures in this species. Given that both mean temperatures and the frequency with which heatwaves occur are increasing, the data presented in this chapter suggest that population persistence in southern pied babblers may be compromised via thermal constraints on successful reproduction.

5.2 Introduction

Anthropogenic climate change is affecting wildlife populations around the world (Saino et al., 2011; Iknayan & Beissinger, 2018; Ripple et al., 2019; Rosenberg et al., 2019), in part via impacts of altered temperature and rainfall patterns on reproductive success (Stevenson & Bryant, 2000; Cahill et al., 2013; Cunningham et al., 2013; Paniw et al., 2019; van de Ven, Fuller, et al., 2020). Accurately predicting how climate change will influence reproduction, and hence population persistence, requires an understanding of the mechanistic links between weather and reproductive outcomes (Conradie et al., 2019; Ratnayake et al., 2019). Therefore, research priorities include determining the mechanisms by which temperature and rainfall affect reproductive outcomes via direct effects on offspring size and daily growth rates, as well as indirectly via effects on parental care strategies (Buchholz et al., 2019).

Adverse weather conditions can impair nestling development (Mainwaring et al., 2016; Imlay, Mills Flemming, Saldanha, Wheelwright, & Leonard, 2018) by forcing nestlings to trade-off between devoting energy to thermoregulation or to growth (Dawson, Lawrie, & O'Brien, 2005). Specifically, high temperatures constrain nestling growth (Cunningham et al., 2013; Mainwaring & Hartley, 2016; Andreasson et al., 2018), result in smaller nestlings overall (Salaberria et al., 2014; Wada et al., 2015; Rodriguez & Barba, 2016), alter corticosterone levels (Newberry & Swanson, 2018; Crino, Driscoll, Brandl, Buchanan, & Griffith, 2020), and reduce survival probabilities (Greño, Belda, & Barba, 2008; Zuckerberg, Ribic, & McCauley, 2018). Rainfall often has a positive effect on nestling development (Wiley & Ridley, 2016) and survival (Skagen & Yackel Adams, 2012; Mares et al., 2017), at least in arid and semi-arid ecosystems, presumably due to increased food availability after rain (Cumming & Bernard, 1997; Hidalgo Aranzamendi et al., 2019), although see Morganti et al. (2017) and Cox et al. (2019) for effects of rainy weather in temperate environments. During droughts, nest outcomes can

be severely compromised (Morrison & Bolger, 2002; Conrey et al., 2016; Cruz-McDonnell & Wolf, 2016).

The above effects of temperature and rainfall on nestlings may be direct due to impacts on nestling physiology, or indirect via, for example, impacts on parental behaviour (Drent & Daan, 1980; Salaberria et al., 2014). Several recent studies suggest that negative effects of adverse weather can be moderated by adjustments in parental care strategies including brooding (S. A. Oswald, Bearhop, Furness, Huntley, & Hamer, 2008; Mainwaring & Hartley, 2016) and provisioning (Auer & Martin, 2017; Sofaer et al., 2018). Other studies indicate that birds trade off foraging behaviour against thermoregulation (Bladon et al., 2019), particularly when provisioning nests where they reduce provisioning rates as temperatures increase (Cunningham et al., 2013; Wiley & Ridley, 2016; van de Ven et al., 2019). Cooperatively-breeding species may respond differently to non-cooperative species, because the amount of care that dependent young receive can be affected by both the number (Russell et al., 2002; van de Ven, Fuller, et al., 2020) and behaviour (Canestrari, Chiarati, et al., 2008; Ridley & Raihani, 2008; Lu, Yu, & Ke, 2011) of helpers present. The investment in young provided by helpers may be additive (Canestrari, Marcos, et al., 2008; Pike et al., 2019; van Boheemen et al., 2019), or compensatory, enabling breeders to reduce their investment while young receive a similar amount of care overall, a behavioural pattern termed 'load-lightening' (Crick, 1992; Langmore et al., 2016). Thus, helpers may benefit the brood, resulting in nestlings that are heavier and more likely to survive (Ridley & Raihani, 2007b; Meade et al., 2010; van de Loock et al., 2017), or they may benefit the breeding pair, resulting in improved survival of breeding adults between years (Langmore et al., 2016).

Southern pied babblers *Turdoides bicolor* ('pied babblers') are cooperative breeders endemic to the Kalahari, which is a semi-arid ecosystem characterised by hot summers and periodic droughts (van Wilgen et al., 2016). Rainfall is extremely variable between years (MacKellar et al., 2014) and, over the

last 20 years, high temperature extremes within the Kalahari have increased in both frequency and severity (Kruger & Sekele, 2013), also see Chapter 3. Pied babblers have natural variation in group size (Raihani & Ridley, 2007b), enabling comparisons between smaller and larger groups within a population. All adult group members contribute to parental care (Ridley & Raihani, 2007b). Previous research on this species has shown that, in larger groups, there are lower rates of nestling predation (Raihani & Ridley, 2007b) and higher fledging rates (Ridley, 2016), dependent young are provisioned for longer (Ridley & Raihani, 2007b), and inter-brood intervals are shorter (Ridley & Raihani, 2008). However, irrespective of group size, high air temperatures during early development result in reduced provisioning rates to nestlings (Wiley & Ridley, 2016), smaller nestlings (Wiley & Ridley, 2016), reduced likelihood of fledging at least one chick per breeding attempt (Chapter 3), and compromised adult foraging efficiency and mass maintenance (du Plessis et al., 2012).

I have used detailed nestling morphometric data and adult behaviour data collected from individually marked and habituated pied babblers over three austral summer breeding seasons to explore the mechanisms by which temperature, rainfall, and group size might influence the transition from hatching to fledging in a cooperatively breeding bird. Specifically, I used confirmatory path analysis (Shipley, 2009; Larson et al., 2015) to empirically test whether temperature, rainfall, and group size influence fledging probabilities via effects on nestling mass and structural size or via changes in adult parental care behaviour. I further explored weather and group size effects on nestling daily growth rates and the foraging and provisioning behaviour of adult group members. I predicted that high temperatures and low rainfall would correlate with reduced provisioning effort and compromised nestling growth, size, and survival, while I expected larger group sizes to have the opposite effect.

5.3 Materials and Methods

5.3.1 Study site and system

Fieldwork was conducted with a habituated population of individually marked pied babblers at the Kuruman River Reserve (33 km^2, KRR; 26°58'S, 21°49'E) in the southern Kalahari. See Chapter 1 for a detailed description of the study site and study species.

5.3.2 Data collection

Data were collected for each austral summer breeding season between September 2016 and February 2019 (three breeding seasons in total).

Nestling size and daily growth rates

To identify climatic and social factors associated with nestling size and daily growth rates, I monitored all nests initiated in the study population during each breeding season to determine hatching dates (*n* = 99 nests in total). Nestlings were measured (body mass, tarsus length, and wing length) between 06h00 and 07h00 (morning) and again between 18h00 and 19h00 (evening) on the 5th day after hatching (d5, representing growth during a fast growth phase) and the 11th day after hatching (d11, representing growth during an asymptote phase). Body mass measurements (± 0.1 g) were taken by weighing nestlings on a top-pan scale. Tarsus length was measured (± 0.1 mm) using clock-dial vernier calipers and wing length (± 0.1 mm) using a stopped rule. Data are presented for right tarsus and right wing. Natal group size (the number of adults present during the period between hatching and fledging) and brood size (the number of nestlings in the brood on the measurement day) were recorded for each brood on each measurement day.

Nestling size was recorded as evening body mass, tarsus length, and wing length measurements, representing nestling mass and size at the end of a full day of provisioning by adults. Nestling daily growth rates were calculated as percentage change (Δ) in body mass, tarsus length, and wing length between morning and evening measurements, standardised for differences in the time between measurements using the equation presented by du Plessis et al (2012):

$$\Delta = 100[(x_2 - x_1)/x_2]/[\Delta_t/12]$$

where Δ_t = number of hours between t_1 (time of morning measurement) and t_2 (time of evening measurement); x_1 = mass, tarsus, or wing length measurement at t_1 and x_2 = measurement at t_2.

Provisioning data

I additionally recorded all provisioning visits to the nests during the morning (08h00 to 09h30), at midday (12h00 to 13h00), and in the afternoons (15h00 to 16h30) on d5 and d11, between morning and evening nestling measurements. Data on provisioning visits were collected using a combination of video cameras (Sony HDR-XR160E) placed on a tripod 4–6 m from the nest and nest watches undertaken by one human observer with binoculars, seated 15–20 m from the nest. Provisioning data were captured using CyberTracker software (v3.448; www.cybertracker.org) on a smartphone. It was not possible to consistently identify the provisioning bird or to estimate the biomass provisioned from the distances at which I observed the nests, so the only provisioning data available for d5 and d11 is the number of provisioning visits to the nest per unit time observed.

Adult behaviour data

To determine effects of weather and social factors on the proportion of time adult birds allocated to parental care vs. self-maintenance, I conducted up to 4 x 20-minute continuous time-activity focal

behaviour observations (Altmann, 1974) within each of 6 focal sessions per day. I focused on groups with 7- to 9-day-old nestlings, i.e. between the days on which I had collected nestling morphometric measurements. Focal sessions lasted two hours each, with the first starting at 07h00 and the last starting at 17h00. I collected behaviour data from both members of the dominant pair and up to two subordinate adults (one of each sex where possible), allowing for inclusion of sex and rank in analyses. When group size was = 3 adult individuals, the pair and the single adult subordinate were studied; when group size was = 4, the pair and both subordinate adults were studied; when group size was > 4, the pair and two subordinate adults of opposite sex (where possible) were studied. I observed each focal individual once within each of the six daily focal sessions, and randomised the order in which each individual was observed within each focal session (*sensu* du Plessis et al (2012)). In this way, I collected approximately six focal behaviour observations per bird per day, spread evenly across the day to minimise time of day effects on summarised measurements. From these data, I could estimate individual investment in young at the nest (including number of provisioning visits to the nest, biomass caught vs. provisioned, and time spent attending the nest for each individual), but not the total number of provisions made to the nest by all group members on that day (because I had to concentrate on one focal bird at a time). All birds for which I had fewer than four focal observations per day were removed from the analyses (n = 6 of 68). I captured the data on an Android smartphone (Mobicel Trendy), using Prim8 software (M. McDonald & Johnson, 2014), in which the duration of each observed behaviour is recorded to the nearest second.

For analyses of time budgets, I summed time observed foraging (foraging effort, including searching for and handling prey), attending the nest (all visits to the nest, including provisioning and brooding), resting (preening, standing, and perching), and engaging in other activities (e.g. walking, flying, on sentinel duty, interacting with neighbouring groups), and calculated the proportion of time

allocated to each set of activities across all six focals, at the scale of a 'focal day'. During each focal behaviour observation, I collected detailed information for each successful foraging event, including the size class of each item caught and whether or not the item was provisioned to the nest. I converted prey captures to biomass (wet g) using the calculations from Raihani & Ridley (2007a). I recorded foraging success as total biomass caught per bird per day, and provisioning rates to the nest as total biomass provisioned per bird per day, i.e. at the scale of the focal day made up of six 20 min focal observations taken at intervals throughout the day. While there were time of day effects on foraging behaviour (e.g. foraging success, one-way ANOVA $F_{5,489} = 5.390$, $p < 0.001$; Fig. 5.1A), sampling evenly across the day per individual ensured minimal time of day biases on data collected ($F_{5,489} = 1.283$, $p = 0.269$; Fig. 5.1B), such that differences between days could be attributed to factors occurring on that day, rather than being artefacts of the time of day at which data were collected. Data analysed at the scale of the focal day are therefore comparable between birds and between days because I collected the same quantity of data per bird and per session across days.

Temperature and rainfall

Daily maximum temperature (T_{max}, in °C) and rainfall (mm) data were collected from an on-site weather station at the KRR (Vantage Pro2, Davis Instruments, Hayward, USA) as described in Chapter 1. Temperature variables included in statistical models were T_{max} on the measurement day and rainfall summed for the 60 days prior to initiation of the breeding attempt ($Rain_{60}$), to allow for delays between rainfall and invertebrate emergence in the Kalahari (Cumming & Bernard, 1997; Ridley & Child, 2009).

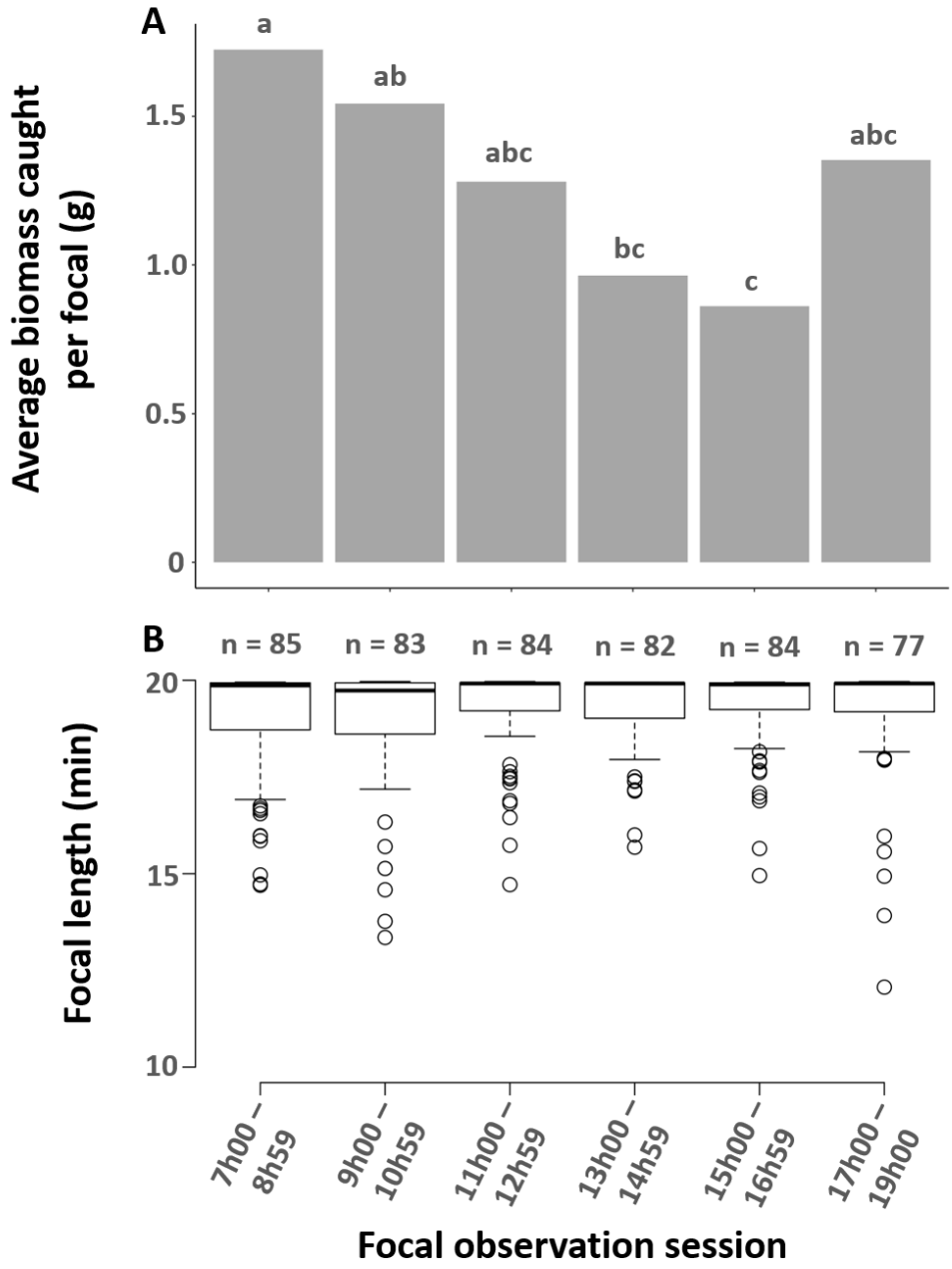


Figure 5.8: (A) average biomass caught per focal, and (B) focal length for each focal observation session. Post-hoc comparisons (Tukey HSD) show which focal sessions differed significantly from one another with regards to average biomass caught (A). Because focal data were collected evenly across all times of day, these differences in prey capture rates between focals are unlikely to affect comparisons between different days at the scale of whole days.

5.3.3 Statistical analyses

Statistical analyses were conducted in the R statistical environment, v 3.6.0 (R Core Team, 2017). The range of group size values in my final data set for this chapter was limited, such that I was not able to fit interactions (Leon & Heo, 2009; Champely et al., 2018) between climatic factors and group size in the models in order to directly test my primary hypothesis regarding the potential buffering effect of larger group size in pied babblers (Cohen's $f^2 > 0.36$ for all analyses). Specifically, most 'hot nests' (nests with live nestlings at temperatures ≥ 35.5°C) with nestlings that survived long enough to be measured were produced by groups with four adults (Fig. 5.2A). Only two breeding attempts by groups other than those with four adults (both with six adults) survived long enough during hot weather for me to measure the nestlings or record adult parental care behaviours. Only one group of three produced young at rainfall < 100mm, and no groups of six adults produced young at rainfall > 100mm (Fig. 5.2B).

Nestling mass, size and survival, days 5 and 11

In Chapter 3, I showed that pied babbler nestling mass is influenced by environmental factors and that fledgling survival to nutritional independence (~90 days after fledging) is influenced by nestling mass. Individuals that were heavier as nestlings were more likely to survive to nutritional independence. In this chapter, I test the hypothesis that nestling mass would likewise be important for predicting survival to fledging, and extend this analysis to include nestling structural size (evening measurements of tarsus and wing length) as well. I undertook a series of confirmatory path analyses to test whether and to what extent the impacts of weather conditions on nestling mass and structural size are direct (i.e. could be inferred to result from physiological limitations) or indirect (i.e. are mediated via changes in adult behaviour and therefore provisioning rates to nestlings). The path analysis approach was a useful starting point for the analyses in this chapter, allowing me to use single

complex models to test multiple hypothesised direct and indirect effects of temperature, rain, group size, brood size, and provisioning rates on nestling mass and structural size, and on the fledging success of individual nestlings measured on the 5th and 11th days after hatching. I used the R package *piecewiseSEM* (Lefcheck, 2016), which can accommodate a range of error structures. This is necessary because the response variables in the component models all have different distributions (see below). Standardised effect sizes are reported (Leftcheck et al. 2018).

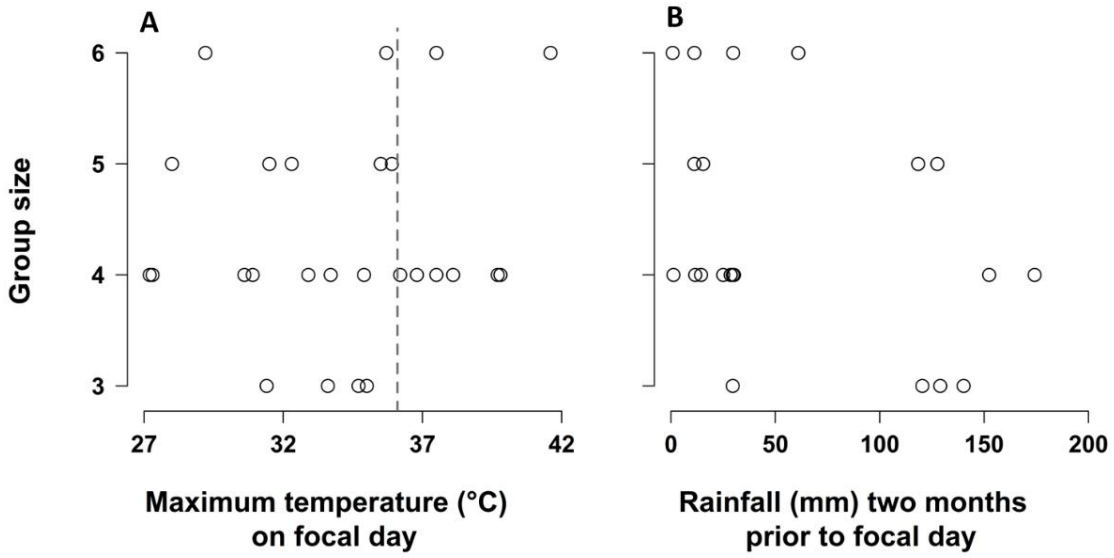


Figure 5.2: Spread of group sizes by (A) temperature on the focal day (dashed line = 35.5°C) and (B) rainfall in the two months prior to the breeding attempt (mm).

Path analysis allowed me to specify and simultaneously quantify all hypothesised relationships, including the indirect effects of weather and group size on survival to fledging via nestling mass or nestling size. Path coefficients are partial regression coefficients and can be interpreted similarly to simple and multiple regression outputs. While model selection processes can be applied to multiple path analyses (Shipley & Douma, 2019), I was not using path analysis to choose between competing

hypotheses in this case and therefore I fit a single path analysis for each nestling age class (5 days and 11 days) and evening measurement (mass, tarsus length, wing length). Statistical significance was taken as $p < 0.05$.

I used the path analyses to test the following statistical hypotheses:

Fledging probability would be negatively affected by low nestling body mass and small structural size (logit);

Nestling body mass and structural size (evening) would be negatively affected by a) high T_{max} on the day of measurement, b) low $Rain_{60}$, c) smaller group size, d) larger brood size, and e) fewer provisioning events (Gaussian);

Number of provisioning events would be negatively affected by a) high T_{max}, b) low $Rain_{60}$, c) smaller group size, and d) smaller brood size (Poisson).

Nestling daily growth rates

In the path analyses I used nestling body mass and structural size measurements taken in the evening on the 5th and 11th day after hatching, as I hypothesised that absolute nestling mass and size at these time points would predict the probability of survival to fledging. In order to further explore and understand the patterns identified in the path analyses (see results – in short, nestling mass was influenced by temperature and influenced survival to fledge for both age classes of nestling), I considered the effect of $Rain_{60}$, T_{max}, brood size, and natal group size on nestling daily growth rates (body mass, tarsus length, and wing length) calculated as the difference between morning and evening measurements on the 5th and 11th day after hatching (see methods). Daily growth rates likely dictate the mass and size that nestlings would have attained by d5 and d11. For this follow-on analysis, I used maximum likelihood linear mixed-effects models (LMMs) with Gaussian error structure in the R

package *lme4* (Bates et al., 2015). In order to account for repeated measures and thus for nonindependence of data, I included brood identity as a random factor, capturing variation by territory/breeding pair while avoiding over-fitting and destabilising the models.

Model selection using the Akaike's information criterion corrected for small sample size (AICc) was used to determine the model/s that best explained patterns of variation in the data. AICc (with maximum likelihood estimation) was used to test a series of models, each representing a biological hypothesis. Lower AICc values were taken to represent more parsimonious models, following Harrison et al (2018a). Where there were several models within 2 AICc of the top model, top model sets were averaged using the package *MuMIn* (Barton, 2015). Model estimates with confidence intervals that did not intersect zero were considered to explain significant patterns in the data (Grueber et al., 2011).

Adult investment in parental care

An important component of the path analyses above was variation in provisioning rates to the nest, data which were collected during three sets of nest watches between morning and evening measurements on each nestling measurement day (see results – in short, provisioning rates varied with temperature and group size and affected nestling mass, and therefore survival, in d11 nestlings). In order to investigate what factors influence adult provisioning decisions, I conducted focal behaviour observations throughout the day between nestling measurement days (on d7-d9 after hatching, see methods). From these data, I was able to construct detailed time budgets of the behaviour of adult pied babblers in groups raising nestlings.

To determine which variables best predicted the proportion of time adults spent foraging, resting, and attending the nest, I fitted binomial GLMMs with Penalised Quasi-Likelihood

(glmmPQL) to analyse the time budget data in the R package *MASS* (Venables & Ripley, 2002). The glmmPQL approach was used to address overdispersion in the data not adequately resolved by the inclusion of an observation level random term while still allowing inclusion of the random term for brood identity. The approach does, however, preclude model selection (Bolker et al., 2009). Proportion of time was modelled as a combined vector of total time spent on the selected activity (seconds) versus total time engaged in other behaviours (seconds). The model included predictor variables T_{max}, $Rain_{60}$, group size, and brood size, as well as sex and rank of the focal bird. Statistical significance was taken as $p < 0.05$.

To determine which variables best predicted biomass caught and biomass provisioned, using the foraging and provisioning data collected during focal observations on d7-d9 after hatching, I fitted GLMMs with a Poisson error distribution (log link) in the package *lme4* (Bates et al., 2015). Model selection was undertaken as described for nestling daily growth rates above. Response variables were rounded to the nearest digit (biomass in g). I considered the influence of the following parameters: T_{max}, $Rain_{60}$, group size, brood size, sex, and rank, and included quadratic terms for T_{max} and group size when there was no significant linear effect and visualisation of the data suggested a non-linear relationship. Model estimates with confidence intervals that did not intersect zero were considered to explain significant patterns in the data (Grueber et al., 2011).

5.4 Results

Maximum temperatures on observation and measurement days ranged from 27.2°C to 41.6°C (mean = 33.7 ± 3.5°C), and $Rain_{60}$ ranged from 0.8 to 174.2 mm (mean = 60.2 ± 55.5 mm). Group sizes averaged 4 ± 1 adults (range: 2 to 6) and brood sizes averaged 3 ± 1 nestlings (range: 1 to 5). Over three breeding seasons during which a total of 99 nests were monitored, 65 clutches hatched. Of these, 52 had nestlings that survived to 5-days-old (first nestling measurement day), 41 had nestlings that

survived to 7- to 9-days-old (adult behaviour observation day), and 38 had nestlings that survived to 11-days-old (second nestling measurement day).

5.4.1 Nestling mass, size, and survival

The path analysis models for nestling mass (evening) for d5 and d11 nestlings explained 11% and 22% of the observed variation in fledging probability respectively (d5*:* $X^2_{10} = 11.95$, $p = 0.288$, Fig. 5.3; d11: $X^2_{10} = 15.78$, $p = 0.106$, Fig. 5.4). Path analysis showed that temperature on the measurement day had the strongest influence on probability of fledging: high temperatures were associated with smaller nestling body mass (on both d5 and d11, which in turn predicted fledging probability) and lower provisoning rates by adults (on d11 only, which in turn predicted smaller nestling mass on d11). Higher $Rain_{60}$, larger group sizes, and larger brood sizes were associated with higher provisioning rates (on both d5 and d11), which in turn predicted larger nestling mass (on d11 only).

Specifically, for both nestling age classes, the number of provisioning visits to the nest declined as T_{max} increased (d5: Est = -0.095, $p < 0.001$; d11: Est = -0.154, $p = 0.002$), and increased with increasing group size (d5: Est = 0.089, $p = 0.018$; d11: Est = 0.155, $p < 0.001$), $Rain_{60}$ (d5: Est = 0.123, $p < 0.001$; d11: Est = 0.232, $p < 0.001$), and brood size (d5: Est = 0.089, $p = 0.004$; d11: Est = 0.127, $p = 0.004$). Nestlings of both age classes were lighter on hot days (d5: Est = -0.519, $p < 0.001$; d11: Est = -0.482, $p = 0.018$). Nestling mass was not affected by number of provisioning visits for d5 nestlings (Est = -0.044, $p = 0.726$), but d11 nestlings were heavier when provisioning visits were more frequent (Est = 0.417, $p = 0.033$). Heavier nestlings were more likely to fledge, and this relationship was detected for both d5 and d11 nestlings (d5: Est = 0.333, $p = 0.042$; d11: Est = 0.478, $p = 0.043$).

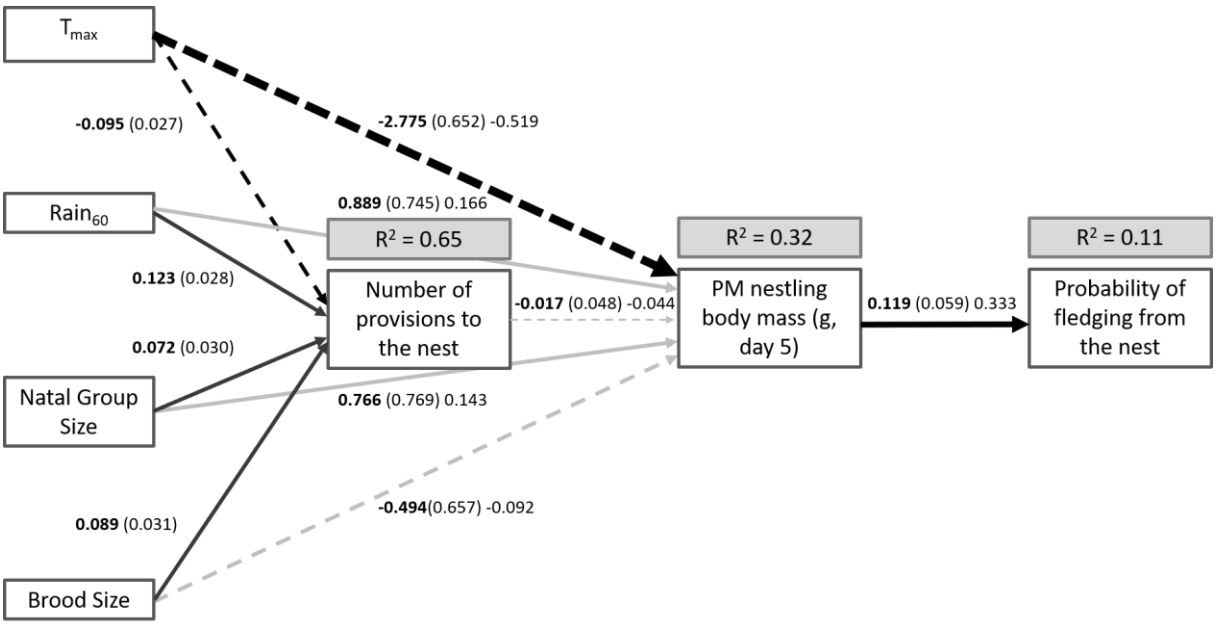


Figure 5.3: Path analysis exploring the effects of environmental factors (temperature and rainfall), group size, and brood size on individual probabilities of fledging via number of provisioning visits and nestling mass (evening) 5 days after hatching. Boxes represent measured variables. Arrows represent unidirectional relationships among variables. Solid arrows denote positive relationships, dashed arrows negative relationships. Unstandardised path coefficients are shown in bold, followed by standard errors in parentheses, and standardised estimates. Standardised Poisson effects could not be calculated in piecewiseSEM*. Non-significant paths are grey. Path thickness has been scaled relative to the absolute magnitude of the standardised estimates, such that stronger effects have thicker arrows.* R^2 *for component models are given in the grey boxes above response variables.*

For d5 nestlings, the strongest relationship identified was the direct effect of temperature on nestling mass (Fig. 5.3). For d11 nestlings, the relationships between temperature and nestling mass, provisioning rates and nestling mass, and nestling mass and fledging probability were all of similar strength (Fig. 5.4). Temperature affected fledging probability indirectly via negative effects of temperature on nestling mass (d5: Est = -0.173, calculated by multiplying standardised estimates along the path as follows: 0.333 * -0.519, see Fig. 5.3; d11: Est = -0.230). For d11 nestlings, number of provisioning visits affected fledging probability indirectly via positive effects on nestling mass and subsequent effects of larger nestling mass on improved fledging probability (Est = 0.199). High temperatures on d11 resulted in smaller nestling mass via reduction in the number of provisioning visits (Est = -0.064). Indirect effects of rainfall (Est = 0.097), group size (Est = 0.065), and brood size

(Est = 0.053) were associated with higher d11 nestling mass via the positive effect of rainfall on number of provisioning visits.

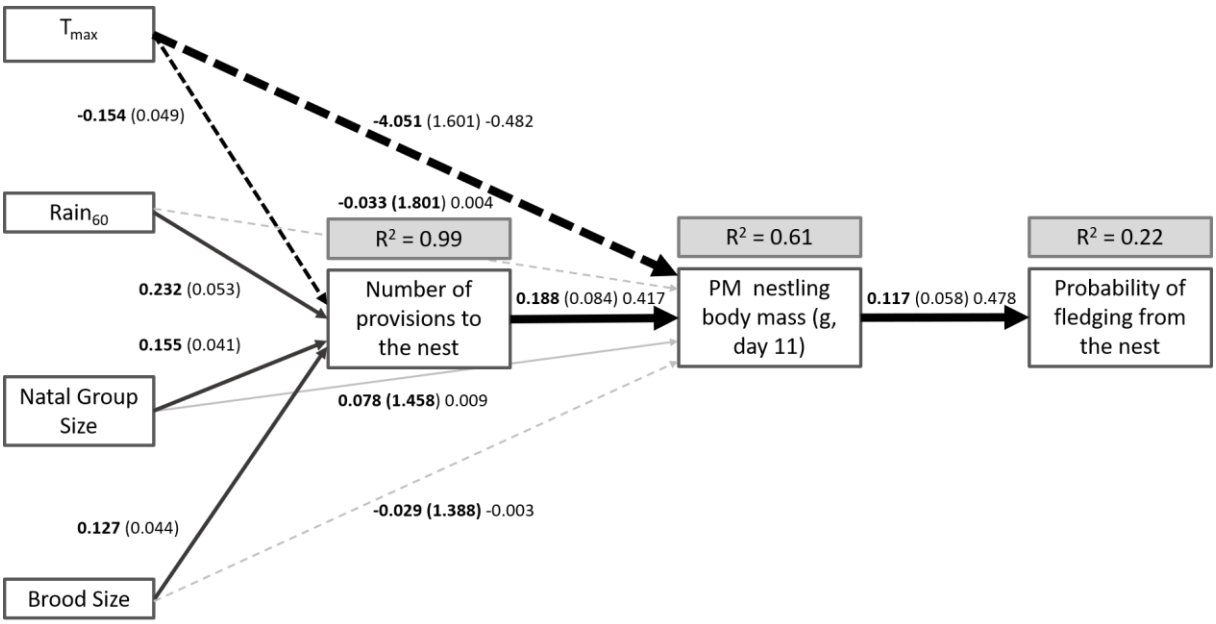


Figure 5.4: Path analysis exploring the effects of environmental factors (temperature and rainfall), group size, and brood size on individual probabilities of fledging via number of provisioning visits and nestling mass (evening) 11 days after hatching. Boxes represent measured variables. Arrows represent unidirectional relationships among variables. Solid arrows denote positive relationships, dashed arrows negative relationships. Unstandardised path coefficients are shown in bold, followed by standard errors in parentheses, and standardised estimates. Standardised Poisson effects could not be calculated in piecewiseSEM. *Non-significant paths are grey. Path thickness has been scaled relative to the absolute magnitude of the standardised estimates, such that stronger effects have thicker arrows.* R^2 *for component models are given in the grey boxes above response variables.*

Path analyses for tarsus length and wing length explained < 4% of the variation in fledging probability in d5 nestlings and 33-36% of the variation in fledging probability in d11 nestlings (X^2_{10} < 15.08, $p > 0.129$ in all cases, Appendix Fig. 5.1-5.4). Relationships between T_{max}, group size, $Rain_{60}$ and brood size were the same as for nestling mass models above. Neither tarsus nor wing length on d5 influenced fledging probabilities, but nestlings with longer tarsi (Est = 0.597, $p = 0.016$) and longer wings (Est = 0.593, $p = 0.021$) on d11 were more likely to fledge. I found no evidence that tarsus or wing length were themselves influenced by T_{max}, $Rain_{60}$, group size, brood size, or number of provisioning visits for either nestling age class.

5.4.2 Nestling daily growth rates

As might be expected, given the strong influence of T_{max} on the measurement day on nestling body mass in the evening identified in the path analyses, T_{max} was the most parsimonious predictor of daily mass gain both in 5-day-old and 11-day-old chicks. Nestlings gained less mass between morning and evening measurements on hotter days.

In 5-day-old nestlings, the single best-fit model for daily mass change contained only T_{max} (model weight = 0.645) and nestlings gained less mass as T_{max} on the measurement day increased (n = 93; Est = -4.043 ± 1.986, 95% CI: -7.922 - -0.151, t = -2.031; Fig. 5.5A). I found no evidence for effects of $Rain_{60}$, brood size, or natal group size (see Appendix Table 5.1 for full model selection outputs). Percentage change in tarsus length and wing length over the same 12 h period in 5-day-old nestlings was not influenced by any of the included predictor variables.

In 11-day-old nestlings, the single best-fit model for daily mass change also contained only T_{max} (model weight = 1.00) and nestlings gained less mass, sometimes even losing mass, on hotter measurement days (n = 77; Est = -7.028 ± 1.122, 95% CI: -8.393 - 4.034, t = -6.262, Fig. 5.5B). Nestling tarsi also grew significantly less on d11 as temperatures increased (top model weight = 0.772; Est = -0.804 ± 0.287, 95% CI: -1.381 - -0.285, t = -2.797; Fig. 5.5C) and, although the effect was not statistically significant, nestling wings also tended to grow less on hotter days (Est = -0.651 ± 0.396, 95% CI: -1.427 - 0.125, t = -1.643; Fig. 5.5D). I found no evidence for effects of $Rain_{60}$, brood size, or natal group size on percentage change in mass, tarsus length, or wing length of 11-day-old nestlings (see Appendix Table 5.2 and Appendix Table 5.3 for full model selection outputs for the mass and tarsus analyses; change in wing length not shown because the top model was the null model).

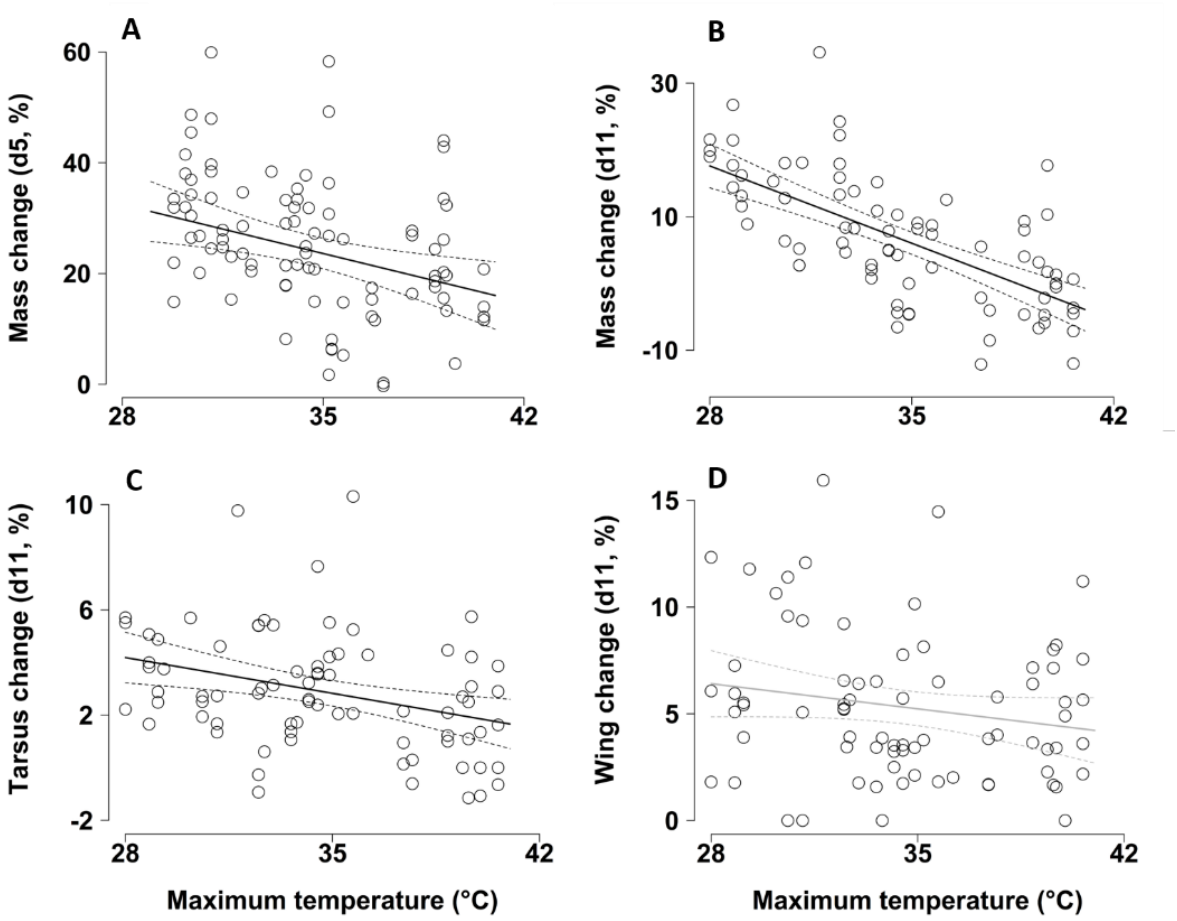


Figure 5.5: The effect of maximum daily temperature (T_{max}, °C) on nestling daily growth rates (% change over a 12 h period). Data points show the % daily mass change of (A) 5-day-old southern pied babbler Turdoides bicolor *nestlings and (B) 11-day-old nestlings as well as the (C) % daily tarsus length change and (D) wing length change of 11-day-old nestlings. Solid lines represent predictions from the models and dashed lines the 95% CIs. The regression line in (D) is greyed out as the trend shown was not statistically significant.*

5.4.3 Adult investment in parental care

I collected 593 focal behaviour observations (mean focal length = 19 ± 1.9 min) over 108 focal days (mean daily observation length over a focal day = 108 ± 17 min) during three austral summer breeding seasons (2016/17 n = 60 days, 2017/18 n = 32 days, 2018/19 n = 16 days). I observed 29 males, 29 females, and 4 individuals of unknown sex. Of these, 27 were dominant individuals and 35 were subordinates.

I observed foraging behaviour in 92.6% of focal observations. The birds spent between 8 and 86% of their time foraging throughout the day (mean = 53% time). The percentage of time spent foraging per focal day tended to be higher for males than females and was significantly lower in larger groups and after rain (Table 5.1; Fig. 5.6), but was not influenced by rank, brood size, or T_{max} (Table 5.1; Fig. 5.6). I observed resting in 97.8% of focals and time spent resting ranged from 3 - 81% time throughout the day (mean = 28%). The percentage of time spent resting per focal day was significantly higher on hot days, after rain, and in larger groups (Table 5.1; Fig. 5.6), but was not influenced by sex, brood size, or rank (Table 5.1; Fig. 5.6). Finally, I observed nest attendance in 54.3% of focals and time spent attending the nest ranged from 0 to 55% time throughout the day (mean = 11%). The percentage of time individuals spent attending the nest per focal day did not vary significantly with any of the predictor variables I included (Table 5.1; Fig. 5.6).

Total biomass caught per observation day averaged 7.0 ± 4.4 g per bird per focal day (n = 108 focal days, range: 0.0-20.3 g). After averaging the two top models (combined weight = 0.784), total biomass caught increased with increasing T_{max} until ~32.3°C, after which it declined with increasing T_{max} (Z = 3.980, p < 0.001; Table 5.2, Fig. 5.7A). The effect of group size was also quadratic: birds in intermediate-sized groups caught less biomass per day than birds in larger and smaller groups (Z = 3.621, p < 0.001; Table 5.2, Fig. 5.7B). I found no evidence that biomass caught per day was influenced by sex, rank, brood size, or rainfall (see Appendix Table 5.4 for full model selection outputs).

Table 5.5: GLMM with Penalised Quasi-Likelihood (glmmPQL) model outputs for factors influencing proportion of time spent foraging, resting, and attending the test. Models fitted to data from 88 days of focal observations on 62 different individuals from 13 groups. Significant terms (p < 0.05) are highlighted in bold. Random term: brood identity.

Model	Parameters	estimate	SE	t-value	P-value
Proportion time spent foraging	*Intercept*	-0.047	0.109	-0.437	0.664
	Brood size	0.157	0.092	1.701	0.105
	Group size	**-0.275**	**0.090**	**-3.049**	**0.007**
	Maximum temperature	-0.114	0.094	-1.221	0.227
	Rainfall two months prior	**-0.322**	**0.093**	**-3.476**	**0.003**
	Rank	-0.013	0.102	-0.132	0.895
	Sex (Male)	0.208	0.105	1.986	0.051
Proportion time spent resting	***Intercept***	**-0.965**	**0.134**	**-7.226**	**0.000**
	Brood size	-0.176	0.104	-1.689	0.108
	Group size	**0.364**	**0.100**	**3.625**	**0.002**
	Maximum temperature	**0.247**	**0.109**	**2.259**	**0.027**
	Rainfall two months prior	**0.437**	**0.104**	**4.222**	**0.001**
	Rank	0.154	0.133	1.153	0.254
	Sex (Male)	-0.049	0.138	-0.356	0.723
Proportion time spent attending the nest	***Intercept***	**-1.768**	**0.168**	**-10.507**	**0.000**
	Brood size	-0.019	0.115	-0.164	0.872
	Maximum temperature	-0.208	0.117	-1.781	0.079
	Group size	-0.059	0.119	-0.496	0.626
	Rainfall two months prior	-0.219	0.127	-1.722	0.101
	Rank	-0.284	0.223	-1.275	0.207
	Sex (Male)	-0.403	0.226	-1.779	0.080

Total biomass provisioned to the nest per observation day averaged 1.2 ± 1.1 g delivered to nestlings per adult bird per focal day (n = 108 focal days, range: 0.0-4.5 g). Rank and group size were the most parsimonious predictors of variation in biomass provisioned to the nest (the single best-fit model had a model weight of 0.590; Table 5.3). Subordinate individuals provisioned significantly less (1.0 ± 0.9 g per focal day) than dominant individuals (1.4 ± 1.3 g; Z = -2.228, p = 0.026; Fig. 5.7C). Individuals in larger groups provisioned less than those in smaller groups (Z = -2.133, p = 0.033; Fig.

5.7D). I found no evidence that biomass provisioned per day was influenced by temperature, brood size, rainfall, or sex (see Appendix Table 5.5 for full model selection outputs).

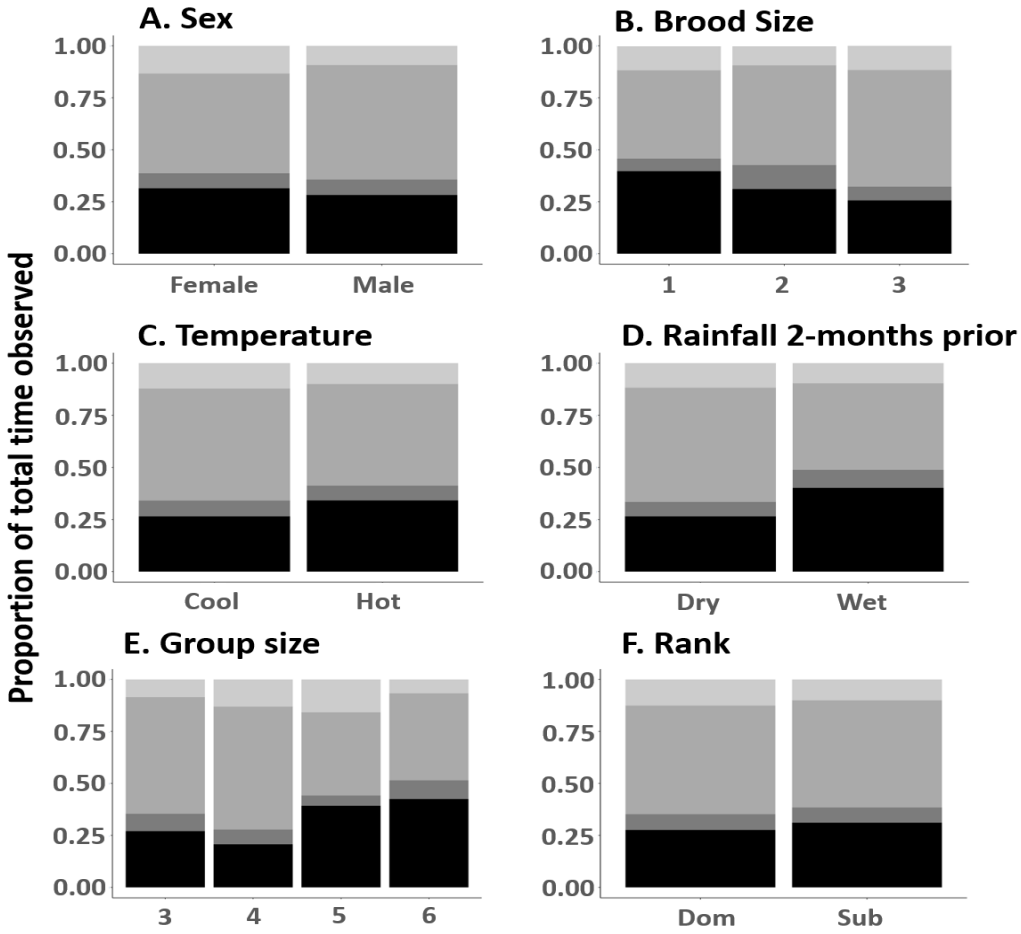


Figure 5.6: Average proportion of time spent resting (black), foraging (medium grey), attending the nest (light grey), and engaging in other activities (narrow dark grey band). Data from 88 days of focal observations on 62 different individuals from 13 groups, attending 23 nests over three breeding seasons.

Table 5.6: Top model sets for factors influencing total biomass caught per day. Model averaging was implemented for models with ΔAICc < 2 of the 'best-fit' model. Significant terms after model averaging are shown in bold. Data from 56 different individuals from 23 nests by 13 groups over 84 focal days.

Model	***AICc***	***ΔAICc***	***ωí***
Null model	438.7	17.28	0.00
Top model set:			
T_{max} ^2 + Group size ^ 2	421.42	0.00	0.55
T_{max} ^2 + Group size ^ 2 + Brood size	421.81	0.39	0.45
Effect size of explanatory terms after model averaging	*Estimate*	*SE*	*95% CI*
Intercept	1.903	0.092	1.719/2.085
T_{max}	**-0.168**	**0.067**	**-0.301/-0.035**
T_{max} ^2	**-0.228**	**0.057**	**-0.341/-0.116**
Group size	**-0.123**	**0.057**	**-0.236/-0.009**
Group size ^ 2	**0.169**	**0.046**	**0.077/0.259**
Brood size	0.094	0.067	-0.039/.227

Table 5.3: Top model sets for factors influencing total biomass provisioned per day. Model averaging was implemented for models with ΔAICc < 2 of the 'best-fit' model. Significant terms after model averaging are shown in bold. Data from 56 different individuals from 22 nests by 13 groups over 84 focal days.

Model	***AICc***	***ΔAICc***	***ωí***
Null model	237.1	5.6	0
Group size + Rank	231.5	0	1
Effect size of explanatory terms after model averaging	Estimate	SE	95% CI
Intercept	0.223	0.177	-0.184/0.539
Rank	**-0.468**	**0.210**	**-0.690/-0.029**
Group size	**-0.334**	**0.157**	**-0.890/-0.063**

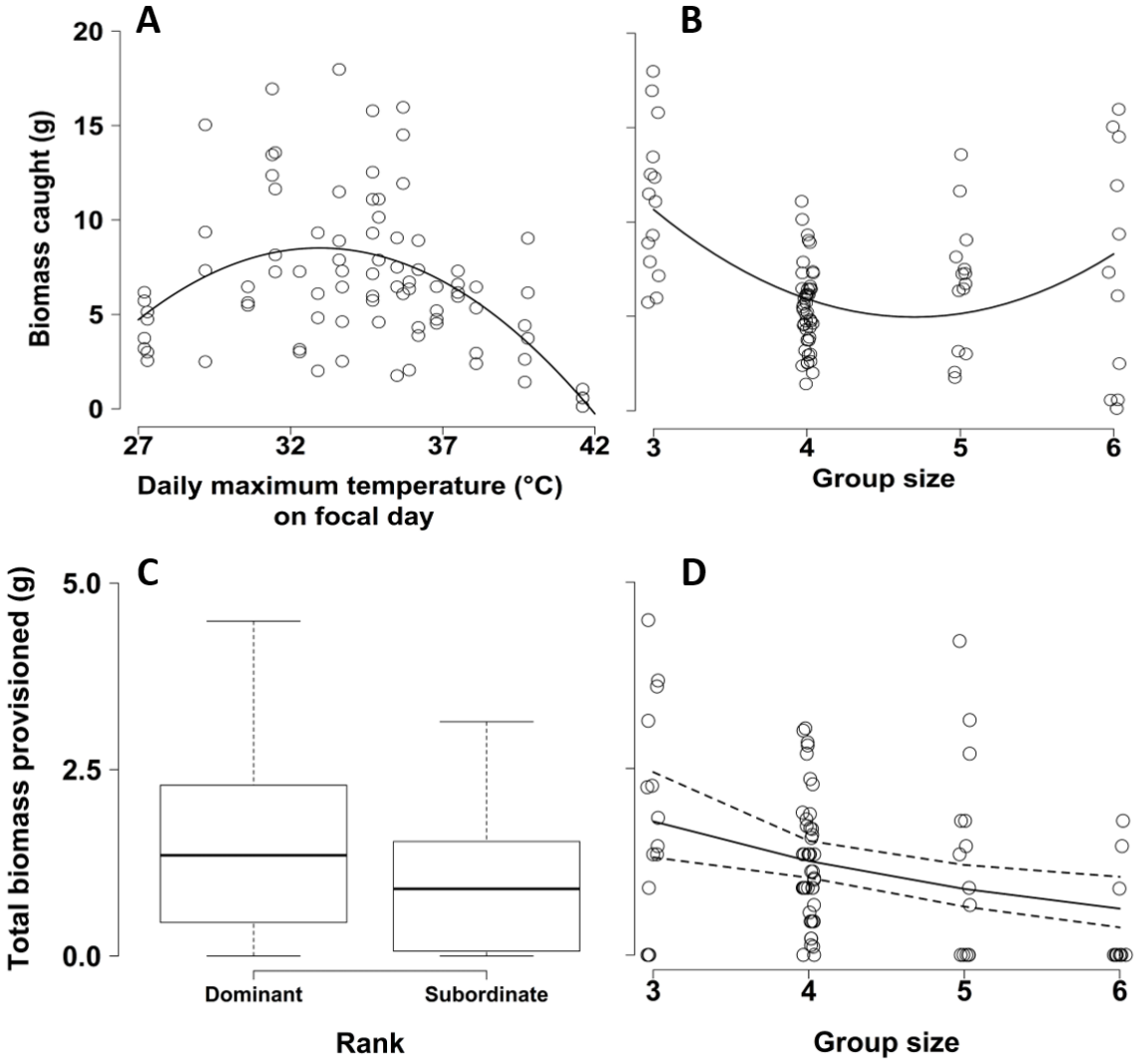


Figure 5.7: Biomass caught per individual per day as a function of daily maximum temperature (A, in °C) and group size (B) on the observation day. Biomass provisioned per individual per day as a function of rank (C) and group size (D) on the observation day.

5.5 Discussion

In this chapter, I have comprehensively investigated environmental (temperature and rainfall) and social (group size) mechanisms influencing survival of young over the development period from hatching to fledging in a cooperatively breeding bird endemic to an arid environment (the southern Kalahari Desert) heavily affected by climate change (Kruger & Sekele, 2013; van Wilgen et al., 2016).

I found that environmental factors, specifically temperature, were more prominent than group size in predicting fledging probabilities. Heavier nestlings were significantly more likely to fledge, consistent with previous studies showing that smaller size in nestlings correlates with reduced survival (Magrath, 1991; Schwagmeyer & Mock, 2008), and this effect was detectable in nestlings as young as five days old (babblers usually fledge at around 15 days of age, see Ridley (2016)). Path analysis showed that high temperatures during the day exerted a strongly negative influence on evening nestling body mass both directly (in both 5-day and 11-day-old nestlings) and indirectly via impacts on adult provisioning rates (in 11-day-old nestlings only); and GLMMs showed that this result was mirrored by (and potentially explained by) compromised diurnal (12hr) mass gain in both 5-day and 11-day-old nestlings on hotter days. Rainfall and group size positively influenced the number of provisioning visits by adults to both 5-day and 11-day-old nestlings, but did not directly influence nestling structural size in the evening (tarsus and wing length) or diurnal growth rates.

5.5.1 Temperature, nestling size and growth, and fledging success

That nestling growth was compromised over the course of a single hot day suggests that isolated hot days are likely to be detrimental to nestling survival regardless of whether or not they occur as part of a heat wave. A possible mechanism underlying mass loss on hot days is dehydration (which I did not measure in nestlings, although see Chapter 4 for dehydration in incubating adults): for example Salaberria et al. (2014) identified a positive relationship between nest heat exposure and nestling dehydration in spotless starlings *Sturnis unicolor*. The effect of temperature on tarsus and wing growth was smaller than for mass, suggesting that pied babbler nestlings prioritise limb growth over mass gain under challenging conditions. This makes sense because individual survival in birds depends strongly on physical traits such as wing length (Naef-Daenzer & Grüebler, 2016; Martin, Tobalske, Riordan, Case, & Dial, 2018). Longer wings allow for improved mobility (Jones et al., 2017), better

competitive and predator avoidance abilities (Greño et al., 2008), synchronous fledging (J Nilsson & Svensson, 1996), and reduced mortality of juveniles (Martin et al., 2018).

My analyses of the effects of temperature on body mass change, tarsus growth and wing growth in 5-day and 11-day-old nestlings are likely to underestimate the real effect of temperature on growth in pied babbler nestlings. As I only measured nestlings twice during the nestling period, I am unable to account for or include the missing weights, tarsus length, and wing lengths of nestlings that did not survive to 5 days or from 5 days to 11 days. It is likely that nestling mass, tarsus length, and wing length may be lower in those nestlings that did not survive, and therefore non-random. If smaller nestlings were more likely to die before measurement on d5 or d11, then the effects presented here (on temperature on mass and size, and of mass and size on survival) are likely to be conservative.

Path analysis suggested that direct effects of temperature on evening mass of both 5-day and 11-day-old nestlings were more important than indirect effects via adult provisioning rates, despite the fact that parental care behaviours mediate effects of weather conditions on nestling growth in other bird species (Weimerskirch, Prince, & Zimmermann, 2000; Tremblay, Thomas, Blondel, Perret, & Lambrechts, 2005; Cunningham et al., 2013). In this study, the number of provisioning visits was only important for predicting evening mass, and thus fledging probability, of 11-day-old nestlings. For the focal behaviour observations, adults in groups with 7- to 9-day-old nestlings, i.e. just before nestling measurements on day 11, spent a larger proportion of time resting on hotter than cooler days. However, they did not significantly reduce the proportion of time spent foraging or attending the nest to achieve this, suggesting that they instead reduced their time spent on other behaviours. High temperatures negatively affected total biomass caught and the number of provisioning visits adults made to the nest (consistent with Wiley & Ridley 2016), but not the total amount provisioned per bird per day. Thus, birds might have been flying to the nest less frequently but taking larger loads each

time. If so, this would imply that the only concession provisioning adults make at high temperatures is to shift from a rate-maximising strategy (frequent visits to the nest) to an efficiency-maximising strategy (providing a consistent amount of food to nestlings, in terms of total biomass per day, while limiting the number of provisioning flights by adults as temperatures rise) as temperatures rise.

Less frequent provisioning trips on hotter days are likely to help birds to avoid raising body temperature by flying (Engel, Biebach, & Visser, 2006), as previously suggested by Wiley & Ridley (2016). However, shifting to an efficiency-maximising strategy appears insufficient to offset the effects of high temperatures on nestling size and daily growth rates. Wet biomass intake may therefore need to increase at high temperatures to maintain nestling mass and sustain growth, due to increased nestling demand for water to aid thermoregulation under hot conditions. If chicks become dehydrated, growth could be hampered by poor physiological performance due to costs associated with dehydration and subsequent high body temperatures (Angilletta, Cooper, Schuler, & Boyles, 2010). If such elevated water demand does exist when hot, the data suggest that provisioning adults appear unable to meet this demand. This is because biomass caught declined with increasing temperature, indicating poorer foraging success and suggesting that there was probably less biomass available to provision to nestlings (Conrey et al., 2016; Dodson, Moy, & Bulluck, 2016; Mella, Possell, Troxell-Smith, & McArthur, 2018). Adults may also be constrained in their ability to provision more water-rich food to nestlings at high temperatures due to the increased costs of flight at high air temperatures (Klaassen, 1995; Powers et al., 2017) and the need to attend to their own water demands (see Chapter 4). Dominant and subordinate individuals may differ in the behavioural adjustments they make in response to high temperatures as the ratio of costs and benefits of helping varies with relatedness to the brood (see Appendix to Chapter 4).

5.5.2 Impacts of group size

Nestling body mass, size and daily growth rates were not affected by group size (also see Wiley & Ridley 2016), suggesting that the benefits of cooperation accrue to adult group members rather than young (Mumme et al., 2015; Langmore et al., 2016). Adult behaviour was affected by group size, since individuals in smaller groups invested more per individual to sustain similar nestling size and growth: they spent more time foraging and less time resting than individuals in larger groups, caught more biomass in total, and provisioned more biomass to young per adult on average than those in larger groups. In summary, nestlings received the same level of care across group sizes, but adults in larger groups invested less per individual in raising young than adults in smaller groups (Savage et al., 2015). This adds further support to previous evidence that 'load-lightening' occurs in pied babblers (Raihani & Ridley, 2008; Ridley & Raihani, 2008; Wiley & Ridley, 2016).

5.6 Conclusion

High temperatures during the nestling period affected the mass, size and number of pied babbler fledglings produced, consistent with prior research on passerines (Greño et al., 2008; Salaberria et al., 2014). This suggests a mechanism by which predicted temperature increases in the Kalahari (MacKellar et al., 2014) could negatively affect population growth and persistence (Cunningham et al., 2013; Conradie et al., 2019). I highlight the need to quantify multiple simultaneous factors that influence fledging probabilities, including adult behaviour, investment in parental care, and offspring growth and development, to identify mechanisms by which birds are at risk under global change. Although parental care strategies are flexible in response to both the weather and social conditions, these strategies have limits. My results suggest that mitigatory actions by provisioning adults (e.g. the behavioural shifts from rate-maximising to efficiency-maximising provisioning strategies documented here) will fail to compensate fully for direct effects of temperature on nestling growth and

development. Repeated exposure to high temperatures during breeding attempts could therefore undermine population replacement via low recruitment of young into the adult breeding population, leading to an increasingly detrimental impact of high temperatures on population persistence over time.

CHAPTER 6: Hot droughts compromise interannual survival across all group sizes in a cooperatively breeding bird

Preamble

In this chapter, I present an analysis of interannual survival and reproduction data using the 15-year Pied Babbler Research Project dataset. I show that hot droughts significantly reduce interannual survival probabilities for both breeding adults and juvenile birds, and that patterns of reproduction are driven primarily by rainfall. Group size does not moderate environmental effects on survival or reproduction. The data from this chapter are published.

Bourne AR, Cunningham SJ, Spottiswoode C, Ridley AR. 2020. Hot droughts compromise interannual survival across all group sizes in a cooperatively breeding bird. *Ecology Letters DOI 10.1111/ele.13604.*

Bourne AR, Cunningham SJ, Spottiswoode C, Ridley AR. 2020. Compensatory breeding in years following drought in a desert-dwelling cooperative breeder. *Frontiers in Ecology and Evolution 8: 190*

6.1 Abstract

Increasingly harsh and unpredictable climate regimes are affecting survival and reproduction across taxa. Comparative research suggests that animals living in harsh and unpredictable environments are more likely to engage in cooperative breeding, implying that cooperative breeding may buffer individuals against negative effects of adverse weather conditions. In this chapter, I have used a 15-year dataset for a cooperatively-breeding bird, the southern pied babbler *Turdoides bicolor*, to determine (i) the impacts of temperature, rainfall, and group size on body mass change, survival, and reproduction, and (ii) whether group size buffers individuals against the impacts of high temperatures and low rainfall. I show that (i) hot and dry conditions, which are expected to increase in frequency in future as a result of anthropogenic climate change, significantly reduced both juvenile and adult growth and survival between years, (ii) wetter conditions and larger group sizes are associated with improved reproductive outcomes, and (iii), contrary to expectations (given prominent theories on the evolution of cooperation), individuals across all group sizes experienced similar effects of adverse weather on survival, growth, and reproduction. I conclude that sociality may not buffer individual group members against adverse current, or future, climate conditions in this study population.

6.2 Introduction

Anthropogenic climate change is affecting population dynamics across taxa (du Plessis et al., 2012; Allen et al., 2015; Rey et al., 2017; Spooner et al., 2018) and understanding life history responses to current environmental conditions is therefore increasingly important for predicting vulnerability to future climate change (Camacho et al., 2018; Conradie et al., 2019). Species living in arid and semi-arid environments are useful models for studying such responses, because these ecosystems are (i) characterised by extremes in temperature and rainfall (McKechnie et al., 2012), and (ii) experiencing rapid increases in temperature and the interannual variability of rainfall as a result of anthropogenic

climate change (Feng & Fu, 2013; Mayaud et al., 2017). Despite evidence that many arid-zone species are well adapted to harsh and unpredictable environments (McKechnie et al., 2016; O'Connor et al., 2017), increasing temperatures and decreasing rainfall have already had far-reaching impacts on behaviour, body condition, growth, and survival in several arid-zone birds (McKechnie & Wolf, 2010; Cunningham et al., 2013; Sunday et al., 2014; Iknayan & Beissinger, 2018). While droughts are a natural feature of arid and semi-arid ecosystems (MacKellar et al., 2014; Tokura et al., 2018), an increase in the frequency of 'hot droughts' – when above-average temperatures and below-average rainfall co-occur (Overpeck, 2013) – is likely in these ecosystems (New et al., 2006; Kruger & Sekele, 2013), with the potential to compromise population persistence (Walther et al., 2002; Sinervo et al., 2010; Cruz-McDonnell & Wolf, 2016; Paniw et al., 2019).

Given the long-term consequences of exposure to heat and drought, life-history traits with the potential to mitigate these impacts are of significant interest. Global comparative studies have shown that the distribution of cooperatively-breeding (Rubenstein & Lovette, 2007; Jetz & Rubenstein, 2011; Lukas & Clutton-Brock, 2017; Shen et al., 2017) and group-living (Griesser et al., 2017) birds and mammals is associated with harsh and highly variable environments, such as arid and semi-arid systems, suggesting that the presence of additional group members buffers against environmental uncertainty (Jetz & Rubenstein, 2011; Russell, 2016; Cornwallis et al., 2017), at least up to an optimal group size (Markham et al., 2015; Ridley, 2016). It has been variously suggested that cooperative breeding evolved in such environments (Rubenstein & Lovette, 2007; Lukas & Clutton-Brock, 2017), enabled species to colonise such environments (Cornwallis et al., 2017), or prevented extinction under increasingly harsh conditions (Russell, 2016; Griesser et al., 2017). One prominent explanation for the occurrence of cooperative breeding in birds is that it represents a 'bet-hedging' strategy (Rubenstein, 2011) whereby dominant individuals share the costs of reproduction with subordinate helpers and are

thus able to breed successfully even when conditions are poor. Cooperation may therefore represent a breeding strategy with the potential to moderate impacts of climate change via task-partitioning (Clutton-Brock et al., 2004; Ridley & Raihani, 2008), improved access to resources (Golabek et al., 2012; Ebensperger et al., 2016), or load-lightening (Crick, 1992), a phenomenon which has been observed in a number of cooperatively-breeding species (Hatchwell, 1999; Mumme et al., 2015; Langmore et al., 2016).

A small number of recent studies empirically test the benefits of cooperation across varying environmental conditions for reproduction (Langmore et al., 2016; Guindre-Parker & Rubenstein, 2018; van de Ven, Fuller, et al., 2020) and extend these analyses to consider adult survival (Guindre-Parker & Rubenstein, 2020). Temperature is, however, rarely included in these analyses despite the fact that thermoregulatory benefits of group living have been demonstrated (Paquet et al., 2016; Mares et al., 2017). I hypothesise that the presence of helpers might be important for buffering social animals against fitness costs of environmental variation by enabling individuals to allocate more time to self-maintenance activities, such as behavioural thermoregulation, and temperature could therefore be an important factor underlying cooperative breeding as a reproductive strategy, driven by the effects of temperature on survival and fecundity in adults (Sinervo et al., 2010; Cunningham et al., 2015).

High temperatures and low rainfall are important environmental conditions which can impact survival and reproduction via trade-offs between mitigating hyperthermia (or dehydration risk) and engaging in essential behaviours, such as foraging or provisioning young (Cunningham et al., 2015; Saracco et al., 2018). Negative consequences of such trade-offs have been recorded in invertebrates (Garcia-Robledo, Chuquillanqui, Kuprewicz, & Escobar-Sarria, 2018), reptiles (Sunday et al., 2014), birds (du Plessis et al., 2012; Edwards et al., 2015), and mammals (Rey et al., 2017), and both acute

and chronic heat exposure negatively impact survival and reproduction in arid-zone species (McKechnie & Wolf, 2010; Cunningham et al., 2013; Wiley & Ridley, 2016; Iknayan & Beissinger, 2018). Droughts are a natural feature of arid and semi-arid ecosystems (MacKellar et al., 2014; Tokura et al., 2018) and have been linked to delayed or failed reproduction (McCreedy & van Riper, 2015; Cruz-McDonnell & Wolf, 2016).

Long-term monitoring of a population of cooperatively-breeding southern pied babblers *Turdoides bicolor* (hereafter 'pied babblers') provides an opportunity to empirically test the impact of environmental conditions on body mass change, survival, and reproductive success between individuals living in groups of different sizes in a cooperatively breeding species. Pied babblers are endemic to the Kalahari Desert in southern Africa – a semi-arid savanna characterised by hot summers, cold winters, and periodic droughts (Hockey et al., 2005). All adult group members participate in cooperative behaviours, including territorial defence, sentinel behaviour, and provisioning of young (Ridley, 2016). A habituated study population and a comprehensive 15-year life history database mean that high-resolution, individual-level data on survival and reproduction are available (Ridley, 2016). Larger mass is likely to be beneficial in this species as heavier pied babblers are more likely to disperse successfully into breeding positions (Ridley, Raihani, & Nelson-Flower, 2008). Mass loss likely indicates physical stress as pied babblers lose weight when provisioning young (Wiley & Ridley, 2016) or defending contested territories (Humphries, 2013), and when they are evicted from their groups (Ridley et al., 2008) or experience high temperatures (du Plessis et al., 2012). High temperature extremes have increased in frequency and severity at the study site over the last two decades (van de Ven, 2017) and rainfall is extremely variable from year to year (MacKellar et al., 2014). In this species, high temperatures and/or drought increase the risk of local extinction (Wiley, 2017), reduce offspring provisioning rates, resulting in smaller nestlings (Wiley & Ridley, 2016), limit foraging

efficiency (du Plessis et al., 2012), lower daily energy expenditure (Bourne et al., 2019), and decrease the effort invested in territorial defence (Golabek et al., 2012).

In this chapter, I explore how temperature, rainfall, and group size affect within-season body mass change (ΔM_b), interannual survival, and reproduction in pied babblers, and whether costs of high temperatures or low rainfall are ameliorated by group size. Specifically, I expected negative effects of high temperatures, and positive effects of high rainfall and larger group sizes on (i) ΔM_b in juveniles and in breeding adults, (ii) survival of juvenile birds from nutritional independence at 90 days of age to recruitment into the adult population at one year of age, (iii) survival of breeding adult birds from one breeding season to the next, and (iv) reproductive effort (number of breeding attempts) and success (number of young surviving to nutritional independence). I consider the relative influence of weather conditions within vs. between annual cycles (consecutive austral summer breeding seasons) on reproductive effort and success, exploring the potential for compensatory mechanisms in response to severe weather conditions characteristic of semi-arid environments, specifically high temperatures and drought (Jetz & Rubenstein, 2011; Lerch, Nolting, & Abbott, 2018). If cooperation helps to buffer against environmental effects, then individuals in larger groups should experience fewer negative consequences of high temperatures and/or low rainfall, i.e. I then further predicted an interaction between group size and environmental factors.

6.3 Materials and methods

6.3.1 Study site and system

Fieldwork was undertaken at the 33 km^2 Kuruman River Reserve (KRR; 26°58'S, 21°49'E) in the southern African Kalahari. See Chapter 1 for a detailed description of the study site and study species.

6.3.2 Data collection

Data were collected for each austral summer breeding season from September 2005–February 2019 (14 breeding seasons in total), of which I collected all the data from September 2016 onwards.

Body mass measurements

Nestlings were weighed to 0.1 g on a top-pan scale at 11 days post-hatching ($Mass_{11}$, representing asymptote mass). Body mass data were collected from 90 (± 15) day-old birds ($Mass_{90}$) by enticing individuals to stand on a top pan balance in exchange for a small food reward (Ridley, 2016), and from adult breeding birds from the beginning (during the months of September or October, $Mass_{Oct}$) and end (during the months of February or March, $Mass_{Mar}$) of each breeding season in the same way. $Mass_{90,}$ $Mass_{Oct,}$ and $Mass_{Mar}$ were collected at dawn, representing pre-foraging body mass. Multiple pre-forage mass measures per individual within a 30-day measurement window were averaged. Body mass change (ΔM_b) was calculated in grams: for sub-adult birds $\Delta M_{b.Juv} = Mass_{90} - Mass_{11}$, and for adult breeding birds $\Delta M_{b.Adults} = Mass_{Mar} - Mass_{Oct}$.

Life history data

All individuals included in the analyses presented here were sexed and marked using the approaches described in Chapter 1. I recorded natal group size ($G.Size_{Brood}$; number of adults present in each individual's natal group between hatching and fledging; constant during the incubation and chick rearing period for all but five of 147 breeding attempts) and calculated average group size (based on monthly means) for the period between fledge and independence for juveniles ($G.Size_{90}$) and over the breeding season in which breeding was monitored for adults ($G.Size_{BrSeas}$). Variations in group size due to older juveniles reaching 1 year of age or dispersal of subordinate adults were observed for 58 of 147 breeding attempts and 62 of 177 group breeding seasons respectively.

(i) Juvenile birds

All nests initiated in the study population during each breeding season were monitored to determine hatching dates. Natal group size ($G.Size_{Brood}$) and brood size (number of nestlings in the brood 11 days post-hatch) were recorded for each brood. Each brood was checked daily from 14 days post-hatching onwards, to determine fledging dates.

Presence/absence of fledglings was noted during weekly visits after fledging. Pied babbler fledglings are considered nutritionally independent (receiving < 1 feed per hour) by 90 days of age, and referred to at that point as juveniles (Ridley & Raihani, 2007b). Presence/absence of juvenile pied babblers (age > 90 days) was recorded at one year (± 15 days) post hatching; at this age individuals have survived through their first winter and are defined as sexually mature adults (Ridley, 2016).

Presence/absence in the population at one year of age represents a 'disappearance rate', likely to be driven primarily by mortality. Dispersal typically occurs after individuals have reached sexual maturity, with the average age at first dispersal being ~2 years (Nelson-Flower et al., 2018). Individuals known to have dispersed before one year of age (n = 1) were excluded from the analysis.

(ii) Adult breeding birds

In each pied babbler group, a single dominant male and female monopolise > 90% of breeding activity (Nelson-Flower et al., 2011). Dominant individuals can be identified unambiguously through incubation behaviour (Ridley, 2016) and distinctive duets (Wiley & Ridley, 2018). Presence/absence of dominant individuals was recorded at the beginning of each breeding season during an annual census, at which point it was possible to determine whether breeding adults had survived over the most recent winter and maintained their dominant status within the group, putting them in the position to breed again. Although dispersal of dominant individuals occasionally occurs, breeding

territory and pair fidelity is high between years (Raihani et al., 2010; Wiley & Ridley, 2018) and overwinter disappearance is therefore likely to be driven primarily by mortality. Age was calculated as the difference in days between known hatch date and 1 September of each breeding season and omitted if hatch date was not known. Data for individuals who were dominant for only part of a breeding season due to death (n = 47) or dispersal (n = 9) were excluded from analyses of interannual survival. Analyses do not include subordinate adults because dispersal of subordinate adults of both sexes is common in this species (Ridley et al., 2008; Raihani et al., 2010) and easily confounded with mortality (Layton-Matthews, Ozgul, & Griesser, 2018).

Breeding effort and success

Nest-building and incubation were recorded during weekly monitoring visits. Number of breeding attempts for each group was defined as the number of discrete clutches laid and incubated per group per breeding season. Breeding success was defined as the total number of nutritionally independent (i.e. 90-day-old) young raised per group per season (*sensu* Ridley & Raihani 2007).

Temperature and rainfall

On-site weather data were collected as described in Chapter 1. Daily maximum temperatures were averaged for the periods between hatching and fledging (mean $T_{maxBrood}$), between fledging and independence (mean T_{max90}), over the breeding season (Sept – Mar, Mean $T_{maxBrSeas}$), and in the previous breeding season (previous Sept – Mar, Mean $T_{maxBrSeas\text{-}1}$). Rainfall was summed for the 60 days prior to initiation of the breeding attempt from which each individual fledged ($Rain_{60}$) (to allow for delays between rainfall and invertebrate emergence; Cumming & Bernard, 1997; Ridley & Child, 2009), for the period between fledging and independence ($Rain_{90}$), over the breeding season ($Rain_{BrSeas}$), and in the previous breeding season ($Rain_{BrSeas\text{-}1}$).

List of symbols and abbreviations

$G.Size_{Brood}$	Number of adults in the natal group at start of breeding attempt
$G.Size_{90}$	Average number of adults in the natal group between fledge and independence
$G.Size_{BrSeas}$	Average number of adults in the natal group over the breeding season
$Mass_{11}$	Nestling body mass (0.1g) collected 11 days after hatching
$Mass_{90}$	Body mass data (0.1g) collected from 90 (± 15) day-old birds
$\Delta M_{b.Juv}$	Change in juvenile body mass (g), calculated as $Mass_{90}$ - $Mass_{11}$
$Mass_{Oct}$	Body mass data (0.1g) collected from adults at the beginning of the breeding season (average morning mass, Sept and Oct)
$Mass_{Mar}$	Body mass data (0.1g) collected from adults at the end of the breeding season (average morning mass, Feb and Mar)
$\Delta M_{b.Adults}$	Change in adult body mass (g), calculated as $Mass_{Mar}$ - $Mass_{Oct}$
Mean $T_{maxBrood}$	Average daily maximum temperatures between hatching and fledging
Mean T_{max90}	Average daily maximum temperatures between fledging and nutritional independence at 90 days of age
Mean $T_{maxBrSeas}$	Average daily maximum temperatures between the start (Sep) and the end (Mar) of the breeding season
Mean $T_{maxBrSeas-1}$	Average daily maximum temperatures between the start (Sep) and the end (Mar) of the breeding season immediately preceding the season in which breeding was monitored
$Rain_{60}$	Total rainfall in the 60 days prior to initiation of the breeding attempt from which each individual fledged
$Rain_{90}$	Total rainfall between fledging and nutritional independence at 90 days of age
$Rain_{BrSeas}$	Total rainfall between the start (Sep) and the end (Mar) of the breeding season
$Rain_{BrSeas-1}$	Total rainfall between the start (Sep) and the end (Mar) of the breeding season immediately preceding the season in which breeding was monitored
$Drought_{BrSeas}$	Occurrence of a meteorological drought (rainfall < 135.75mm) within the breeding season
$Drought_{BrSeas-1}$	Occurrence of a meteorological drought (rainfall < 135.75mm) within the preceding breeding season

The presence or absence of a meteorological drought within a breeding season ($Drought_{BrSeas}$) or previous breeding season ($Drought_{BrSeaso-1}$) was defined as ≤ 75% of average precipitation between September and March each year (≤ 137.75 mm), using long term data for the 30-year period 1984–2013 to determine average precipitation in the region, following Mayaud et al (2017). Long term rainfall data for the region, used to determine the 30-year average of precipitation, was obtained from a South African Weather Services weather station at Twee Rivieren (~120k from the study site; available until 2013). Exploratory data analysis indicated that weather conditions in the preceding

breeding season were only important for analyses of reproductive effort and success and so these parameters were only included in the reproduction models.

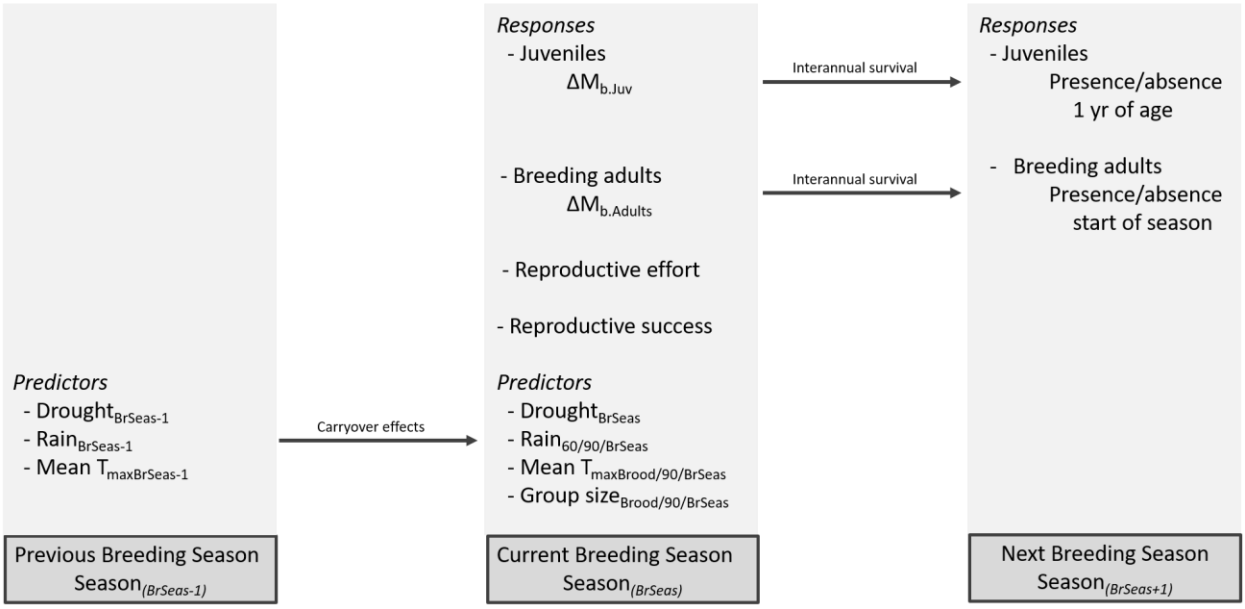


Figure 6.1: Summary of time windows of analysis for Chapter 6.

6.3.3 Statistical analyses

Statistical analyses were conducted in R v 3.4.1 (2017). Mixed effects models, using the package *lme4* (Bates et al., 2015), were used for all analyses. Model selection with Akaike's information criterion corrected for small sample size (AICc) and maximum likelihood estimation was used to test a series of models to determine which model/s best explained patterns of variation in the data. Lower AICc values were considered to represent more parsimonious models, following Harrison et al (2018a), and where multiple models were within 5 AICc of the top model, top model sets were averaged using the R package *MuMIn* (Barton, 2015). Model terms with confidence intervals not intersecting zero were considered to explain significant patterns in the data (Grueber, Nakagawa, Laws, & Jamieson, 2011). All rainfall measures were highly correlated with drought within the same seasonal cycle ($F_{1,247\text{-}350}$ >

37.611, $p < 0.001$), since these variables represent the same pattern in different ways, and rainfall and drought were therefore not included in the same additive models (Harrison et al., 2018a).

Sensitivity power analyses confirmed that I had sufficient sample size to detect 1) small to moderate main effects in all analyses (Cohen's $f^2 < 0.14$ in all cases), 2) moderate to very large effects of two-way interactions in ΔM_b analyses ($f^2 = 0.27$ for fledglings, $f^2 = 0.62$ for adults), 3) small to moderate effects of two-way interactions in interannual survival analyses ($f^2 < 0.15$ for juveniles, $f^2 = 0.09$ for breeding adults), and 4) moderate to large effects of two-way interactions in analyses of reproductive effort ($f^2 = 0.19$) and reproductive success ($f^2 = 0.29$).

Where interannual survival probabilities for juveniles and breeding adults were influenced by interactions, I used the R package *lsmeans* (Lenth, 2016) to predict survival probabilities based on different values of the interacting factors.

Body mass change: To determine which variables predicted $\Delta M_{b.Juv}$ and $\Delta M_{b.Adults}$, I used maximum likelihood linear mixed-effects models (LMMs) with a Gaussian distribution. For juveniles ($n = 129$), I considered the influence of $G.Size_{90}$, $Drought_{BrSeas}$, $Rain_{60}$, $Rain_{90}$, mean T_{max90}, sex, brood size, and the interactions between weather variables and group size on $\Delta M_{b.Juv}$, with brood identity nested within group identity included as a random term to account for repeated measures and thus for nonindependence of data. For adults ($n = 74$ measurements from 46 different individuals), I considered the influence of $G.Size_{BrSeas}$, $Drought_{BrSeas}$, $Rain_{BrSeas}$, mean $T_{maxBrSeas}$, sex, and the interactions between weather variables and group size on $\Delta M_{b.Adults}$, including individual identity nested within group identity as a random term. Weather parameters refer to the breeding season in which ΔM_b was measured (Fig. 6.1).

Survival: Non-monitoring periods over winter prevented detailed time-step survival analyses, such as Cox proportional hazards models (D. R. Cox, 1972; Austin, 2017; Guindre-Parker & Rubenstein, 2020), for both juveniles and adults. Therefore, to determine which variables predicted interannual survival of known individuals in the study population, I used generalised linear mixed-effects models (GLMMs) with a binomial distribution (binary response; survived = 1, died = 0) and a logit link function.

Juveniles: For juvenile birds, interannual survival was measured as survival from the time of nutritional independence (90 days post-fledging) to the date (± 15 days) in the following breeding season on which they reached one year of age. I considered the influence of the following parameters on survival to one year for the period (a) between hatching and fledging (n = 247 individuals): $G.Size_{Brood}$, $Rain_{60}$, $Drought_{BrSeas}$, mean $T_{maxBrood}$, sex, $Mass_{11}$, brood size, and the two way interactions amongst all group size and weather variables; and (b) between fledging and nutritional independence (n = 229 individuals): $G.Size_{90}$, $Rain_{90}$, $Drought_{BrSeas}$, mean T_{max90}, sex, $Mass_{11}$, brood size, and the two way interactions among all group size and weather variables. Drought parameters refer to the breeding season in which an individual fledged. Brood identity nested within natal group identity was included as a random term in both analyses.

Breeding adults: For breeding adults, interannual survival was measured from the end of a breeding season in which they had attempted to breed to the beginning of the subsequent breeding season. I considered the influence of the following parameters on interannual survival (n = 352 interannual survival records from 136 different individuals): $G.Size_{BrSeas}$, $Drought_{BrSeas}$, $Rain_{BrSeas}$, Mean $T_{maxBrSeas}$ and sex. Weather parameters ($Drought_{BrSeas}$, $Rain_{BrSeas}$, Mean $T_{maxBrSeas}$) refer to the breeding season in which an individual's breeding activity was

monitored (Fig. 6.1). Individual identity nested within group identity was included as a random term.

I tested for the influence of ΔM_b on interannual survival probabilities for both juveniles and breeding adults separately, using univariate binomial GLMMs with logit link function, due to much smaller sample sizes for body mass than for presence/absence data.

Number of breeding attempts & breeding success: To determine which variables predicted (a) number of breeding attempts and (b) breeding success per group per year, I used GLMMs with a Poisson distribution (log link). Groups in which the breeding pair split during the breeding season (n = 18 of 177) were excluded from the analysis because the continuity of the breeding pair is an important determinant of reproductive success in pied babblers (Wiley & Ridley, 2018). $G.Size_{BrSeas}$, $Rain_{BrSeas}$, $Rain_{BrSeas-1}$, $Drought_{BrSeas}$, $Drought_{BrSeas-1}$, Mean $T_{maxBrSeas}$ and Mean $T_{maxBrSeas-1}$ and the interactions between weather variables and group size were included as predictor variables and group identity as a random effect in both analyses. Weather parameters refer to the breeding season in which breeding activity was monitored (Drought/Rain/mean $T_{maxBrSeas}$) and the breeding season before that (Drought/Rain/mean $T_{maxBreSeas-1}$; Fig. 6.1).

6.4 Results

Average summer maximum temperature at the study site from 2005–2019 was 34.2 ± 0.9°C (range in annual average summer maximum temperatures: 32.4–36.5°C), summer rainfall averaged 185.4 ± 86.2 mm (range: 64.4–352.1 mm), and droughts occurred in 5 of 14 breeding seasons studied (Fig. 6.2A). Group size varied between groups and between breeding seasons, averaging 4.2 ± 1.4 adults per group across all breeding seasons (range: 2-9 adults; Fig. 6.2B), but did not differ significantly between drought and not-drought years ($F_{1,164}$ = 0.754, p = 0.387). Between 2005 and 2019, the largest group

averaged 5.4 ± 2.3 adult group members (range across 11 breeding seasons: 2.3-9), while the smallest group averaged 3.3 ± 0.9 members (range across 12 breeding seasons: 2-5).

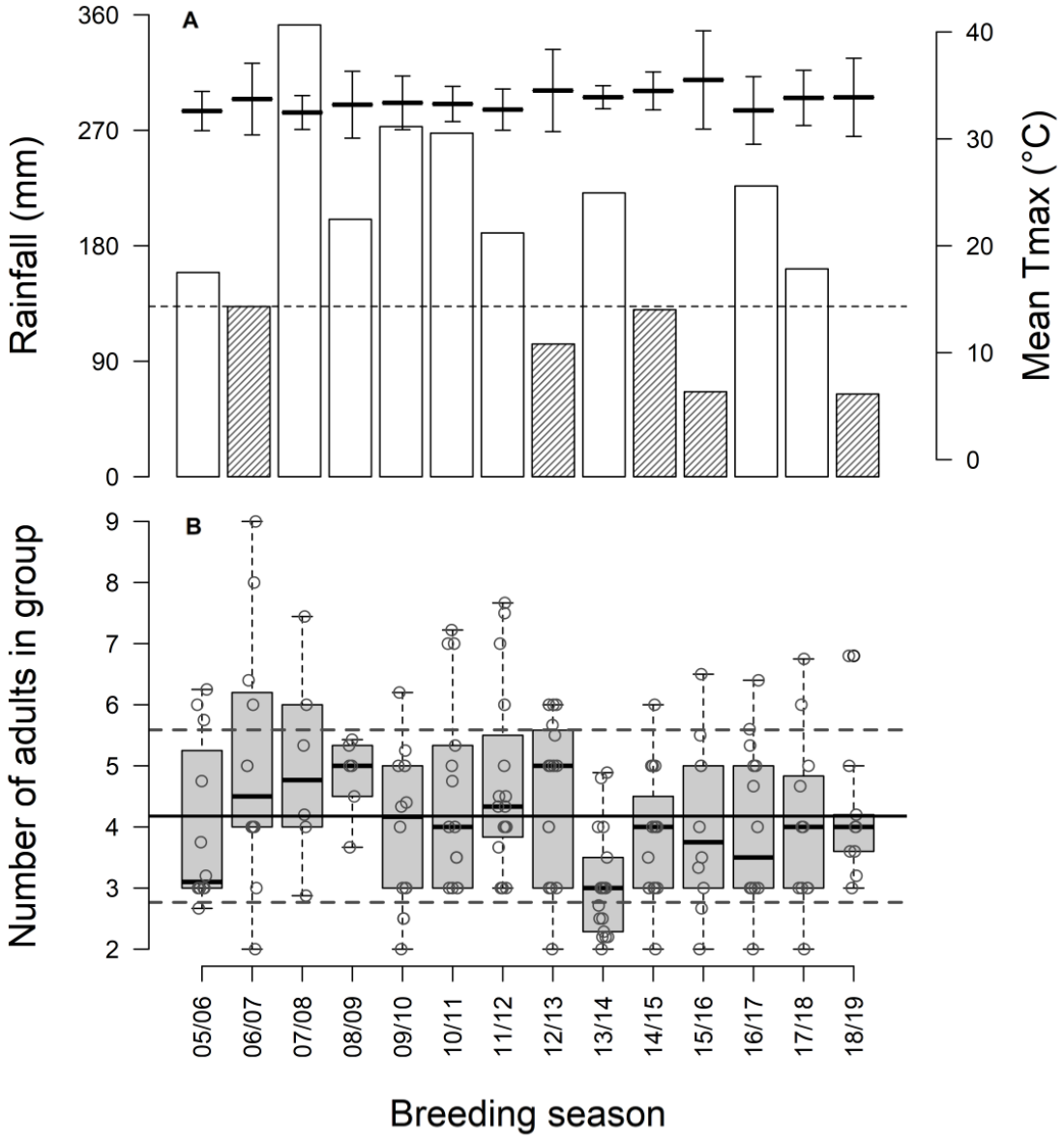


Figure 6.2: (A) Average maximum temperature (black dashes ± 1 SD) and total rainfall (vertical bars: no colour = no drought, hatched = drought) for each austral summer breeding season studied from 2005 to 2019. Dashed horizontal line represents rainfall = 137.75 mm; years with rainfall < 137.75 mm were classified as drought years. (B) Boxplots show median (black line), first and third quartiles (box), and interquartile range (whiskers) for the distribution of average group size across each breeding season. Open circles represent data points (jittered for improved visibility) and lines present the study-wide average group size (solid horizontal line) ± 1 SD (dashed horizontal lines).

6.4.1 Change in body mass

Fledglings that survived to 90 days were heavier as nestlings (mean $Mass_{11}$ = 40.0 ± 5.5 g, n = 270) than those that did not survive (37.4 ± 7.3 g, n = 295; LMM with brood identity as the random term: Est = 2.403 ± 0.526, t = 4.566, 95% CI 1.371 - 3.437). Individuals gained significantly more mass between fledge and independence during wetter periods and when they were raised in larger broods (Table 6.1, Fig. 6.3). Juvenile body mass change did not vary with sex, group size or temperature between fledge and independence, and I did not find any evidence of an interaction between group size and weather (see Appendix Table 6.1 for full model selection output).

High temperatures and low rainfall during the breeding season were associated with body mass loss in breeding adults (Table 6.2; Fig. 6.4). Body mass change did not vary with sex nor was the influence of weather variables on $\Delta M_{b.Adults}$ moderated by group size (see Appendix Table 6.2 for full model selection output).

Table 6.1: Top LMM model sets for factors influencing body mass change in juveniles (n = 129 individuals from 78 nests by 25 groups over 14 breeding seasons). Model averaging was implemented on all models with ΔAICc < 5. Significant terms after model averaging are shown in bold. Null models shown for comparison with top model sets.

Models	***AICc***	***ΔAICc***	***ωí***
Null model	828.73	17.97	0.00
Top model set:			
$Rain_{60}$ + $Rain_{90}$ + Brood size	810.76	0.00	0.71
$Rain_{90}$ + Brood size	813.82	3.06	0.15
$Rain_{60}$ + $Rain_{90}$	815.41	4.65	0.07
$Rain_{60}$ + Brood size	815.57	4.81	0.06
Effect size of explanatory terms after model averaging	*Effect*	*SE*	*95% CI*
Intercept	29.466	0.732	28.016/30.915
Brood size	**1.467**	**0.714**	**0.059/2.875**
$Rain_{60}$	1.085	0.716	-0.327/2.497
$Rain_{90}$	**1.439**	**0.696**	**0.065/2.814**

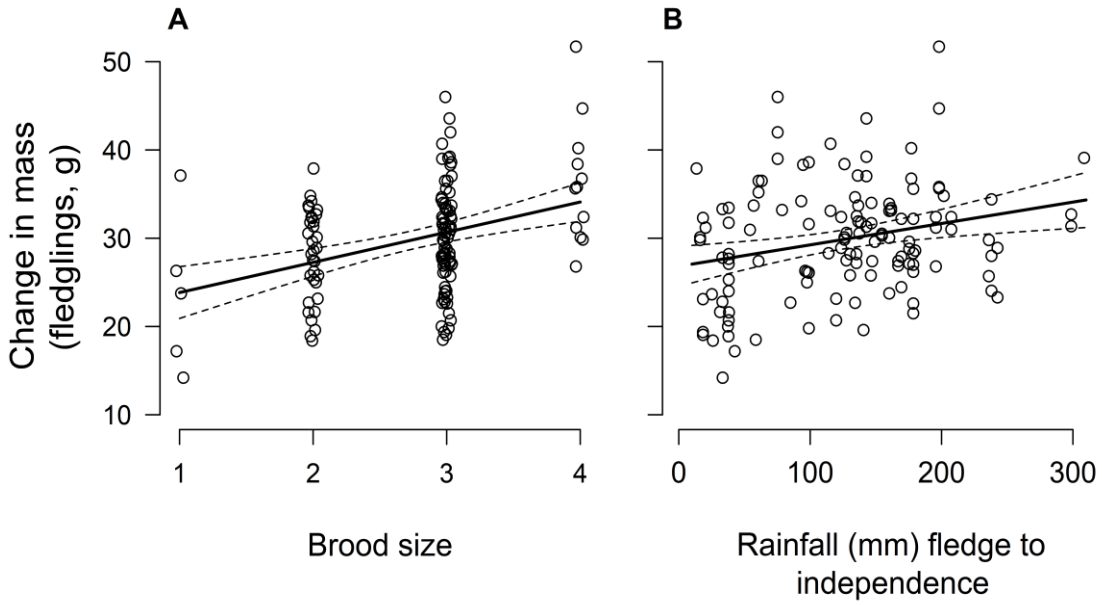


Figure 6.3: Change in body mass in southern pied babbler Turdoides bicolor *fledglings between the fledging and nutritional independence in relation to (A) brood size and (B) rainfall (mm) between the fledging and nutritional independence. Data points in (A) are jittered for improved visibility. Model fit lines and confidence intervals are generated from the models presented in Table 6.1.*

Table 6.2: Top LMM model sets for factors influencing body mass change in adults (n = 74 measurements from 46 different individuals at 20 distinct groups over 10 breeding seasons). Model averaging was implemented on all models with ΔAICc < 5. Significant terms after model averaging are shown in bold. Null models shown for comparison with top model sets.

Models	***AICc***	***ΔAICc***	***ωí***
Null model	408.99	12.14	0.00
Top model set:			
Mean $T_{\mathbf{MaxBrSeas}}$ + $Rain_{BrSeas}$	396.86	0.00	0.76
Mean $T_{\mathbf{MaxBrSeas}}$ + $Rain_{BrSeas}$ + $G.Size_{BrSeas}$	399.12	2.26	0.24
Effect size of significant explanatory terms	*Effect*	*SE*	*95% CI*
Intercept	0.334	0.444	-0.553/1.221
Mean $T_{MaxBrSeas}$	**-1.531**	**0.411**	**-2.349/-0.711**
$Rain_{BrSeas}$	**1.415**	**0.402**	**0.612/2.218**
$G.Size_{BrSeas}$	-0.004	0.217	-0.437/0.429

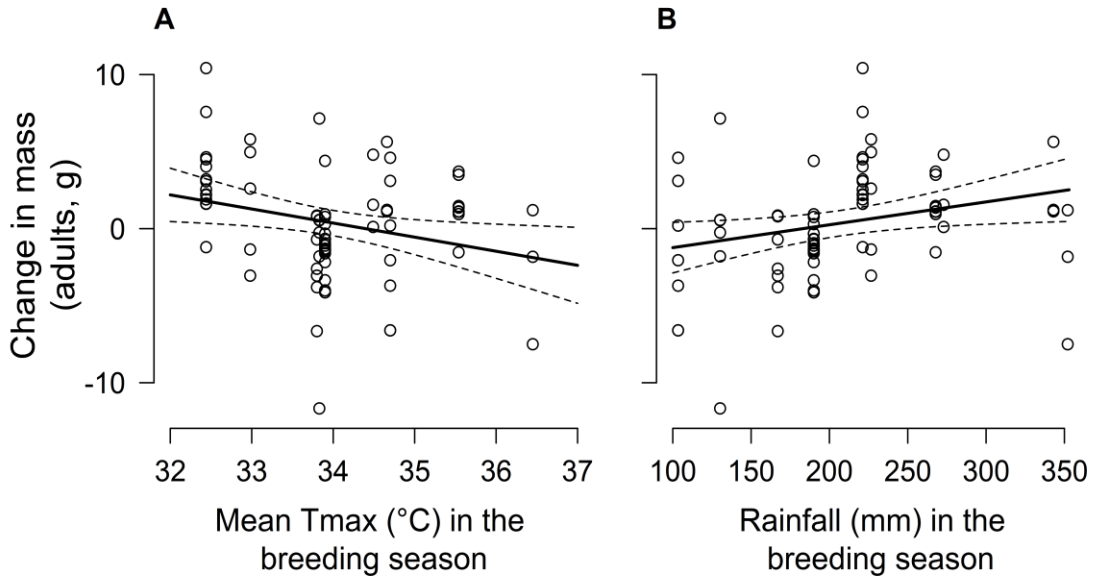


Figure 6.4: Change in body mass in breeding southern pied babbler Turdoides bicolor *adults between the start and end of the breeding season in relation to (A) average daily maximum temperatures and (B) total rainfall (mm) during the breeding season.*

6.4.2 Survival: juveniles

Of 596 nestlings of known $Mass_{11}$, 254 (42.6%) survived to nutritional independence at 90 days. Of these, 173 (68.1%) were present in the study population one year post-hatching. Natal group size ranged from 2–9 adults (mean = 4.4 ± 1.5). The likelihood of a 90-day-old juvenile surviving to one year of age increased as rainfall prior to the breeding attempt from which they fledged increased ($Rain_{60}$; Table 6.3, Fig. 6.5A). However, juveniles that experienced high temperatures as nestlings (mean $T_{maxBrood}$) were less likely to survive to adulthood (Table 6.3, Fig. 6.5B; see Appendix Table 6.3 for full model selection output).

Individuals were less likely to survive to one year of age when they were exposed to high temperatures between fledging and independence (mean T_{max90}) and drought conditions within the breeding season overall ($Drought_{BrSeas}$). The effect of $Drought_{BrSeas}$ on juvenile survival to adulthood

was influenced by temperature: mean probability of survival was high (0.90 ± 0.05) when juvenile birds had experienced both $Drought_{BrSeas}$ and relatively cool mean daily maximum temperatures as a dependent fledgling (mean T_{max90}), whereas mean probability of survival was very low (0.12 ± 0.08) when juvenile birds had experienced $Drought_{BrSeas}$ in addition to high mean T_{max90} (Table 6.4, Fig. 6.5C). This represents a more than seven-fold decrease in recruitment of juveniles into the adult population during periods when both drought and high temperatures were experienced compared to periods when drought occurred but temperatures were mild. Survival to one year of age did not vary with $Mass_{11}$, sex, brood size, or group size in either analysis and I found no evidence that group size between fledge and independence interacted with environmental conditions to influence survival to adulthood (see Appendix Tables 6.3-6.4 for full model selection output). Additionally, survival to one year of age was not influenced by $\Delta M_{b.Juv}$ (GLMM: Est = 0.003, 95% CI: -0.013 - 0.018, χ = 0.407).

Table 6.3: Top GLMM model sets for the influence of conditions experienced between hatching and fledging on interannual survival of juvenile birds (n = 247 different individuals from 143 broods by 30 distinct groups over 14 breeding seasons). Model averaging was implemented on all models with ΔAICc < 5. Significant terms after model averaging are shown in bold. Null models shown for comparison with top model sets.

Models	***AICc***	***ΔAICc***	***ωí***
Null model	315.40	10.07	0.00
Top model set:			
$Rain_{60}$ + Mean $T_{maxBrood}$ + $Rain_{60}$ * Mean $T_{maxBrood}$	305.33	0.00	0.67
$Rain_{60}$ + Mean $T_{maxBrood}$	307.78	2.45	0.20
$G.Size_{Brood}$ + $Rain_{60}$ + Mean $T_{maxBrood}$	309.84	4.52	0.07
$Rain_{60}$	310.10	4.77	0.06
Effect size of explanatory terms after model averaging	*Effect*	*SE*	*95% CI*
Intercept	0.891	0.206	0.499/1.305
Mean $T_{maxBrood}$	**-0.341**	**0.184**	**-0.702/-0.021**
$G.Size_{Brood}$	0.002	0.045	-0.087/0.091
$Rain_{60}$	**0.492**	**0.191**	**0.116/0.868**
$Rain_{60}$ + Mean $T_{maxBrood}$ + $Rain_{60}$ * Mean $T_{maxBrood}$	-0.280	0.261	-0.793/0.233
*Residual deviance: 277.56 on 241 degrees of freedom (ratio: 1.147)			

Table 6.4: Top GLMM model sets for the influence of conditions experienced between fledging and nutritional independence 90 days later on interannual survival of juvenile birds (n = 229 different individuals from 133 broods by 30 groups over 14 breeding seasons). Model averaging was implemented on all models with ΔAICc < 5. Significant terms after model averaging are shown in bold. Null models shown for comparison with top model sets.

Models	***AICc***	***ΔAICc***	***ωí***
Null model	300.45	17.79	0.00
Top model set:			
$Drought_{BrSeas}$ + Mean T_{max90} + $Drought_{BrSeas}$ * Mean T_{max90}	282.66	0.00	1.00
Effect size of explanatory terms after model averaging	*Effect*	*SE*	*95% CI*
Intercept	0.662	0.164	0.397/1.086
$Drought_{BrSeas}$ (drought = YES)	**1.861**	**0.670**	**0.626/3.502**
Mean T_{max90}	**-0.352**	**0.172**	**-0.719/-0.021**
$Drought_{BrSeas}$ + Mean T_{max90} + $Drought_{BrSeas}$ (drought = YES) * Mean T_{max90}	**-2.761**	**0.852**	**-4.752/-1.257**
*Residual deviance: 270.664 on 223 degrees of freedom (ratio: 1.214)			

6.4.3 Survival: breeding adults

In 264 of 352 cases recording interannual survival (75%; from 136 different individuals), breeding adults were still present at the start of the next breeding season. Breeding adults were less likely to be present at the start of the next breeding season when they had experienced a drought during the breeding season ($Drought_{BrSeas}$, Table 6.5). The effect of $Drought_{BrSeas}$ on the survival of breeding adults was influenced by temperature: mean probability of survival was high (0.81 ± 0.06) when individuals had experienced $Drought_{BrSeas}$ alongside relatively cool mean daily maximum temperatures (mean $T_{maxBrSeas}$), whereas mean probability of survival was low (0.32 ± 0.09; Table 6.5, Fig. 6.6) when individuals experienced drought conditions alongside high mean $T_{maxBrSeas}$ ('hot droughts'). Hot droughts were thus associated with a more than 50% decrease in survival of breeding adults from one year to the next compared to cooler droughts. Interannual survival of breeding adults did not vary with sex or group size and I found no evidence that group size over the breeding season interacted with environmental conditions during the breeding season to influence interannual survival (see Appendix Table 6.5 for full model selection output). Additionally, the probability that breeding adults

would survive to the start of the next breeding season was not influenced by $\Delta M_{b.Adults}$ (GLMM, Est = 0.005, 95% CI: -0.02 - 0.029, χ = 0.39).

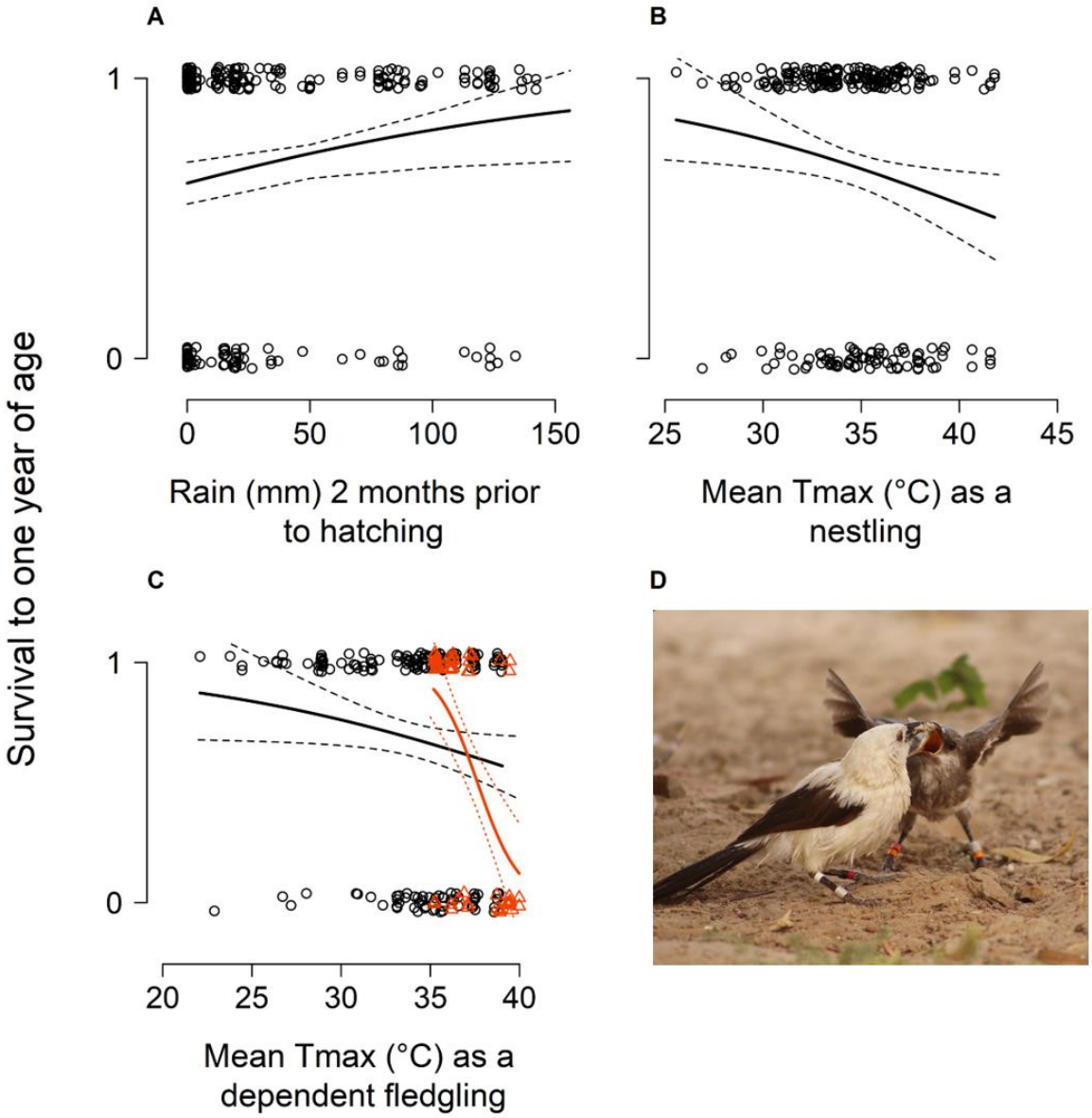


Figure 6.5: Interannual survival (0 = not present, 1 = present) in juvenile southern pied babblers Turdoides bicolor *in relation to (A) rainfall prior to hatching; (B) mean daily maximum temperature between hatching and fledging; and (C) the interaction between temperature between fledge and independence and drought (non-drought breeding seasons: open circles, dashed confidence intervals, black colour; drought breeding seasons: open triangles, dotted confidence intervals, orange colour). Data points are integers (0,1) jittered for improved visibility. Individuals in the study population are uniquely identifiable by their colour and metal ring combinations (D; photograph by Nicholas B. Pattinson).*

Table 6.5: Top GLMM model sets for the influence of conditions experienced during the breeding season on interannual survival of breeding adults (n = 352 measurements of interannual survival from 136 different individuals in 37 distinct groups over 14 breeding seasons). Model averaging was implemented on all models with ΔAICc < 5. Significant terms after model averaging are shown in bold. Null models shown for comparison with top model sets.

Models	***AICc***	***ΔAICc***	***ωí***
Null model	363.5	27.99	0.00
Top model set:			
$Drought_{BrSeas}$ + Mean $T_{maxBrSeas}$ + $Drought_{BrSeas}$ * Mean $T_{maxBrSeas}$	335.5	0.00	1.00
Effect size of explanatory terms after model averaging	*Effect*	*SE*	*95% CI*
Intercept	1.724	0.235	1.299/2.243
$Drought_{BrSeas}$ (drought = YES)	**-1.085**	**0.367**	**-1.895/-0.390**
Mean $T_{maxBrSeas}$	0.349	0.235	-0.086/0.849
$Drought_{BrSeast}$ + Mean $T_{maxBrSeas}$ + $Drought_{BrSeas}$ (drought = YES) * Mean $T_{maxBrSeas}$	**-0.985**	**0.320**	**-1.653/-0.384**
*Residual deviance: 310.478 on 347 degrees of freedom (ratio: 0.895)			

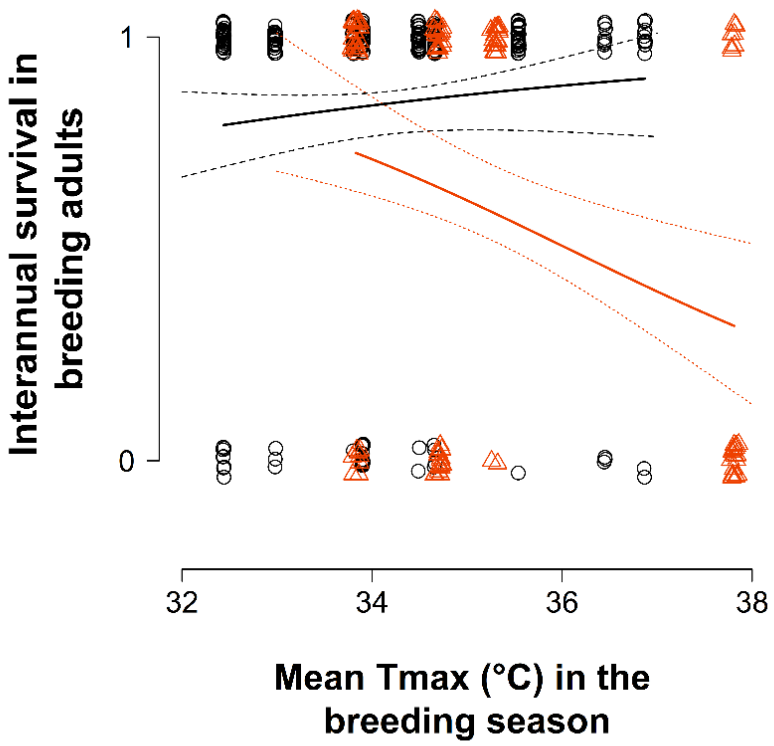


Figure 6.6: Survival of breeding adult southern pied babblers Turdoides bicolor *from one breeding season to the next in relation to temperature and drought conditions during the initial breeding season (non-drought years: open circles, dashed confidence intervals, black colour; drought years: open triangles, dotted confidence intervals, orange colour). Data points are integers (0,1) jittered for improved visibility.*

6.4.4 Breeding activity

The number of breeding attempts per group varied between breeding seasons (range 1–9, mean = 3.4 ± 1.9; *n* = 177 group-seasons), and increased both when there had been a drought in the previous breeding season ($Drought_{BrSeas-1}$, averaging 5.4 ± 1.8 attempts per group in breeding seasons preceded by drought compared to 2.8 ± 1.4 attempts when not preceded by drought) and with rainfall within the current breeding season ($Rain_{BrSeas}$; Table 6.6, Fig. 6.7). I found no evidence for an effect of within-season drought conditions, temperature, group size, or the interaction between group size and environmental factors on the number of breeding attempts per group per season (see Appendix Table 6.6 for full model output).

Table 6.6: Top GLMM model sets for factors influencing number of breeding attempts per group (n = 177 group-seasons from 38 groups over 14 breeding seasons). Model averaging was implemented on all models with ΔAICc < 5. Significant terms after model averaging are shown in bold. Null models shown for comparison with top model sets.

Models	***AICc***	***ΔAICc***	***ωí***
Null model	701.64	68.57	0.00
Top model set:			
$Rain_{BrSeas}$ + $Drought_{BrSeas-1}$	633.07	0.00	0.66
$Rain_{BrSeas}$ + $Drought_{BrSeas-1}$ + $Rain_{BrSeas}$ * $Drought_{BrSeas-1}$	634.42	1.35	0.34
Effect size of explanatory terms after model averaging	*Effect*	*SE*	*95% CI*
Intercept	1.012	0.053	0.907/1.118
$Drought_{BrSeas-1}$ (drought = YES)	**0.419**	**0.088**	**0.246/0.591**
$Rain_{BrSeas}$	**0.259**	**0.047**	**0.167/0.351**
$Rain_{BrSeas}$ + $Drought_{BrSeas-1}$ + $Rain_{BrSeas}$ * $Drought_{BrSeas-1}$ (drought = YES)	0.015	0.036	-0.056/0.086
*Residual deviance: 107.676 on 173 degrees of freedom (ratio: 0.622)			

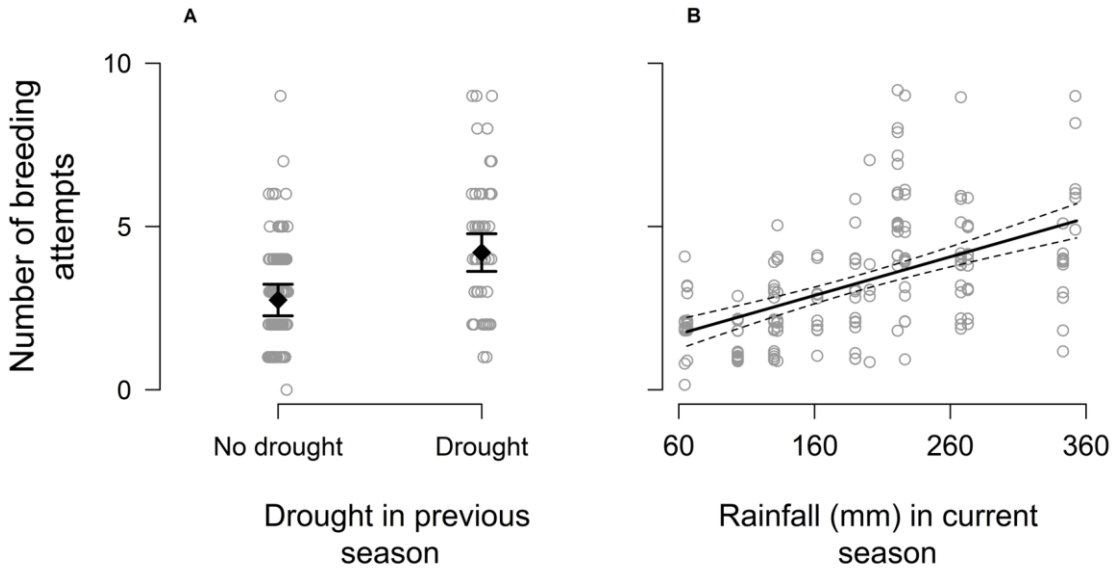


*Figure 6.7: Number of breeding attempts initiated per group per breeding season in relation to (A) the occurrence of drought in a previous breeding season, showing the model-predicted mean (black filled diamond) ± 1.96 * standard error (black whiskers), and (B) rainfall during the current breeding season. Data points are jittered for improved visibility.*

Breeding success per group varied between breeding seasons (range 0–7 surviving independent young produced, mean = 1.6 ± 1.6; n = 144 group-seasons) and, like the number of breeding attempts, increased both when there had been a drought in the previous breeding season ($Drought_{BrSeas-1}$; averaging 2.1 ± 1.8 surviving young per group in breeding seasons preceded by drought compared to 1.3 ± 1.1 attempts when not preceded by drought) and with rainfall within the current breeding season ($Rain_{BrSeas}$; Table 6.7, Fig. 6.8A, Fig. 6.8B). Larger groups produced more surviving young than smaller groups (Table 6.7, Fig. 6.8C), but there was no evidence for an effect of within-season drought conditions, temperature, or interactions between group size and environmental factors on breeding success (see Appendix Table 6.7 for full model output).

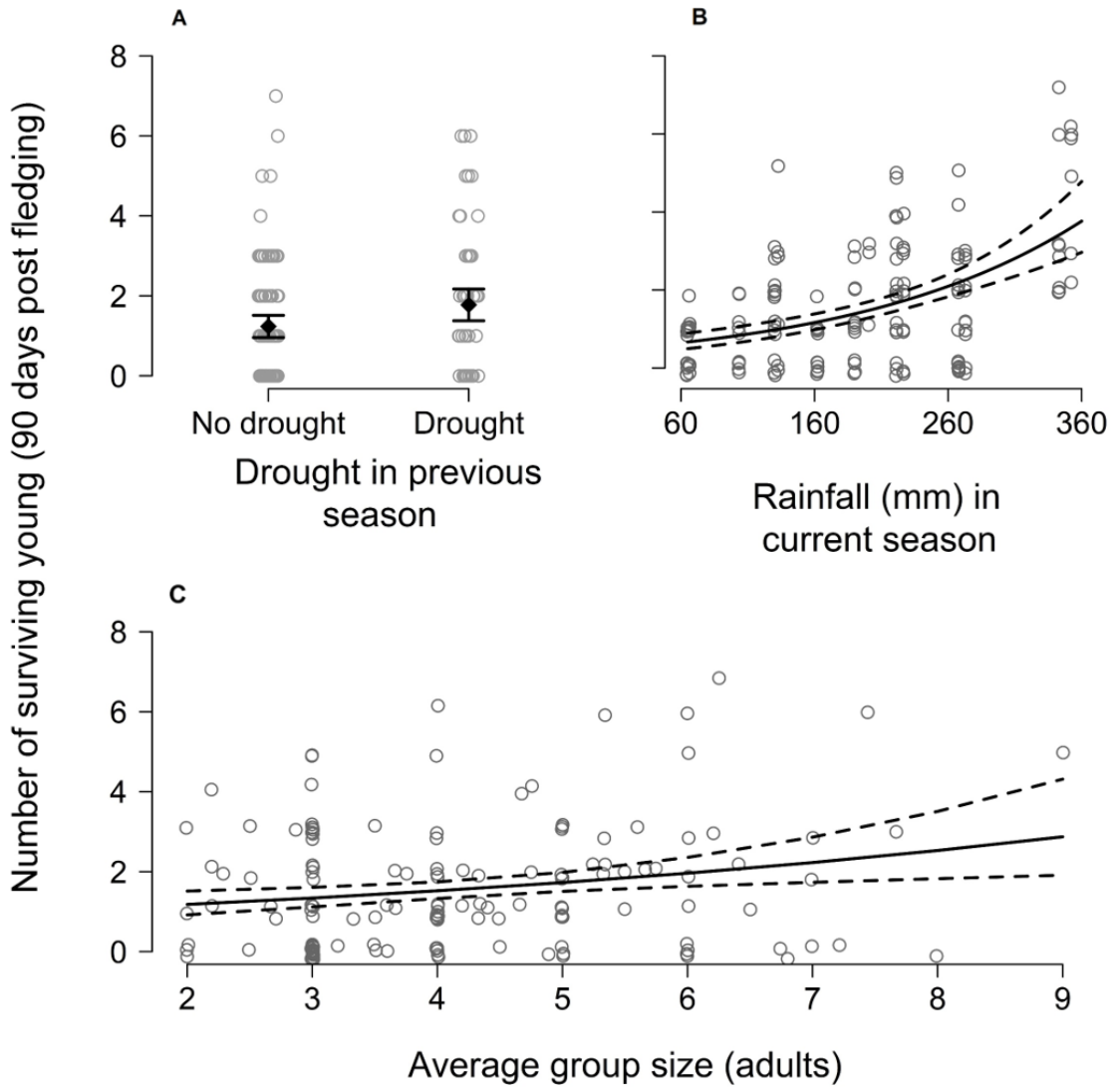


Figure 6.8: Number of surviving young (90 days post fledging) produced per group per breeding season in relation to (A) the occurrence of drought in a previous breeding , showing the model-predicted mean (black filled diamond) ± 1.96 ˟ standard error (black whiskers), (B) rainfall during the current breeding season, and (C) average group size during the current breeding season. Data are jittered for improved visibility.

Table 6.7: Top GLMM model sets for factors influencing number of surviving young produced per group (n = 144 group-seasons from 32 groups over 14 breeding seasons). Model averaging was implemented on all models with ΔAICc < 5. Significant terms after model averaging are shown in bold. Null models shown for comparison with top model sets.

Models	***AICc***	***ΔAICc***	***ωi***
Null model	500.92	53.37	0.00
Top model set			
$Rain_{BrSeas}$ + $Drought_{BrSeas-1}$ + $G.Size_{BrSeas}$	447.55	0.00	0.63
$Rain_{BrSeas}$ + $Drought_{BrSeas-1}$ + $G.Size_{BrSeas}$ + Mean $T_{maxBrSeas-1}$	449.00	1.45	0.31
$Rain_{BrSeas}$ + $G.Size_{BrSeas}$	452.11	4.55	0.06
Effect size of significant explanatory terms	*Effect*	*SE*	*95% CI*
Intercept	0.206	0.103	0.002/0.409
$Drought_{BrSeas-1}$ (drought = YES)	**0.358**	**0.170**	**0.023/0.693**
$Rain_{BrSeas}$	**0.461**	**0.076**	**0.311/0.611**
$G.Size_{BrSeas}$	**0.189**	**0.066**	**0.057/0.319**
Mean $T_{maxBrSeas-1}$	-0.022	0.056	-0.136/0.091
*Residual deviance: 173.634 on 139 degrees of freedom (ratio: 1.249)			

6.5 Discussion

In this chapter, I investigated the potential for group size to buffer against the impacts of climatic factors on body mass change, interannual survival, and reproduction in a cooperatively breeding bird, and present three primary findings. First, environmental conditions significantly affected body mass change and interannual survival in both juveniles and breeding adults as well as reproductive effort and success in pied babblers. Specifically, this finding contributes to a rapidly growing body of literature (Overpeck, 2013; Allen et al., 2015; Cruz-McDonnell & Wolf, 2016) demonstrating that high temperatures and drought occurring concurrently ('hot droughts') have significant impacts on survival in a range of species across taxa. Second, pied babblers initiated more breeding attempts, and bred more successfully, in wetter years and in breeding seasons *following* drought, suggesting the presence of compensatory mechanisms in response to harsh years. Third, I found no evidence that individuals in larger groups were less affected by high temperatures and drought compared to those in smaller

groups: group size did not interact with environmental factors in predicting survival, reproduction, or any of the measures of body mass change that I investigated.

Exposure to high temperatures and low rainfall was strongly associated with reduced growth in juvenile pied babblers and greater body mass loss in breeding adults. Body mass performs well as an index of condition (Labocha & Hayes, 2012), particularly when change *within* individuals is measured over time, and poor body condition has been linked to reduced survival in both adult birds (Gardner et al., 2018) and nestlings (Todd, Poulin, Wellicome, & Brigham, 2003; Schwagmeyer & Mock, 2008). However, the within-individual declines in body mass I report here were not significantly associated with interannual survival in either juvenile or breeding adult pied babblers, suggesting that maintaining larger mass does not buffer pied babblers from the effects of harsh environmental conditions, at least over the measurement windows I used.

In pied babblers, regardless of the proximate cause of death (e.g. predation, lethal dehydration, starvation, injury, disease), exposure to chronic, sublethal effects of high temperatures and low rainfall (particularly in combination) were associated with increased risk of overwinter mortality. Hot and dry conditions experienced between fledge and independence were associated with lower probability of survival to adulthood, and thus reduced recruitment into the population, explaining the overall trend for population decline in below-average rainfall years in this species (Wiley, 2017). Hot droughts also strongly impacted the likelihood of interannual survival in breeding adults. This is particularly concerning because interannual survival rates of breeding adults (compared to non-breeding adult helpers) have the greatest impact on population growth rates in this species, and hence the probability of population persistence through time (Wiley, 2017; Layton-Matthews, Ozgul, & Griesser, 2018).

Droughts are currently a regular, natural feature of the local climate (Tokura et al., 2018). Temperatures in the region have increased in recent decades (van Wilgen et al., 2016) and will continue

to do so (IPCC, 2013), and therefore an increase in the number and frequency of hot droughts can be expected. If this occurs, pied babbler populations are likely to decline as altered drought regimes reduce opportunities for population recovery following hot drought events. Consecutive hot droughts could lead to failed recruitment and population crashes, as has been observed in burrowing owls *Athene cunicularia* (Cruz-McDonnell & Wolf 2016) and is predicted for pied babblers (Wiley, 2017; Conradie et al., 2019).

Rainfall within the breeding season was the most important weather-related predictor of reproductive effort and success in pied babblers, consistent with other studies of birds breeding in subtropical environments (Morrison & Bolger, 2002; Skagen & Yackel Adams, 2012; Zuckerberg et al., 2018; Hidalgo Aranzamendi et al., 2019). Pied babblers breed later into the season when it has rained, and are able to re-clutch while raising dependent fledglings when conditions allow, due to the presence of task partitioning among group members (Ridley & Raihani, 2008; Ridley & van den Heuvel, 2012). An alternative explanation for laying and incubating more clutches and producing more surviving young in wetter years could be that higher numbers of clutches initiated in wetter years indicate higher rates of nest predation, an important cause of reproductive failure in birds (Mayer et al., 2009; DeGregorio et al., 2015; Mortensen & Reed, 2018). Previous research in sociable weavers *Philetairus socius* has shown that reproductive effort (defined as number of clutches laid and incubated) increases when predation is high (Mares et al., 2017). In cases of high reproductive effort in response to high predation risk, the number of fledglings produced per breeding attempt is typically low (Mares et al., 2017), whereas I show here that pied babblers produced more surviving young per breeding attempt in wetter years and other studies suggest that, in arid environments, higher predation rates are often associated with warm, dry weather (McCreedy & van Riper, 2015; Kozma, Burkett, Kroll, Thornton, & Mathews, 2017).

Pied babblers also responded to conditions in previous years, with drought conditions in one breeding season influencing reproductive investment and success in the subsequent breeding season a year later. Pied babblers both initiated more clutches and produced more surviving young in breeding seasons *following* drought in the previous breeding season. This provides evidence of compensatory breeding (see Hatchwell 1999 for compensatory adjustments to parental care in cooperatively breeding birds), with pied babblers responding flexibly to interannual variation in rainfall. An alternative explanation for the pattern that we observed could be that higher numbers of clutches initiated in non-drought years indicate higher rates of nest predation, an important cause of reproductive failure in birds (Mayer et al., 2009; DeGregorio et al., 2015; Mortensen & Reed, 2018). Previous research in sociable weavers (*Philetairus socius*) has shown that reproductive effort (defined as number of clutches laid and incubated) increases when predation is high (Mares et al., 2017). In cases of high reproductive effort in response to high predation risk, the number of fledglings produced per breeding attempt is typically low (Mares et al., 2017).

Additionally, in arid environments, higher predation rates are often associated with warm, dry weather (McCreedy & van Riper, 2015; Kozma et al., 2017). Our results show that pied babblers produced fewer surviving young during droughts and more surviving young per breeding attempt in breeding seasons following a drought. This represents an effect of greater investment in breeding during breeding seasons following a drought, rather than simply more clutches being laid due to higher rates of predation or nest failure. The pattern of producing more surviving young per breeding attempt in breeding seasons following a drought also cannot be explained by years following droughts being significantly wetter (Iknayan & Beissinger, 2018; Sharpe et al., 2019), since droughts were not consistently followed by wetter conditions (Fig. 6.1).I found that larger groups of pied babblers produced more surviving young, a benefit of cooperation that is probably extremely important for

post-drought recovery and overall population persistence in this species (Wiley 2017). The observed group size effect is likely driven by the presence of helpers reducing predation risk at nests (Raihani & Ridley, 2007b; Valencia et al., 2016), and enabling the production of multiple, overlapping broods per breeding season (Ridley & Raihani, 2008; Valencia et al., 2016). Cooperative species also tend to raise more broods to independence per breeding season than non-cooperative species (Ridley & van den Heuvel, 2012). Constraints on independent breeding (Emlen, 1982) can lead to helpers having much lower fitness than if they were able to breed independently, lower per capita reproductive success for the population as a whole, and breeders accruing relatively small inclusive fitness benefits. However, some studies have shown that helping can be evolutionarily stable even when independent breeding is possible (Cockburn, 2002; Riehl, 2013).

Group size did not influence interannual survival or body mass change in either juvenile birds or breeding adults, although larger groups did produce more surviving offspring (also see Ridley 2016; Ridley & van den Heuvel, 2012). Assuming that reproduction is costly (Reznick, 1992; Descamps, Gilchrist, Bêty, Buttler, & Forbes, 2009), the absence of an effect of group size on breeding adult survival could indicate a benefit of cooperation, in that breeders from larger groups may survive equally as well as breeders from small groups, while producing more young.

Critically, however, compensatory breeding in breeding seasons following drought, as well as severe effects of hot droughts on individual survival and body condition, were observed across all group sizes, and were not moderated by the number of helpers present. Therefore, and consistent with the conclusions drawn by van de Ven et al. (2020) for a cooperatively-breeding mammal *Suricata suricatta* and Guindre-Parker & Rubenstein (2020) for superb starlings *Lamprotornis superbus,* larger group size does not buffer against lost reproductive opportunities and compromised survival associated with current environmental variability in the context of a rapidly changing climate. Adverse

effects of environmental conditions on individual body condition and survival are therefore likely driven primarily by physiological tolerance limits (Smit et al., 2018) and resource constraints (Nowakowski et al., 2018) acting on individuals, irrespective of the number of individuals present in their social group. Alternative explanations include that global comparative analyses (Rubenstein & Lovette, 2007; Lukas & Clutton-Brock, 2017) do not predict what occurs in all species and the conditions under which cooperation evolved may have been very different to those which we currently observe at the study site. It is also possible that group size in my study population of pied babblers does not vary enough to allow small buffering effects to be detected. Nonetheless, my finding has some theoretical importance given that prevailing theory of the evolution of cooperative breeding in vertebrates suggests that cooperative breeding either evolved in environments with harsh and unpredictable climates (Rubenstein & Lovette, 2007; Lukas & Clutton-Brock, 2017), enabled species to colonise such environments (Cornwallis et al., 2017), or prevented extinction under increasingly harsh conditions (Griesser et al., 2017).

6.6 Conclusion

The Intergovernmental Panel on Climate Change now predicts with virtual certainty that the incidence of hot extremes will continue to become more frequent, that the length, frequency, and intensity of heatwaves will continue to increase over most land masses, and that hot droughts will become more frequent and severe (IPCC, 2013). As temperatures continue to increase and hot droughts become both more severe and more frequent, compensatory breeding in more productive seasons following droughts, and higher overall offspring production by larger groups overall, may not be sufficient to allow for population recovery between hot droughts. Despite the intuitive appeal of the hypothesis that cooperation should buffer cooperative breeders against some of these effects through reducing impacts on individual group members, I found no evidence this will be the case in

pied babblers. Taken together, the results presented in this chapter raise concerns for the long-term persistence of arid-zone species in the face of changing environmental conditions, and suggest that cooperative life history strategies are unlikely to confer an advantage over alternative breeding strategies in the face of changing environmental conditions and increased frequency of climatic extremes.

CHAPTER 7: General discussion

Preamble

In this chapter, I revisit the thesis rationale in light of the analyses presented in the preceding data chapters (2 through 6). I synthesise the results from all the data chapters under four themes: 1) non-invasive physiological tools and techniques, 2) impacts of climate change on southern pied babblers, 3) benefits of group size in southern pied babblers, and 4) buffering effects of group size on climate impacts. I discuss the implications of my results, both for theory development and conservation, and highlight directions for future research.

7.1 Overview

In this thesis, I have used a novel combination of behavioural ecology, life history, and ecophysiology methods to investigate the potential for sociality to buffer against the impacts of climatic variability and change on survival and reproduction in a cooperatively breeding bird, the southern pied babbler *Turdoides bicolor*. Temperatures above critical thresholds are known to affect the fitness and population persistence of animals by forcing trade-offs between thermoregulation and other essential behaviours (Sinervo et al., 2010; du Plessis et al., 2012; Cunningham et al., 2015; Wiley & Ridley, 2016; Clauser & McRae, 2017; R. L. Carroll et al., 2018; Conradie et al., 2019; van de Ven et al., 2019). Cooperation in social groups allows for the sharing of workload amongst individuals, a phenomenon known as load-lightening (Crick, 1992; Meade et al., 2010; van Boheemen et al., 2019), and may (i) reduce the costs of time spent on thermoregulation and (ii) increase the amount of time available to individual adults for self-maintenance behaviours that could include but are not limited to behavioural thermoregulation. Consequently, I predicted that individual-level sub-lethal costs of exposure to high temperatures and low rainfall would decline with increasing group size, such that pied babblers in larger groups would suffer fewer negative consequences of exposure. Understanding the role of reproductive strategies such as cooperation is important for the conservation, management, and predictive population modelling (Camacho et al., 2018; Conradie et al., 2019) of social species, including humans (Scheffers et al., 2016), in the face of ongoing rapid climate change (Parmesan & Yohe, 2003; IPCC, 2013; Stillman, 2019). Yet, to date there are very few direct empirical tests of the potential for sociality to buffer against climate impacts (Covas et al., 2008; Langmore et al., 2016; Guindre-Parker & Rubenstein, 2020; van de Ven, Fuller, et al., 2020).

In addition to providing an empirical test of the buffering role of group size in a social species, I have also refined, validated, and applied a non-invasive doubly labelled water (DLW) technique for

measuring metabolic rates and water turnover without handling the study animal (Williams et al., 1997; Anava et al., 2000; Scantlebury et al., 2014; Bourne et al., 2019). This technique enabled me to achieve the unusual but increasingly important task of measuring behaviour and physiology in the same individuals at the same time under natural conditions. In a recent review, Stillman (2019) explained that, although physiologists have learned a huge amount about animal performance in response to environmental change, most of these studies are conducted under controlled laboratory or semi-controlled field conditions (Wada et al., 2015; Whitfield, Smit, McKechnie, & Wolf, 2015; McWhorter et al., 2018). There is an urgent need for physiologists to characterise shifts in performance in animals from uncontrolled wild populations (Breuner & Hahn, 2003; Stillman, 2019). While attempts have been made to study behaviour and physiology simultaneously in the same individuals in captivity (van de Ven, Martin, Vink, McKechnie, & Cunningham, 2016; Cunningham, Thompson, & McKechnie, 2017; Weaver, Gao, & McGraw, 2018; Glassman, Hagmann, Qadri, Cook, & Romero, 2019) and at the same time under natural conditions but in different individuals (Cooper et al., 2019; Lavergne et al., 2019; Smit et al., 2019), this study is the first to achieve highly detailed, concurrent behavioural and physiological measurements in a wild population of birds without handling of any kind.

In this chapter, I discuss the implications of my analyses in all the preceding chapters in terms of the methodological contribution of the non-invasive DLW technique I developed and implemented, and with regard to what I have learned about the impacts of climate change, benefits of group size, and buffering effect of group size on climate impacts using pied babblers as a model species. I make several suggestions for future research and conclude with a general statement about the potential impacts and utility of this work.

7.2 Non-invasive physiology

In Chapter 2 of this study I demonstrated that a DLW technique based on oral dosing and faecal sampling, (and thus requiring no handling of the study animals whatsoever), produces similar measurements to those produced using traditional methods in the same individuals at the same time, and is both practically feasible in the field and sufficiently sensitive to detect an expected relationship between daily energy expenditure and air temperature (Bourne et al., 2019). In Chapter 4, I presented a practical application of the method to my research question, further demonstrating the utility and feasibility of the technique. There is a growing realisation that behaviour provides the context within which to interpret physiological responses to environmental variation, and vice versa (Mariette et al., 2018; McKechnie, 2019; Ribeiro et al., 2019; Pattinson et al., 2020), and several recent studies of global change either call for (Camacho et al., 2018; Knapp et al., 2018; Buchholz et al., 2019; Stillman, 2019) or attempt (Cooper et al., 2019; Lavergne et al., 2019; Smit et al., 2019) concurrent measurement of behaviour and physiology in the same individuals under natural conditions. Reducing disturbance is important for improving both animal welfare in research (Romero & Reed, 2005; Pavlova et al., 2018) and the biological relevance of physiology data collected in the field (Butler et al., 2004; Speakman & Hambly, 2016; Glassman et al., 2019).

My non-invasive DLW technique substantially reduces the disturbance normally associated with measuring field metabolic rates and water turnover in free-living animals using DLW, enabling the collection of behaviour and physiology data from the same individuals at the same time under natural conditions. Metabolic rates and water turnover can be correlated directly not only with observed natural behaviour but with environmental variables such as temperature and rainfall to allow a more nuanced interpretation than is possible with traditional methods. For example, my field application of this technique (Chapter 4) provided insights into the water costs of incubation at high

temperatures that would have been impossible to obtain using traditional approaches. Non-invasive DLW is, therefore, potentially very useful for behavioural ecologists and ecophysiologists who wish to explore the physiological correlates of behavioural strategies and/or natural environmental conditions without unduly disrupting the behaviour (or influencing the physiological response) of their study organisms.

7.3 Climate impacts

In the most optimistic of global warming scenarios available today, mean temperatures are predicted to increase between 2 and 4°C above pre-industrial levels by the year 2100, and heat waves and droughts are predicted to increase in both frequency and severity (Meehl & Tebaldi, 2004; IPCC, 2013; Ummenhofer & Meehl, 2017; Heffelfinger et al., 2018; Stillman, 2019; Szejner, Belmecheri, Ehleringer, & Monson, 2019). Although acute, lethal effects of high temperatures and drought as a direct result of dehydration, starvation, and hyperthermia currently do occur in wild populations (Knight, 1995; McKechnie & Wolf, 2010; Boyles, Seebacher, Smit, & Mckechnie, 2011; Rey et al., 2017), they are relatively uncommon. Far more common, and with potentially pernicious long-term consequences that are not yet fully understood, are the chronic, sub-lethal effects of high temperatures and drought acting on individuals via effects on body condition (Sharpe et al., 2019; van de Ven et al., 2019), reproduction (Grant, Grant, Keller, & Petren, 2000; Nardone, Ronchi, Lacetera, Ranieri, & Bernabucci, 2010; Reyna & Burggren, 2012; Cunningham et al., 2013; McCreedy & van Riper, 2015; Conrey et al., 2016; Wiley & Ridley, 2016), foraging efficiency (du Plessis et al., 2012; Cunningham et al., 2015; Edwards et al., 2015), predation risk (Cox, Thompson, & Reidy, 2013; Rauber, Clutton-Brock, & Manser, 2019), interannual survival (Salaberria et al., 2014; Tanner et al., 2016; Woodworth, Norris, Graham, Kahn, & Mennill, 2018), and, ultimately, population persistence (Cruz-McDonnell & Wolf, 2016; Heffelfinger et al., 2018; Saracco et al., 2018; Paniw et al., 2019).

In this thesis, I have presented strong evidence for chronic and severe sub-lethal effects of high temperatures and drought on reproduction and interannual survival in pied babblers. The total number of days during the breeding season (Oct–Mar) exceeding 35.5°C, identified previously as a critical temperature threshold for mass maintenance and parental investment in pied babblers (du Plessis et al., 2012; Wiley & Ridley, 2016), has been increasing at my Kalahari field site, and rainfall has been decreasing (Chapter 3); also see van de Ven (2017). High mean air temperatures (>35.5°C during incubation, >37.3°C for nestlings, and >36.6°C for dependent fledglings) were significantly associated with higher mortality risk during early development in pied babblers (Chapter 3). I identified a thermal limit of 38°C (mean daily maximum temperature), above which all breeding attempts failed (Chapter 3). I have shown that high air temperatures during incubation periods are associated with a) very high nest operative temperatures, exceeding limits of thermoneutrality for incubating adults and probable lethal limits for embryos, b) difficulty maintaining body mass and water balance in incubating birds, and c) unusually extended incubation recesses (Chapter 4). It is likely that these behavioural and physiological responses to high temperatures contribute to reduced hatching success during hot incubation periods. During the nestling period, high air temperatures were associated with compromised nestling growth both directly and via reduced provisioning effort by adults, leading to reduced fledging success (Chapter 5). High temperatures between fledging and nutritional independence were associated with reduced body mass gain and lower recruitment into the adult population (Chapter 6). High temperatures during the breeding season were associated with body mass loss and reduced interannual survival in breeding adults (Chapter 6). In summary, high temperatures were the dominant factor influencing reproductive failure and mortality during all the life stages I studied.

I also investigated the impacts of other weather-related factors, and how these interacted with high temperatures to influence survival and reproduction in pied babblers. Higher rainfall positively influenced nest outcomes (Chapter 3), parental care behaviour (Chapter 4), and the number of surviving young per breeding attempt (Chapter 6). These results suggest that the greater availability of food resources following rain (Cumming & Bernard, 1997) could at least partially buffer the impacts of high temperatures (Naef-Daenzer & Grüebler, 2016), and are consistent with other studies in which breeding birds respond flexibly and opportunistically to changes in their environment (Morrison & Bolger, 2002; Hidalgo Aranzamendi et al., 2019). However, when droughts (breeding seasons with ≤135.75 mm of rainfall between September and March) occurred in combination with high average daily maximum temperatures (> ~38°C), the effect of temperature was exacerbated, and interannual survival of both juveniles and breeding adults was severely compromised (Chapter 6).

With temperatures increasing rapidly in the Kalahari (van Wilgen et al., 2016), and hot droughts predicted to become ever more frequent and severe (IPCC, 2013), pied babblers may increasingly experience conditions that inhibit both successful breeding and the interannual survival of two important age classes: juveniles recruiting into the adult population and experienced breeding adults. The impacts of hot droughts on the interannual survival of experienced breeding adults is particularly concerning as it is these birds that have the greatest potential to impact on population growth rates during good years, influencing recovery after extreme events (Wiley 2017). Pied babblers are relatively long-lived and well adapted to the natural variability of their arid environment (Ridley, 2016), but an increase in the frequency and severity of hot weather extremes (Stillman, 2019), especially hot droughts (Enright, Fontaine, Bowman, Bradstock, & Williams, 2015), could undermine population recovery after extreme events (Wiley, 2017), and population growth and persistence overall (Conradie et al., 2019), leading ultimately to localised extinctions for this species.

7.4 Benefits of cooperation

In cooperatively breeding species, more than two individuals rear a single brood (Cockburn, 2006; Riehl, 2013). Usually, dominant individuals breed with the help of subordinate, sexually mature but non-breeding individuals (Cockburn, 2002) who may or may not be related to the dominant individuals (Riehl, 2013; Nelson-Flower & Ridley, 2016; Griesser et al., 2017). Cooperative breeders may be able to produce more young per breeding season than pair-breeding species with a similar ecology (Ridley & van den Heuvel, 2012) or breed equally well across different years in highly variable environments (Rubenstein & Lovette, 2007; Jetz & Rubenstein, 2011). In pied babblers, dominant pairs monopolise >95% of breeding (Nelson-Flower et al., 2011) and each group contains only one monogamous dominant pair (Wiley & Ridley, 2018). Previous research on this species has shown that larger group sizes are associated with reduced nestling predation (Ridley & Raihani, 2007b), load-lightening behaviours characterised by reduced per-individual investment in parental care and resulting in lower body mass loss per individual during breeding (Ridley, 2016), reduced likelihood of group-level extinction (Ridley, 2016), and the ability to produce multiple broods per season (Ridley & Raihani, 2008).

In this thesis, I additionally show that larger group sizes were associated with higher survival probabilities for pied babbler nestlings and fledglings (Chapter 3) and confirm that larger groups produce more surviving young than smaller groups (Chapter 6). Nestling body mass, size, and daily growth rates (Chapter 5), and fledgling growth rates (Chapter 6), were not affected by group size (also see Wiley & Ridley 2016). I found that nestlings received the same level of care across group sizes, and that adults in larger groups invested less per individual in raising young than adults in smaller groups (Chapter 4 and 5). Specifically, individuals in larger groups spent less time foraging and more time resting, and provisioned less of the biomass they caught on average, than those in smaller groups

(Chapter 5). My results thus further support the occurrence of 'load-lightening' in pied babblers (Raihani & Ridley, 2008; Ridley & Raihani, 2008; Wiley & Ridley, 2016). I have also confirmed that pied babbler pairs do not breed as successfully as groups with one or more helpers (Chapter 3; Ridley 2016) and so benefit from help when breeding (Lucas & Keller, 2019).

7.5 Buffering effects of sociality

This thesis provides one of the few direct empirical tests of the potential for sociality, specifically group size, to buffer against climate impacts. I aimed both to investigate the ability of a cooperatively breeding species to respond to climate change (Kruuk et al., 2015; Langmore et al., 2016; van de Ven, Fuller, et al., 2020) and to provide insight into the mechanisms underlying the established but poorly understood association between cooperation and highly variable environments in mammals and birds (Rubenstein & Lovette, 2007; Rubenstein, 2011; Cockburn & Russell, 2011; Cornwallis et al., 2017; Lukas & Clutton-Brock, 2017; Lin et al., 2019; Downing et al., 2020). I predicted that load-lightening with respect to behaviours shared amongst adult group members, such as incubation and offspring provisioning, would reduce the costs of thermoregulation for individuals in large groups. I expected that costs of high temperatures and low rainfall would be reduced for offspring in larger groups because reduced input from individual adults would be buffered by the inputs of all the other group members. For individual adults, I expected that sharing the load of parental care and other group-directed behaviours amongst larger numbers of fellow group members would enable each individual to spend more time on self-maintenance, thus improving survival. Individuals in larger groups may have more time for thermoregulation (resting, seeking shade), allowing for improved regulation of body temperature and better physiological performance. In Chapter 5, I presented strong evidence of load-lightening in pied babblers (individuals in larger groups provisioned less and rested more than those in smaller groups), providing further support for the idea that the benefits of cooperation may

result in fewer negative consequences of hot and dry conditions for individuals in larger groups. In summary, I expected to find an interaction between weather variables (temperature and rainfall) and group size such that negative impacts of high temperatures and low rainfall would be smaller for individuals in larger versus smaller groups.

However, I found no evidence for an interaction between climatic variables and group size on any of the life history parameters I measured. Temperature was the dominant factor determining variation in all the responses I measured: negative effects of high temperatures were observed across all group sizes, and temperature effects were consistently stronger than group size effects. Group size did not interact with environmental factors in predicting survival (Chapter 6), reproduction (Chapter 3), parental care behaviour (Chapter 4, Chapter 5), physiological responses (Chapter 4), or any of the measures of body mass change that I investigated (Chapter 4, 5, and 6). This was despite considerable statistical power to detect interactions should they have been present, particularly for the long-term data presented in Chapters 3 and 6. The lack of an interaction between weather-related and social factors suggests that physiological tolerance limits (Smit et al., 2018) and resource constraints (Nowakowski et al., 2018) at high temperatures and low rainfalls exceed any potential buffering effect of larger group sizes in this cooperatively-breeding species (van de Ven, Fuller, et al., 2020).

It is also possible that group size does not adequately capture the benefits of sociality, or that group size in this population of pied babblers does not vary enough to allow small buffering effects to be detected. Additionally, recent studies (Shen et al., 2017; Shen & Rubenstein, 2019) show that social species are distributed widely in both stable, benign environments and harsh, fluctuating environments. For example, cooperatively breeding starlings (Rubenstein & Lovette, 2007; Guindre-Parker & Rubenstein, 2020), meerkats (Paniw et al., 2019; van de Ven, Fuller, et al., 2020), and babblers (Keynan & Ridley, 2016; Ridley, 2016; Russell, 2016) tend to inhabit fluctuating

environments with highly variable rainfall (Jetz & Rubenstein, 2011; Lukas & Clutton-Brock, 2018), but cooperatively breeding hornbills (Gonzalez et al., 2013) and cichlid fishes (Dey et al., 2017) predominantly live in temporally stable environments. This paradox of environmental quality and sociality emerges because there are many different types of grouping benefits (Nelson-Flower et al., 2018; Lin et al., 2019; Shen & Rubenstein, 2019). The patterns detected by global comparative studies may, therefore, not mean that buffering effects of larger group sizes should be expected in all cooperatively breeding species in fluctuating environments.

7.6 Future research

Throughout this thesis, I have presented novel findings combining behavioural ecology, life history study, and ecophysiology to investigate the potential for sociality to buffer against the impacts of climate variability and change in pied babblers. The insights gained through my research also resulted in a suite of new questions that could inform future research on the vulnerability of arid-zone birds to climate change, the benefits of help in cooperatively-breeding species, and the application of non-invasive physiology methods in the wild. Possible directions for future, complementary research include:

a) The effect of temperature and rainfall on group size itself, because, although not statistically significant (Chapter 1, Chapter 6), I observed that both average group size and the spread of group sizes were smaller in the two hotter and drier years during which I collected my field data (Chapter 5). Group size co-varying with temperature and rainfall could have masked buffering effects of group size in those years. While I am confident that the observed lack of a buffering effect of group size relates to physiological tolerance limits and resource constraints acting on individuals at high temperatures and during drought (Chapter 6), a

follow-up study could usefully consider effects of variation in group size within and between years, along with demographic causes of smaller group size.

b) The impacts of group size and/or the interaction between group size and weather on survival of subordinate birds, because subordinates appear to benefit from load-lightening in larger groups (Chapter 5, Appendix to Chapter 4). The benefits of load-lightening during adverse weather may be one reason for subordinate individuals to stay in their natal groups rather than disperse, although I could not test for this here because of the difficulty of distinguishing mortality from dispersal in subordinate birds (Chapter 6).

c) The impacts of weather variables such as temperature and rainfall on prey availability, since impacts of temperature and rainfall on foraging and provisioning behaviour (Chapter 5) and body mass (Chapter 4 and Chapter 6) may be mediated by fluctuating prey availability (Cumming & Bernard, 1997; Hidalgo Aranzamendi et al., 2019), something I did not measure in this study.

d) The influence of nest microsite selection (tree species, orientation, thermal properties, height) on nest outcomes, since the impacts of temperature and rainfall on nest outcomes (Chapter 3) and incubation behaviour (Chapter 4) may be mediated by variation in predation risk and thermal exposure given different choices of nest site (Inouye, Huntly, & Inouye, 1981; Souza & Santos, 2007; Goodenough, Maitland, Hart, & Elliot, 2008; Mainwaring et al., 2016; R. L. Carroll et al., 2018).

e) The influence of drought frequency (Enright et al., 2015) on population growth and persistence (Wiley, 2017; Layton-Matthews et al., 2018; Paniw et al., 2019), because hot droughts occurring too frequently, or to close together, seem a likely route for localised extinctions in pied babblers given the significant effect of hot droughts on survival of both juveniles and breeding adults (Chapter 6).

f) Detailed predictive modeling of population viability under different climate scenarios (Conradie et al., 2019) informed by the temperature thresholds identified in Chapters 3-6.

g) Patterns of individual incubation effort in pied babblers (see Appendix to Chapter 4) and how these vary with temperature, rainfall and group size, because the fact that I did not find evidence of a buffering effect of group size on the thermoregulatory costs of incubation may reflect pied babblers sharing incubation effort unequally between group members (Ridley & Raihani, 2008), with some individuals carrying higher costs of breeding than others (Canestrari, Chiarati, et al., 2008; Wiley & Ridley, 2016).

h) Sex differences in nestling development and survival to independence (Chapter 5) or adulthood (Chapter 6) in relation to environmental conditions, because pied babblers in the study population demonstrated a slightly female-skewed sex ratio (unpublished data) and evidence for male-biased mortality in this highly monomorphic species (Ridley, 2016) would provide support for a physiological, rather than sexual size dimorphism, basis of sex-specific responses to adversity (Clutton-Brock, Albon, & Guinness, 1985; Sheldon, Merila, Lindgren, & Ellegren, 1998; Kruuk et al., 2015), and thus warrant further investigation.

i) The influence of territory quality on survival (Chapter 3 and Chapter 6) and reproduction (Chapter 3, 4, 5, and 6), because the observed relationship between larger numbers of helpers and improved reproductive success (Chapter 6) could be the result of helpers boosting productivity, which I have assumed here, or of helpers accumulating on productive territories (Cockburn et al., 2008). Some indications of territory quality that could be usefully explored as an alternative explanation for the apparent benefits of larger group size include resource availability, [e.g. food, water, nesting sites (Ens, Kersten, Brenninkmeijer, & Hulscher, 1992; Canestrari, Chiarati, et al., 2008; van Boheemen et al., 2019)], occupancy or size (Sergio & Newton, 2003; Mumme et al., 2015; Nado et al., 2018), predation risk (Tieleman et al., 2008;

Martin, Oteyza, Boyce, Lloyd, & Ton, 2015; Lee & Lima, 2016), and the presence or absence of thermal refugia (J. M. Carroll, Davis, Elmore, Fuhlendorf, et al., 2015; Bailey et al., 2019).

j) A laboratory experiment comparing daily energy expenditure (DEE) measurements using the non-invasive method described here with concurrent measures made by indirect respirometry (Tomlinson et al., 2013) or an energy balance feeding trial (Speakman & Racey, 1988), and/or comparing oral dosing with injecting the dose, would further validate the non-invasive DLW technique I presented in Chapter 2.

k) A field trial in which DEE was measured in the same individuals using both the non-invasive technique described in Chapter 2 and the traditional DLW technique would further enhance understanding of the extent to which measurements of DEE in the field are actually affected by handling stress, and thus inform the extent to which trickier non-invasive techniques such as those I describe are really necessary (Speakman & Hambly, 2016).

l) Testing the non-invasive DLW technique with frugivores, nectarivores, and/or granivores, with very different diets and potentially much less predictable or much higher water turnover rates (Bradshaw & Bradshaw, 2007), and with insectivores with predictable water turnover rates but different foraging habits (Cunningham et al., 2015; Sharpe et al., 2019; Stofberg, Cunningham, Sumasgutner, & Amar, 2019), will be important to determine the limits to general applicability of the non-invasive DLW technique in birds.

m) Further study of the interesting instances where isotope enrichments in consecutive faecal samples appeared to decline transiently (Chapter 2), reversing and rising again in subsequent samples, in order to understand whether this had to do with processes of osmoregulation as well as water and nutrient absorption in the gut of the birds (Levey & Karasov 1994; McWhorter, Caviedes-Vidal & Karasov 2009), or some other set of biological processes.

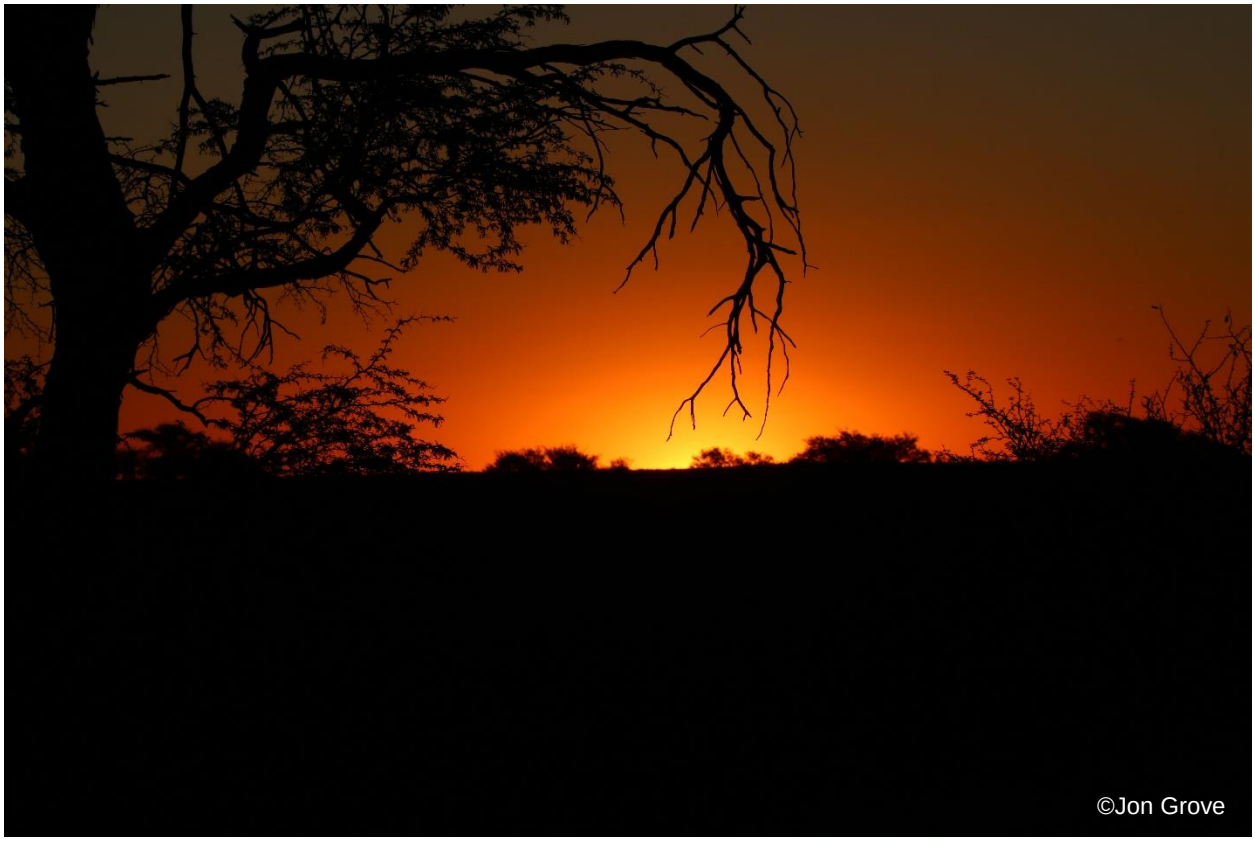
n) Finally, an investigation into what else could be measured in faeces of pied babblers and other animals, and applied to questions of global change, that may extend the applicability of non-invasive sampling and advance understanding of animal stress responses under natural conditions. Examples include measurement of glucocorticoid levels (Jepsen et al., 2019), DNA (King et al., 2018), and diet (Procházka et al., 2010; Mansor, Abdullah, Halim, Nor, & Ramli, 2018).

I have started work on some of the above ideas for future research with students [(i), and (n)] and colleagues [(a), (d), (g), (h), and (l)].

7.7 Conclusion

It has been argued that cooperative breeding could be a bet-hedging strategy, to reduce reproductive variance in the face of unpredictable rainfall, and therefore food availability (Rubenstein & Lovette, 2007). Extending this idea, I have further proposed that thermoregulation could be a crucial mechanism underlying the large-scale pattern, whereby cooperative breeding occurs with disproportionate frequency in highly variable environments (Jetz & Rubenstein, 2011; Cornwallis et al., 2017; Lukas & Clutton-Brock, 2017), driven by the effects of temperature on survival and reproduction. I tested this hypothesis by looking for impacts of temperature, rainfall, and group size (and the interactions between them) on reproduction, growth, and survival in pied babblers. In each chapter, I have demonstrated that temperature is the dominant driver: while higher rainfall and larger group sizes brought benefits, particularly for successful reproduction, negative effects of high temperature were consistently more important for predicting the full range of responses I measured. I found no evidence that larger group sizes moderated the effects of temperature or rainfall: individuals in all group sizes responded similarly to the pressures of high temperature and low rainfall.

The Intergovernmental Panel on Climate Change now predicts with virtual certainty that the incidence of hot extremes will continue to become more frequent, that the length, frequency, and intensity of heatwaves will continue to increase over most land masses, and that hot droughts will become more frequent and severe (IPCC, 2013). At higher average and extreme temperatures, and as hot droughts become both more severe and more frequent, bird species in arid and semi-arid environments, such as pied babblers, may increasingly experience temperatures that do not permit successful breeding and that severely constrain growth and survival. Given the lack of evidence for a moderating effect of group size throughout the analyses presented in this study, I conclude that thermal tolerance limits and resource constraints acting on individuals will be more important than whether or not a species is cooperative. As the climate continues to change, rainfall becomes less predictable, and temperatures increase further, species employing cooperative breeding strategies may fare no better in the face of rapid anthropogenic climate change than species employing non-cooperative breeding strategies.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APPENDIX to CHAPTER 3

Model output tables

Table 3.1: Full GLMM model outputs for analyses of survival probabilities from initiation of incubation to hatching. Data from 492 breeding attempts by 50 groups over 14 breeding seasons. Random terms: Group identity and Year.

Models	***AICc***	***ΔAICc***	***weight***
Null model	606.8	4.98	0.040
Mean T_{maxInc}	601.8	0.00	0.483
Natal group size	607.1	5.22	0.036
$Rain_{60}$	608.8	6.91	0.015
Mean T_{maxInc} * Natal group size	603.6	1.73	0.203
Mean T_{maxInc} * $Rain_{60}$	603.5	1.66	0.210
$Rain_{60}$ * Natal group size	609.2	7.31	0.012

Table 3.2: Full GLMM model outputs for analyses of survival probabilities from hatching to fledging. Data from 341 hatched nests by 46 groups over 14 breeding seasons. Random terms: Group identity and Year.

Models	***AICc***	***ΔAICc***	***weight***
Null model	456.5	19.75	0.000
Mean $T_{maxBrood}$	458.6	21.78	0.000
Mean $T_{maxBrood}$ ^2	439.4	2.60	0.214
Natal group size	452.9	16.10	0.000
$Rain_{60}$	458.4	21.63	0.000
Mean $T_{maxBrood}$ + Mean $T_{maxBrood}$ ^2 + Natal group size	436.8	0.00	0.785
Mean $T_{maxBrood}$ * Natal group size	455.5	18.69	0.000
Mean $T_{maxBrood}$ * $Rain_{60}$	461.3	24.55	0.000
$Rain_{60}$ * Natal group size	456.3	19.46	0.000

Table 3.3: Full GLMM model outputs for analyses of survival probabilities from fledging to nutritional independence. Data from 372 fledglings from 34 groups over 14 breeding seasons. Random terms: Group identity and Year.

Models	***AICc***	***ΔAICc***	***weight***
Null model	460.2	139.21	0.000
Mean T_{max90}	450.9	129.92	0.000
Natal group size	462.2	141.21	0.000
$Rain_{90}$	332.0	11.05	0.004
$Mass_{11}$	450.5	129.92	0.000
$Mass_{11}$ + $Rain_{90}$	328.6	7.62	0.016
Mean T_{max90} + $Rain_{90}$	331.2	10.25	0.004
Mean T_{max90} + $Mass_{11}$	442.3	121.32	0.000
Mean T_{max90} + $Mass_{11}$ + $Rain_{90}$	328.2	7.23	0.019
Mean T_{max90} * Natal group size	453.0	132.09	0.000
Mean T_{max90} * $Rain_{90}$	323.5	2.54	0.200
Mean T_{max90} * $Mass_{11}$	444.0	123.04	0.000
$Rain_{90}$ * Natal group size	333.6	12.68	0.001
$Rain_{90}$ * $Mass_{11}$	327.8	6.83	0.023
Natal group size * $Mass_{11}$	445.8	124.89	0.000
Mean T_{max90} * $Rain_{90}$ + $Mass_{11}$	321.0	0.00	0.710
Natal group size * $Mass_{11}$ + $Rain_{90}$	329.8	8.89	0.008
Natal group size * $Mass_{11}$ + Mean T_{max90}	436.5	115.53	0.000
Natal group size * $Mass_{11}$ + $Rain_{90}$ + Mean T_{max90}	328.6	7.66	0.015

APPENDIX to CHAPTER 4

I have included information in this appendix that is additional to the model output tables that make up the appendices to all other chapters. Here I include:

- the full model selection and output tables for all the relevant analyses in Chapter 4
- a series of additional analyses for the section in Chapter 4 dealing with the proportion of time that nests were attended in order to provide several ways to approach and visualise the data depending on which aspect of incubation constancy one is most interested in
- anecdotal evidence of apparent dehydration in pied babblers that incubated for long periods of time to support the results of physiological analyses in Chapter 4 showing that pied babblers incubating for long periods of time failed to maintain water balance on hot days.
- a discussion of some additional exploratory analyses considering differences in investment in incubation by dominant and subordinate individuals which, while not the main focus of Chapter 4 and so not included there, are relevant to the research question overall and perhaps of interest for future research.

Model output tables

Table 4.1: Full GLMM model outputs for analyses of survival probabilities from initiation of incubation to hatching. Data from 99 breeding attempts by 23 groups over 3 breeding seasons. Random terms: Nest identity.

Model terms	***AICc***	***ΔAICc***	***weight***
Null model	134.0	15.90	0.000
Season	137.7	19.57	0.000
T_{max}	118.1	0.00	0.817
Group size	135.9	17.79	0.000
Group size + Group size^2	135.8	17.66	0.000
T_{max} + Group size + T_{max} * Group size	121.2	3.00	0.182
Season + Group size + Season * Group size	140.4	22.28	0.000
Model	***AICc***	***ΔAICc***	***weight***
Null model	134.0	18.10	0.00
Top models:			
T_{max}	115.9	0.00	1.00
Effect size of explanatory terms after model averaging	Estimate	SE	95% CI
Intercept	10.676	2.669	5.728/16.274
T_{max}	**-0.303**	**0.079**	**-0.467/-0.157**

Table 4.2: Full GLMM model outputs for analyses of proportion of time that clutches were incubated. Data from 46 observation days at 35 breeding attempts by 15 groups over 3 breeding seasons. Random terms: Nest identity.

Model terms	***AICc***	***ΔAICc***	***weight***
Null model	376.6	12.08	0.001
Season	379.4	14.93	0.000
T_{max}	364.5	0.00	0.498
Group size	378.7	14.19	0.000
Group size + Group size^2	373.8	9.35	0.005
T_{max} + Group size + Group size^2	364.6	0.17	0.457
T_{max} + Group size + T_{max} * Group size	369.6	5.14	0.038
Season + Group size + Season * Group size	385.0	20.55	0.000
Model	***AICc***	***ΔAICc***	***weight***
Null model	376.6	12.13	0.00
Top models:			
T_{max}	364.47	0.00	0.520
T_{max} + Group size + Group size^2	364.64	0.17	0.480
Effect size of explanatory terms after model averaging	Estimate	SE	95% CI
Intercept	6.084	0.855	4.379/7.788
T_{max}	**-1.588**	**0.466**	**-2.528/-0.648**
Group size	0.259	0.419	-0.576/1.095
Group size ^ 2	-0.633	0.771	-2.156/0.889

Higher temperatures were associated with more frequent incubation recesses (Est = 0.406 ± 0.182, 95% CI: 0.039, 0.772, z = 2.172; Table 3, Fig. 1), longer total durations of incubation recesses (Wilcoxon rank sum W = 890, p = 0.012 comparing durations between hot and cools days using 35.5°C as the threshold; Table 4, Fig. 2), and a higher probability of observing any incubation recesses at all (Est = 1.498 ± 0.712, 95% CI: 0.061, 2.934, z = 2.043; Table 5, Fig. 3).

The babblers leave their nests unattended infrequently, averaging 2 ± 2 times a day where no group members are incubating the clutch (range: 0 – 9). After averaging the two top models (combined weight = 0.760), only T_{max} significantly predicted the number of time that clutches were left unattended, with the number increasing as temperatures rose (Table 3, Fig. 1). At temperatures

exceeding 35.5°C, identified as a critical temperature threshold in pied babblers (du Plessis et al., 2012; Wiley & Ridley, 2016), the number of times that clutches were left unattended averaged 3 (± 2, range: 0 – 9), whereas on cool days (maximum temperates < 35.5°C) the number of times that clutches were left unattended averaged < 1(± 2, range: 0 – 8). I only recorded clutches being left unattended on more than 2 occasions on cool days twice across three breeding seasons – both of these nests were the first nests of inexperienced pairs from groups primarily made up of siblings rather than offspring.

Table 4.3: Full GLMM model outputs for analyses of the number of times a day that clutches were left completely unattended. Data from 46 observation days at 35 breeding attempts by 15 groups over 3 breeding seasons. Random terms: Nest identity.

Model terms	***AICc***	***ΔAICc***	***weight***
Null model	167.9	4.17	0.057
Season	170.4	6.75	0.016
T_{max}	164.6	0.86	0.300
Group size	169.6	5.93	0.024
Group size + Group size^2	166.0	2.34	0.143
T_{max} + Group size + Group size^2	163.7	0.00	0.460
Model	***AICc***	***ΔAICc***	***weight***
Null model	167.90	4.20	0.00
Top models:			
T_{max} + Group size + Group size^2	163.70	0.00	0.610
T_{max}	164.56	0.86	0.390
Effect size of explanatory terms after model averaging	Estimate	SE	95% CI
Intercept	-0.243	0.395	-1.032/0.545
T_{max}	**0.406**	**0.182**	**0.039/0.772**
Group size	-0.264	0.261	-0.782/0.254
Group size ^ 2	0.325	0.329	-0.327/0.976

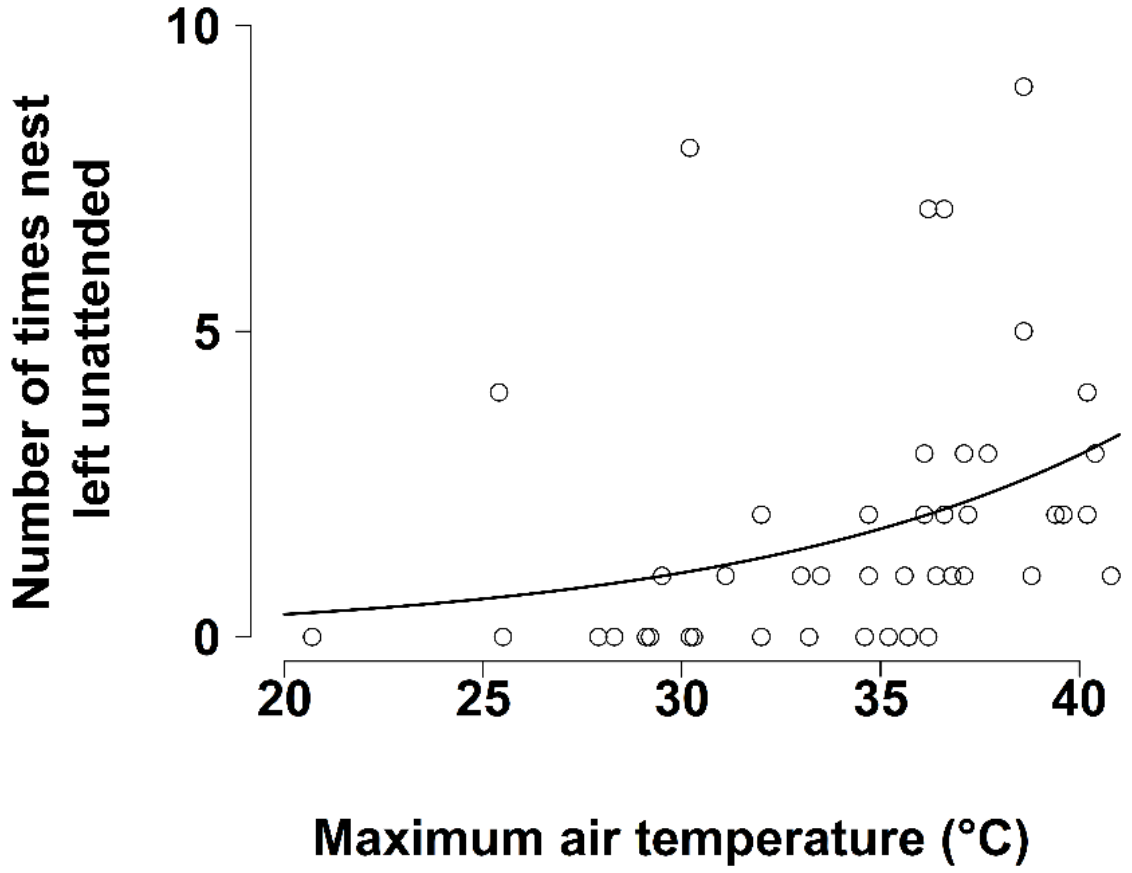

Figure 4.9: Number of times that the clutch was left unattended by maximum temperature on the observation day. Data from 46 observation days at 35 nests over 3 breeding seasons.

The duration of time periods during which clutches were left unattended ("incubation recesses") was usually quite short (n = 83; mean = 22 ± 37.9 min; range: 1 – 265 min) – 80.7% of these periods were shorter than 30 min. The average duration of incubation recesses was significantly longer on hot days (mean = 26.3 ± 42.6 min; range: 1 – 265 min) than on cool days (9.1 ± 10.4 min; range: 1 – 37 min; Wilcoxon rank sum $W = 890$, $p = 0.012$). Most of the time, clutches were left unattended for less than 30 min in total per day – we recorded clutch non-attendance totalling longer than 30 min per day on only 15 of 46 observation days. Thirteen of these occurred on days where

maximum air temperatures exceeded 35.5°C and the other two were the nests of the inexperienced pairs from groups primarily made up of siblings rather than offspring described above. Days with no or very short total time periods for which clutches were left unattended (n = 24 with total non-attendance < 10 min) tended to be cooler (18 of 24 days had maximum temperatures < 35.5°C, mean = 33.1 ± 4.3°C; Wilcoxon rank sum $W = 104$, $p = 0.003$). These data are modelled as the inverse of nest attendance, with proportion of time that clutches were left unattended as the response and with the same results: after averaging the two top models (combined weight = 0.993), only T_{max} significantly predicted the proportion of time that clutches were left unattended, with proportion time unattended increasing as temperatures rose (Table 4, Fig. 2).

Table 4.4: Full GLMM model outputs for analyses of the proportion of time that clutches were left completely unattended. Data from 46 observation days at 35 breeding attempts by 15 groups over 3 breeding seasons. Random terms: Nest identity.

Model terms	***AICc***	***ΔAICc***	***weight***
Null model	376.6	12.08	0.001
Season	379.4	4.93	0.000
T_{max}	364.5	0.00	0.518
Group size	378.7	14.19	0.000
Group size + Group size^2	373.8	9.35	0.005
T_{max} + Group size + Group size^2	364.6	0.17	0.475
Model	***AICc***	***ΔAICc***	***weight***
Null model	376.6	12.13	0.00
Top models:			
T_{max}	364.47	0.00	0.520
T_{max} + Group size + Group size^2	364.64	0.17	0.480
Effect size of explanatory terms after model averaging	Estimate	SE	95% CI
Intercept	-6.084	0.855	-7.788/-4.379
T_{max}	**1.588**	**0.466**	**0.648/2.528**
Group size	-0.259	0.419	-1.095/0.576
Group size ^ 2	0.633	0.771	-0.889/2.156

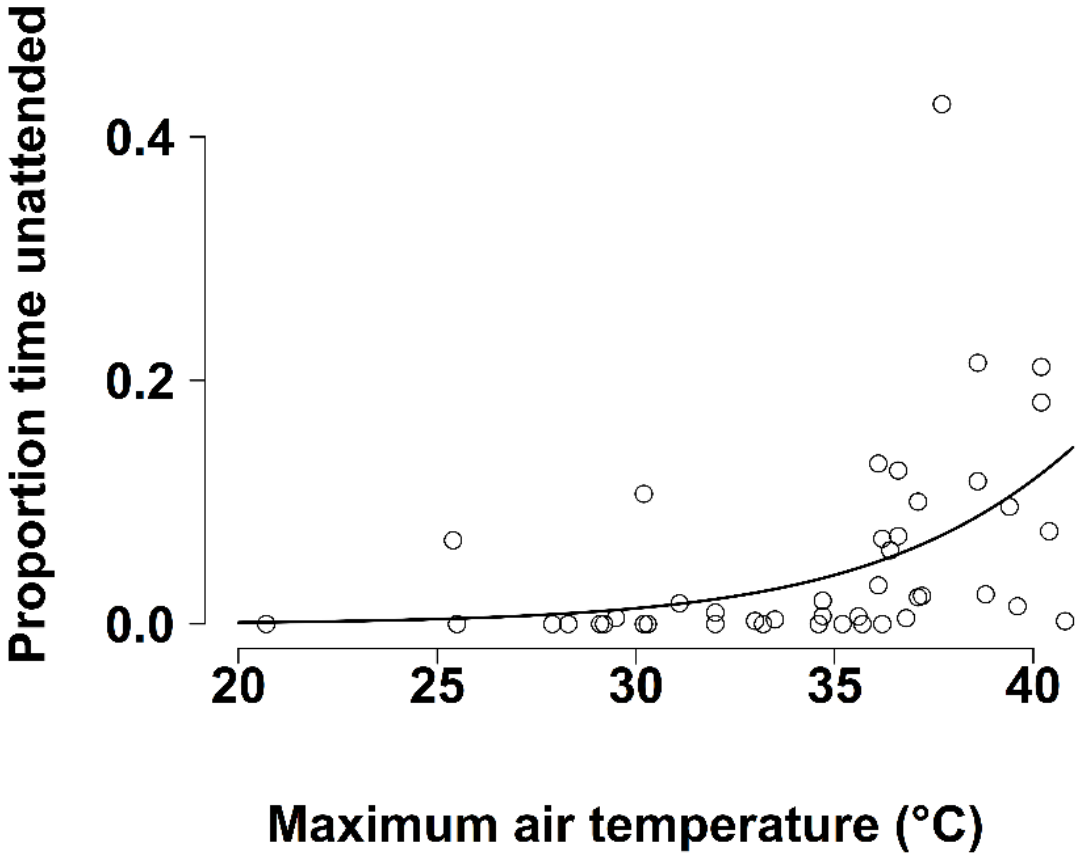

Figure 4.2: Proportion of time that the clutch was left unattended by maximum temperature on the observation day. Data from 46 observation days at 35 nests over 3 breeding seasons.

Clutches were not left unattended at all on 16 of the observation days. These days were all signficantly cooler (mean = 31.1 ± 4.3°C) than the days on which clutches were left unattended at least once (mean = 36.0 ± 3.6°C; Wilcoxon rank sum $W = 75.5$, $p = 0.001$, n = 31). After averaging the two top models (combined weight = 0.993), only T_{max} significantly predicted the probability of observing that clutches were left unattended at all, with the probability of at least on period of non-attendance increasing as temperatures rose (Table 5, Fig. 3). 78.6% of clutches that ultimately failed to hatch (n = 14) were left unattended at least once on our obervation days, whereas clutches that

ultimately hatched (n = 21) were less likely to be left unattended - only 52.4% of hatched nests were left unattended at least once on our observations days. The difference is not statistically significant ($X^2_1 = 1.473, p = 0.225$).

Table 4.5: Full GLMM model outputs for analyses of whether or not clutches were left completely unattended at all. Data from 46 observation days at 35 breeding attempts by 15 groups over 3 breeding seasons. Random terms: Nest identity.

Model terms	***AICc***	***ΔAICc***	***weight***
Null model	62.9	12.10	0.001
Season	64.6	13.71	0.001
T_{max}	51.8	0.92	0.382
Group size	64.9	14.01	0.001
Group size + Group size^2	59.1	8.23	0.010
T_{max} + Group size + Group size^2	50.8	0.00	0.605
Model terms	***AICc***	***ΔAICc***	***weight***
Null model	62.90	12.05	0.00
Top models:			
T_{max} + Group size + Group size^2	50.85	0.00	0.610
T_{max}	51.77	0.92	0.390
Effect size of explanatory terms after model averaging	Estimate	SE	95% CI
Intercept	0.173	0.772	-1.364/1.709
T_{max}	**1.498**	**0.712**	**0.061/2.934**
Group size	-0.345	0.529	-1.405/0.714
Group size ^ 2	0.786	0.819	-0.841/2.412

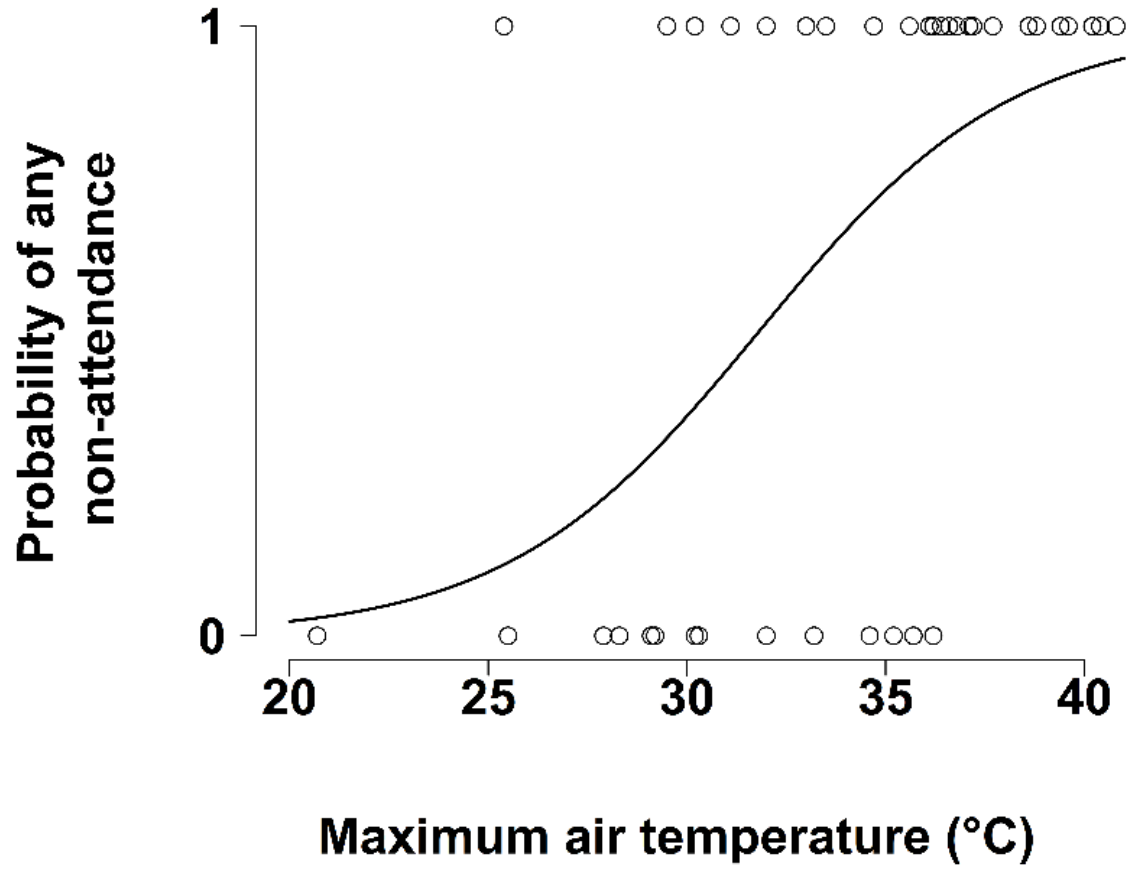

Figure 4.3: Whether or not a clutch was left unattended at all by maximum temperature on the observation day. Data from 46 observation days at 35 nests over 3 breeding seasons.

Table 4.6: Paired t-tests comparing air temperatures (Air temo) and black bulb temperature (BB temp) for each hour of the day. Data are 1,023,981 temperature records from 23 nests in Vachellia erioloba *by 14 groups over 3 breeding seasons.*

Hour	N	Air temp mean	BB temp mean	Mann Whitney U	P value
6 AM	1,518	19.2	20.1	43932	< 0.001
7 AM	1,518	21.4	22.9	19863	< 0.001
8 AM	1,518	24.0	27.1	9600	<0.001
9 AM	1,518	26.0	30.3	6707	<0.001
10 AM	1,539	27.8	32.8	7003	<0.001
11 AM	1,560	29.2	33.8	8357	<0.001
12 PM	1,560	30.5	37.0	11664	<0.001
1 PM	1,560	31.5	38.2	11698	<0.001
2 PM	1,560	32.2	37.7	15821	<0.001
3 PM	1.560	32.6	36.9	31493	<0.001
4 PM	1,560	32.3	36.1	55564	<0.001
5 PM	1,554	32.0	34.0	98050	<0.001
6 PM	1,542	31.1	31.8	260135	<0.001
7 PM	1,804	28.9	29.0	760973	0.022

Table 4.7: Full LMM model outputs for analyses of variation in daily energy expenditure in birds from groups incubating clutches. Data from 68 measurements from 45 different individuals at 33 breeding attempts by 15 groups over 3 breeding seasons. Random terms: Bird identity.

Model terms	***AICc***	***ΔAICc***	***weight***
Null model	92.5	14.09	0.000
Season	93.2	14.75	0.000
T_{max}	78.4	0.00	0.553
Group size	91.2	12.77	0.001
Sex	95.6	17.22	0.000
Rank	96.3	17.85	0.000
T_{max} + Group size	82.4	3.99	0.075
T_{max} + Season	80.0	1.58	0.251
Group size + Season	89.7	11.25	0.002
T_{max} + Group size + Season	82.8	4.36	0.063
T_{max} + Group size + T_{max} * Group size	83.4	4.96	0.046
Season + Group size + Season * Group size	97.5	19.08	0.000
T_{max} + Group size + Season + T_{max} * Group size	87.1	8.68	0.007
Model	***AICc***	***ΔAICc***	***weight***
Null model	92.5	14.08	0.00
Top models:			
T_{max}	78.42	0.00	0.69
T_{max} + Season	80.00	1.58	0.31
Effect size of explanatory terms	Estimate	SE	95% CI
Intercept	1.117	0.754	-0.361/2.595
T_{max}	**-0.223**	**0.046**	**-0.315/-0.131**
Season (2016-17)	0.428	0.638	-0.823/1.679
Season (2017-18)	0.550	0.818	-1.054/2.155
Season (2018-19)	0.508	0.755	-0.971/1.987

Table 4.8: Full LMM model outputs for analyses of variation in water balance in birds from groups incubating clutches. Data from 69 measurements from 45 different individuals at 33 breeding attempts by 15 groups over 3 breeding seasons. Random terms: Bird identity.

Model terms	***AICc***	***ΔAICc***	***weight***
Null model	-131.0	0.00	0.945
Season	-117.6	13.34	0.001
T_{max}	-121.6	9.38	0.009
Group size	-121.4	9.53	0.008
Sex	-123.2	7.78	0.019
Rank	-123.0	7.96	0.018
T_{max} + Group size + T_{max} * Group size	-102.9	28.09	0.000
Season + Group size + Season * Group size	-92.0	38.95	0.000
Model	***AICc***	***ΔAICc***	***weight***
Top models:			
Null model	-131.34	0.00	1.00
Effect size of explanatory terms	Estimate	SE	95% CI
Intercept	1.025	0.011	1.004/1.045

Table 4.9: Full LMM model outputs for analyses of variation in mass change between days in individuals from groups incubating clutches (temperature < 36.1˚C). Data from 72 individuals at 22 breeding attempts by 12 groups over 3 breeding seasons. Random terms: Nest identity.

Model terms	***AICc***	***ΔAICc***	***weight***
Null model	317.5	1.12	0.215
Season	316.4	0.00	0.377
T_{max}	320.5	4.13	0.048
Group size	320.1	3.71	0.059
Sex	319.3	2.91	0.088
Rank	319.3	2.92	0.088
T_{max} + Group size + T_{max} * Group size	325.5	9.10	0.004
Season + Group size + Season * Group size	318.6	2.27	0.121
Model	***AICc***	***ΔAICc***	***weight***
Top models:			
Season	316.36	0.00	0.640
Null model	317.48	1.12	0.36
Effect size of explanatory terms	Estimate	SE	95% CI
Intercept	0.258	0.378	-0.485/0.999
Season (2016-17)	-0.189	0.509	-1.205/0.827
Season (2017-18)	0.782	0.717	-0.632/2.195
Season (2018-19)	0.507	0.473	-0.425/1.439

Table 4.10: Full LMM model outputs for analyses of variation in mass change between days in individuals from groups incubating clutches (temperature ≥ 36.1˚C). Data from 48 individuals at 15 breeding attempts by 10 groups over 3 breeding seasons. Random terms: Nest identity.

Model terms	***AICc***	***ΔAICc***	***weight***
Null model	223.6	4.63	0.063
Season	224.5	5.51	0.040
T_{max}	219.0	0.00	0.633
Group size	225.9	6.94	0.020
Sex	222.9	3.96	0.087
Rank	224.9	5.91	0.033
T_{max} + Group size + T_{max} * Group size	222.4	3.45	0.113
Season + Group size + Season * Group size	226.9	7.95	0.012
Model	***AICc***	***ΔAICc***	***weight***
Null model	223.6	5.60	0.00
Top model:			
T_{max}	218.0	0.00	1.00
Effect size of explanatory terms	Estimate	SE	95% CI
Intercept	-0.365	0.315	-1.009/-.251
T_{max}	**-0.926**	**0.318**	**-1.609/-0.303**

Examples of apparent dehydration in pied babblers

Examples of apparent dehydration in incubating pied babblers were collected in an ad hoc manner during full days of behavioural observation.

Example 1, 29 October 2016: The dominant female of a group consisting of three adult pied babblers incubated for four straight hours (12h12 – 16h17) during the hottest part of the day on a day where the daily maximum air temperature was 40.2°C [pied babblers exhibit compromised foraging efficiency and an resultant inability to maintain body mass overnight at temperatures > 35.5°C (du Plessis et al., 2012)]. She panted 88.1% of the time during that particular incubation period [she was clearly visible in the nest from an observation point 10-15 m away; panting is an evaporative cooling behaviour used to maintain body temperature in a variety of mammals and birds (Schmidt-Nielson, 1990)]. When she left the nest at 16h17, she exhibited signs of severe heat stress and dehydration,

including loss of coordination and diarrhoea (McKechnie et al., 2017). She was not replaced by another group member at this time and left the nest unattended for ~2 h returning shortly after sunset, at 18h51, to incubate overnight. Soon after alighting from the nest she began to move towards the nearest water source, a livestock trough ~300 m away, taking more than an hour to travel the required distance. She had lost 3.9 g by the following day, and DLW analysis showed that she had a negative water balance (0.874).

Example 2, 16 December 2018: At another group of pied babblers (group size = 7), I observed milder signs of dehydration [sluggishness, sunken eyes (Sharpe et al., 2019)] in the dominant female after she had incubated for almost 4 hours in the afternoon (13h45-17h30) on a hot day (40.4°C). When she left the nest, she was not replaced by another group member. She sat motionless in the shade for ~1 h before returning to the nest after sunset to incubate overnight. This group does not have access to standing water in their territory and the bird was not observed drinking after leaving the nest. She had lost 1.4 g by the following day, and DLW analysis showed that she had a negative water balance (0.908).

Example 3, 4 January 2018: At a third group of pied babblers (group size = 6 adults), I recorded unusual incubation behaviour followed by nest abandonment during a breeding attempt that took place during a heat wave. Both male and female dominant individuals were observed flying to drink water immediately after completing incubation bouts, and the pair left the nest unattended for extended periods of time – up to 4 h. They did not replace each other immediately after completing incubation, as is usual for pied babblers, but only after the nest had been left unattended for at least 40 min. The dominant female did most of the incubating compared to the dominant male (6.9 vs. 0.9 h). Daily maximum air temperatures on nine of the eleven days between initiation of incubation and failure of the breeding attempt exceeded 35.5°C (the average maximum temperature for the incubation

period was 37.1°C). The nest was abandoned after five consecutive days > 35.5°C, evidenced by the fact that we found two unhatched eggs in the nest after the group had ceased incubation. The hottest day of the heat wave (40.6°C) occurred the day before the nest was abandoned. The dominant female had lost 1.9 g and the dominant male had lost 3.4 g by the following day. Water balance was not measured in either bird on that day.

Exploratory evidence that pied babblers share incubation effort unequally

To determine whether individual incubation effort varied by sex, rank, and group size, I started by constructing a dataset on the proportion of time adult birds allocated to different activities. I collected these data during up to 4 x 20-minute continuous time-activity focal behaviour observations (Altmann, 1974) within each of 6 focal sessions per day (n = 65 focal days, see Chapter 4 for details on the method). I summed time observed foraging (foraging effort; including searching for and handling prey), attending the nest (all visits to the nest including incubating and shading), resting (preening, standing, and perching), and engaging in other activities (e.g. walking, flying, on sentinel duty, interacting with neighbouring groups), and calculated the proportion of time allocated to each set of activities across all of the focals collected on the focal day. I explored main effects using binomial GLMMs with Penalised Quasi-Likelihood (glmmPQL) in the MASS package (Venables & Ripley, 2002).

Pied babblers in incubating groups spent 36.8 ± 13.5% of their time foraging, 26.2 ± 11% time resting, 27.7 ± 19.6% of their time incubating the eggs, and the remaining time engaged in other activities. Subordinate birds spent significantly more time foraging (42.1 ± 13.7%) and significantly less time incubating (18.2 ± 18.6%) than dominant birds (31.3 ± 11%; 37.4 ± 15.7%; Table 11, Fig.

4). Both members of the dominant pair incubated at every nest on every observation day, and for at least an hour everyday (range: 55 – 535 min; mean = 251 ± 107 minutes; vs. subordinates range: 0 – 521 min; mean = 104 ± 124 min). Many subordinate individuals did not incubate at all: in group sizes of six adults, subordinate individuals were observed not incubating at all 65% of the time (31 out of 48 observation days). Birds also spent significantly more time foraging (44.6 ± 15.3%) and less time incubating (23.8 ± 20.9%) in the summer of 2017/18 (165.2mm) than in the wetter summer of 2016/17 (226.6mm; 33 ± 13.6%; 30.2 ± 20.8%; Table 11, Fig. 4). Time spent foraging (36.1 ± 8.6%) and incubating (26.9 ± 17%) in the driest summer 2018/19 (88.4mm) did not differ significantly from either of the preceding years. Proportion of time spent resting did not vary significantly by any of the predictors included in the model.

Table 4.11: glmmPQL model outputs for factors influencing proportion of time spent a) foraging, b) resting, and c) attending the test. Models fitted to data from 65 days of focal observations on 46 different individuals from 40 nests by 15 groups over 3 breeding seasons.

Model	Parameters	estimate	SE	t-value	p-value
Proportion time spent foraging	*Intercept*	-0.957	0.127	-7.514	0.000
	Maximum temperature	0.111	0.067	1.651	0.113
	Rank (Subordinate)	**0.419**	**0.116**	**3.603**	**0.002**
	Sex (Male)	0.024	0.119	0.202	0.841
	Group size	0.026	0.073	0.360	0.721
	Season (2017/18)	**0.591**	**0.165**	**3.575**	**0.001**
	Season (2018/19)	0.084	0.158	0.529	0.599
Proportion time spent resting	*Intercept*	-1.251	0.154	-8.114	0.000
	Maximum temperature	0.104	0.085	1.228	0.232
	Rank (Subordinate)	0.219	0.131	1.668	0.109
	Sex (Male)	0.098	0.134	0.738	0.469
	Group size	0.107	0.092	1.162	0.253
	Season (2017/18)	-0.028	0.217	-0.128	0.899
	Season (2018/19)	0.112	0.202	0.556	0.582
Proportion time spent attending the nest	*Intercept*	-0.199	0.235	-0.847	0.403
	Maximum temperature	-0.248	0.133	-1.867	0.075
	Rank (Subordinate)	**-1.041**	**0.223**	**-4.679**	**0.000**
	Sex (Male)	-0.346	0.221	-1.562	0.133
	Group size	-0.186	0.150	-1.238	0.224
	Season (2017/18)	**-0.748**	**0.363**	**-2.063**	**0.046**
	Season (2018/19)	0.064	0.322	0.198	0.844

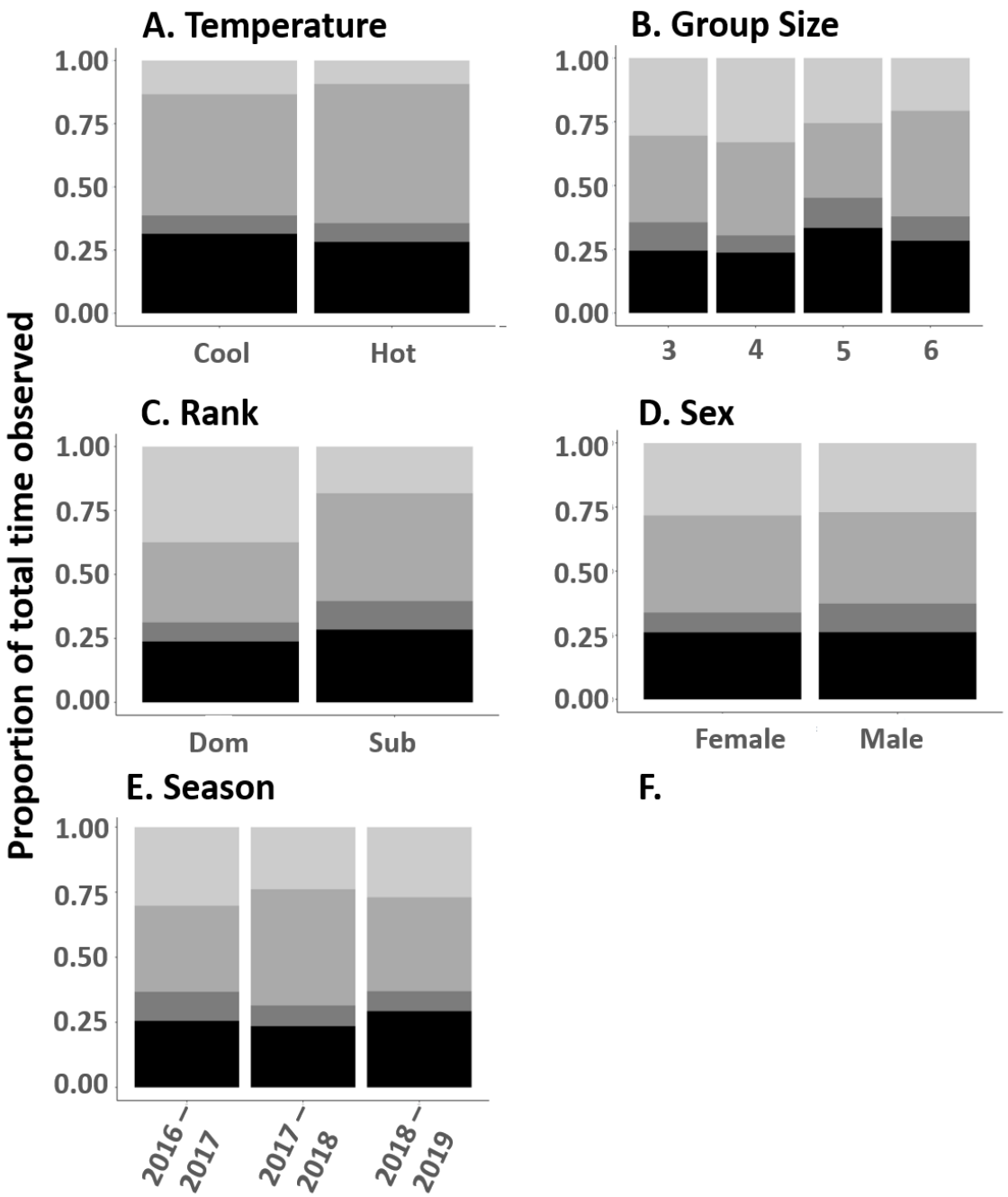

Figure 4.4: Average proportion of time spent resting (black), foraging (medium grey), attending the nest (light grey), and engaging in other activities (narrow dark grey band). Data from 65 days of focal observations on 46 different individuals from 40 nests by 15 groups over 3 breeding seasons.

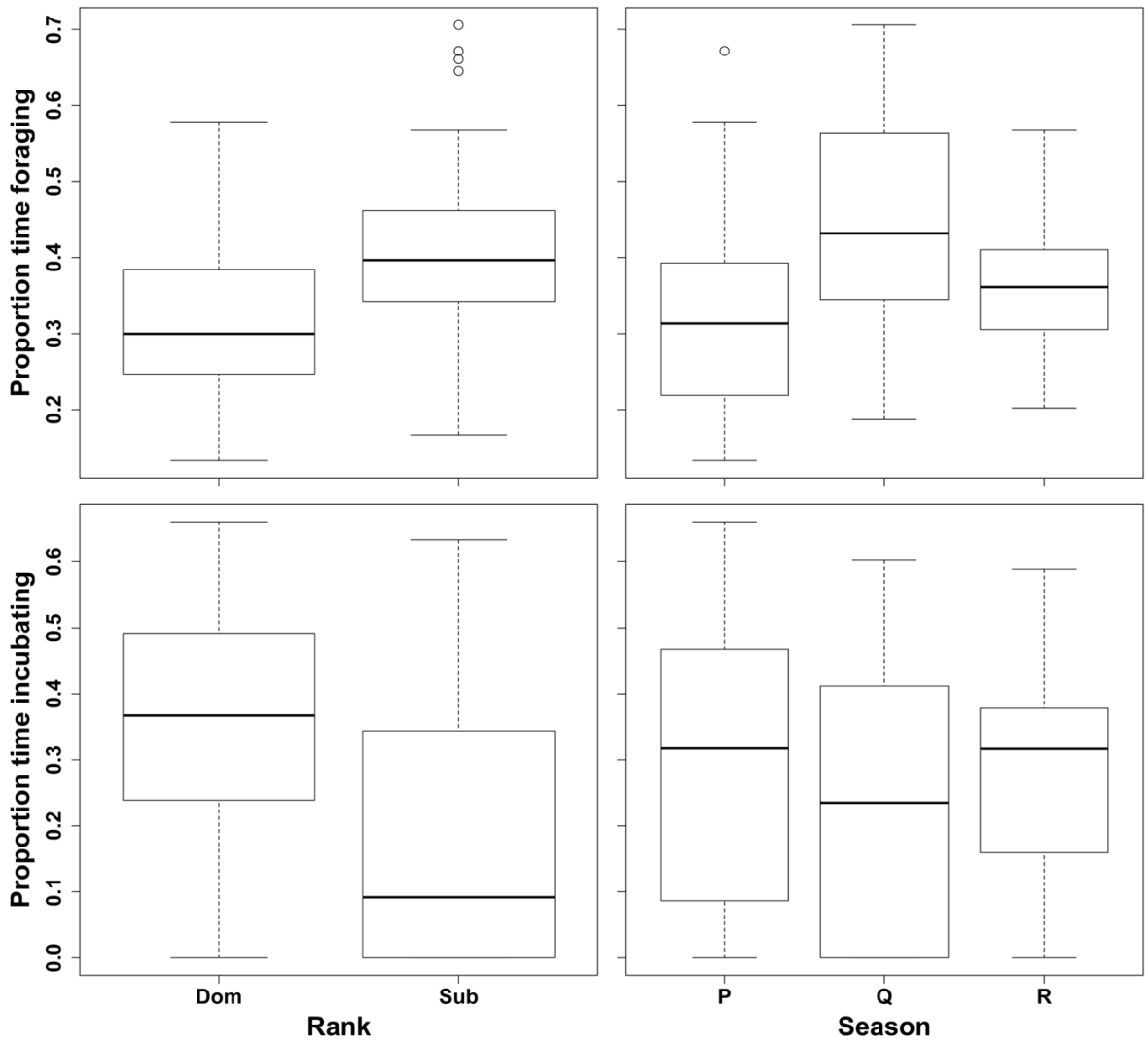

Figure 4.5: Proportion of time spent foraging (top panels) and attending the nest (bottom panels) in relation to rank (left panels) and season (right panels; P = summer 2016/17, Q = summer 2017/18, R = summer 2018/19). Data from 65 days of focal observations on 46 different individuals from 40 nests by 15 groups over 3 breeding seasons.

Separate GLMM analyses for the interactions between predictor variables showed that rank interacted with temperature (Est = 0.719 ± 0.021, z = -33.612, $p < 0.001$): while the proportion of time individuals spent incubating generally decreased as temperatures increased, subordinates decreased their proportion of time incubating more than dominants (towards zero at very high temperatures; Fig. 4.6). While there was no statistically significant effect of an interaction between rank and group size (Est = -0.708 ± 0.948, z = -0.7472, $p < 0.455$), dominant individuals spent a fairly

consistent ~30% time incubating across all group sizes but subordinate individuals tended to decrease their proportion of time spent incubating as group sizes increased. For example, subordinate individuals in groups of three adults spent a similar proportion of time incubating to dominant individuals (around 25.9 ± 20.9%), whereas subordinate individuals in groups of six adults spent only 4.5 ± 9.2% time incubating on average.

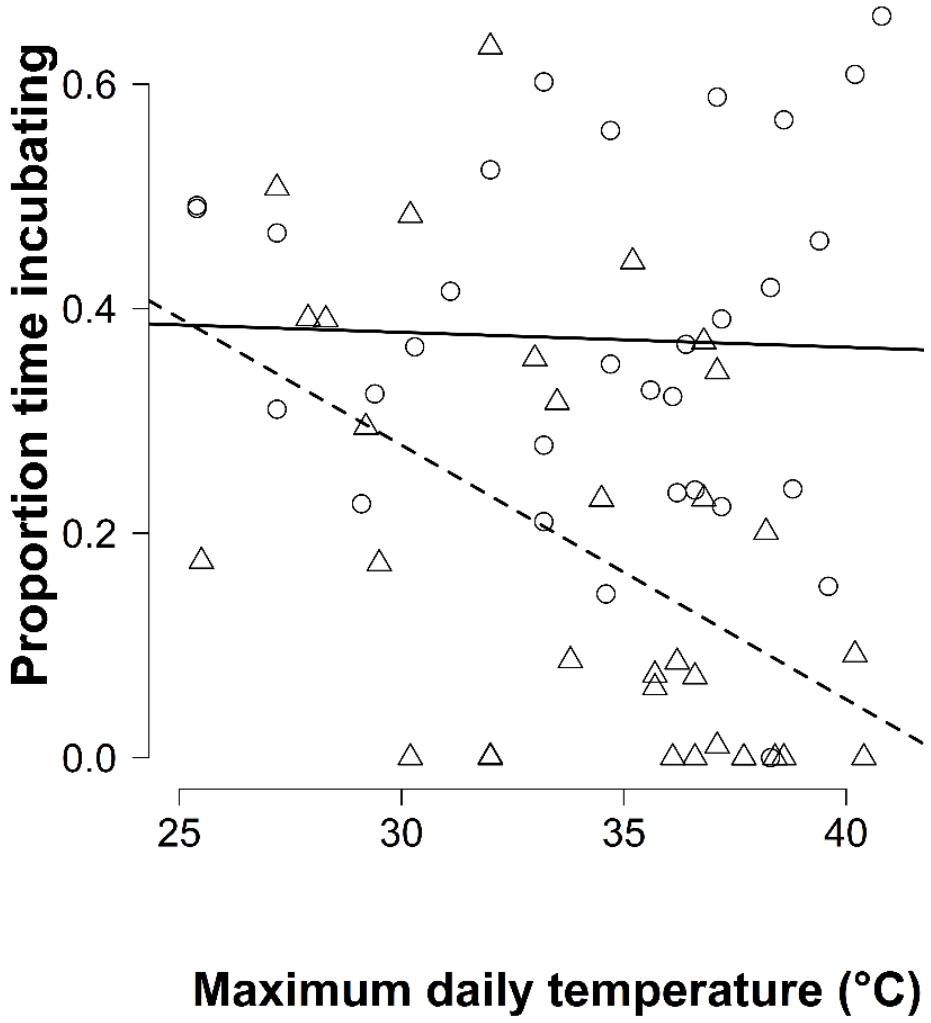

Figure 4.6: Proportion of time spent incubating as a function of temperature, modelled separately for dominant (open circles, solid line) and subordinate (open triangle, dashed line) individuals. Data from 65 days of focal observations on 46 different individuals from 40 nests by 15 groups over 3 breeding seasons.

I also collected data on incubation bouts and recesses for all group members, including details on which individuals incubated on observation days and for how long (see Chapter 4 methods for details). Individual incubation bouts were quite variable in length (n = 437; mean = 80.1 ± 76.4 min; range: 1 – 420 min), split fairly evenly between relatively short incubation bouts (<60 min, n = 235) and more sustained incubation bouts (>=60 min, n = 203). Average duration of incubation bouts did not differ significantly between hot days (≥ 35.5°C; mean = 87.3 ± 88.4 min; range: 1 – 420 min) and cool days (< 35.5°C; 73.8 ± 63.6 min; range: 1 – 302 min; Wilcoxon rank sum W = 24562, p = 0.546). Total incubation effort (as time spent incubating in minutes) per adult individual per day averaged 171 ± 138 minutes (or 2.9 ± 2.3 h, range 0 - 8.9 h). Observation time ranged from 12 to 14 hours (mean = 13.4 ± 0.4 h), so proportion time spent incubating per adult individual per day averaged 21.4 ± 17.1%.

Sub-adult individuals generally incubated for short periods at a time (n = 18 incubate bouts, mean = 18.4 ± 15.4 min; range: 2 – 54 min), and for relatively short periods in total (n = 8 observation days, mean = 23.5 ± 17.4 min; range 3 – 54 min; excludes one juvenile individual from a group of three adults that incubated for 120 min in total). Once sub-adult incubators are excluded the total number of birds that incubated per observation day averaged 3.5 (± 0.9 min; range: 2 – 6; n = 46 observation days). Number of incubators per day approximated number of adult group members for group sizes of 3 – 5 adults (three = 3.4, four = 3.9, five = 4.6), but not for group sizes of 6 adults (six = 3.6) – suggesting that individuals in larger groups may be able to take days off from incubating or avoid incubating altogether. In 93% of groups with three adults, all adults incubated every observation day (n = 14 observation days). All adults incubated every observation day in only 70% of groups with four adults (n = 17), 60% of groups with five adults (n = 5), and zero groups with six adults (n=11), suggesting that pied babblers share the workload of incubation unequally and / or can spread the work

load of incubation between individuals on time scales longer than single days when there more than enough helpers in the group.

Number of incubators per day varied by season with significantly more incubators per day in summer 2018/19 (the driest year; 4 ± 0.94, $p = 0.023$) than in summer 2016/17 (3.1 ± 0.75), and no difference between summer 2016/17 or summer 2017/18 (3.3 ± 0.91) or summer 2017/18 and summer 2018/19 (Fig. 7). In summer 2016/17 and summer 2017/18, the average difference between group size and number of incubators was ~1 (i.e. not all adult group members incubated on a given observation day). In summer 2018/19, the average difference between group size and number of incubators was ~0.5 (i.e. it was more likely for all adult group members to incubate on a given observation day).

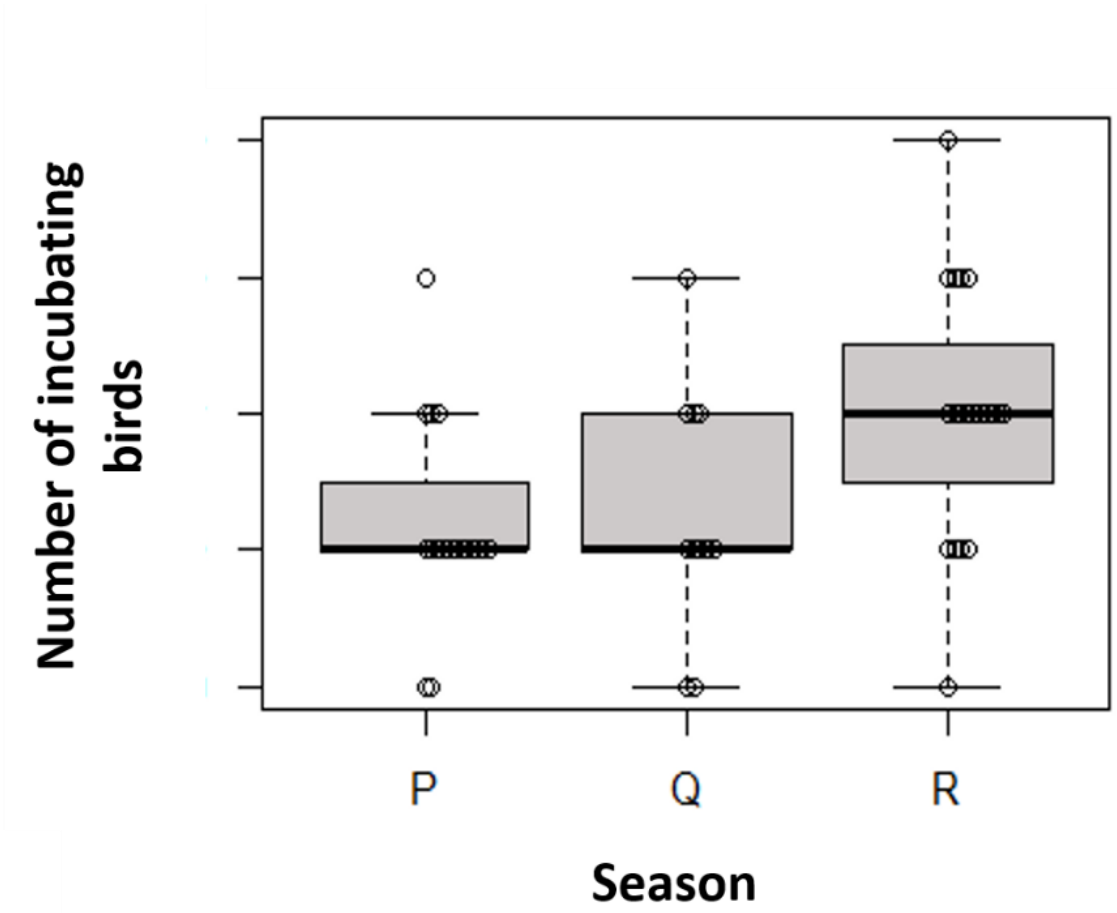

Figure 4.7: number of incubating birds per observation day as a function of breeding season (P = summer 2016/17, Q = summer 2017/18, R = summer 2018/19). Data from 46 observation days.

APPENDIX to CHAPTER 5

Path analysis diagrams for nestling size

Tarsus length, d5

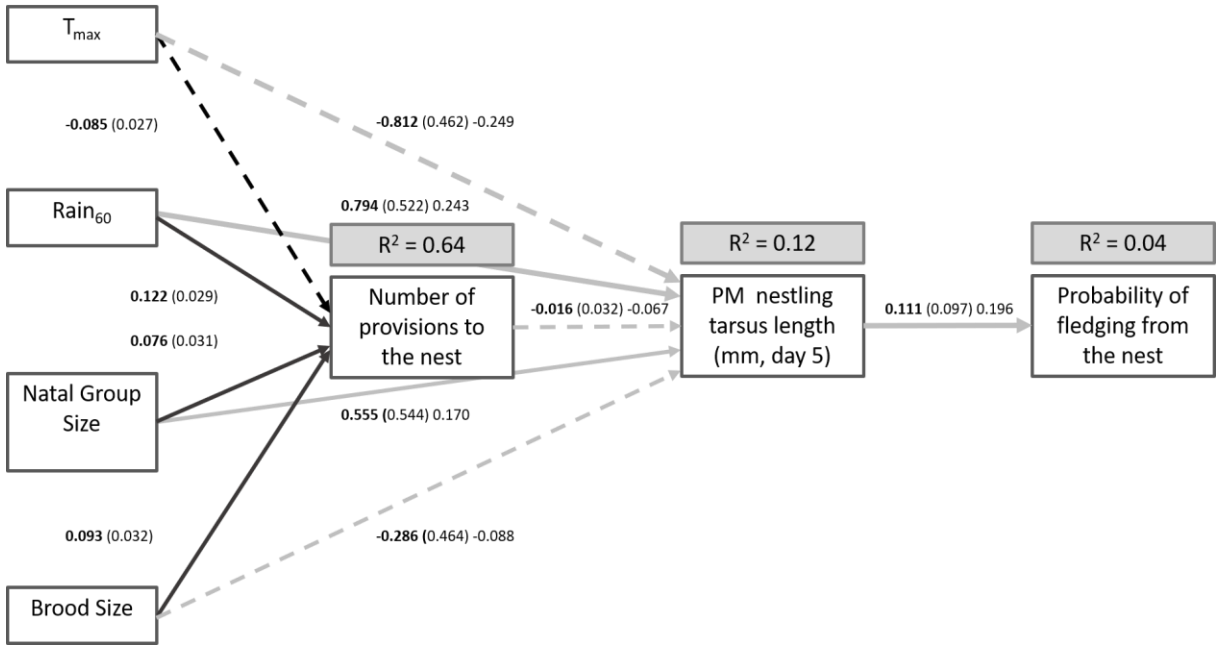

Figure 5.1: Path analysis exploring the effects of environmental factors (temperature and rainfall), group size, and brood size on individual probabilities of fledging via number of provisions and nestling tarsus length (evening) 5 days after hatching. Boxes represent measured variables. Arrows represent unidirectional relationships among variables. Solid arrows denote positive relationships, dashed arrows negative relationships. Unstandardised path coefficients are shown in bold, followed by standard errors in parentheses, and standardised estimates. Standardised Poisson effects could not be calculated in piecewiseSEM*. Non-significant paths are grey. Path thickness has been scaled relative to the absolute magnitude of the standardised estimates, such that stronger effects have thicker arrows.* R^2 *for component models are given in the grey boxes above response variables. Model fit:* $X^2 = 14.83$, $df = 10$, $p = 0.139$.

Wing length, d5

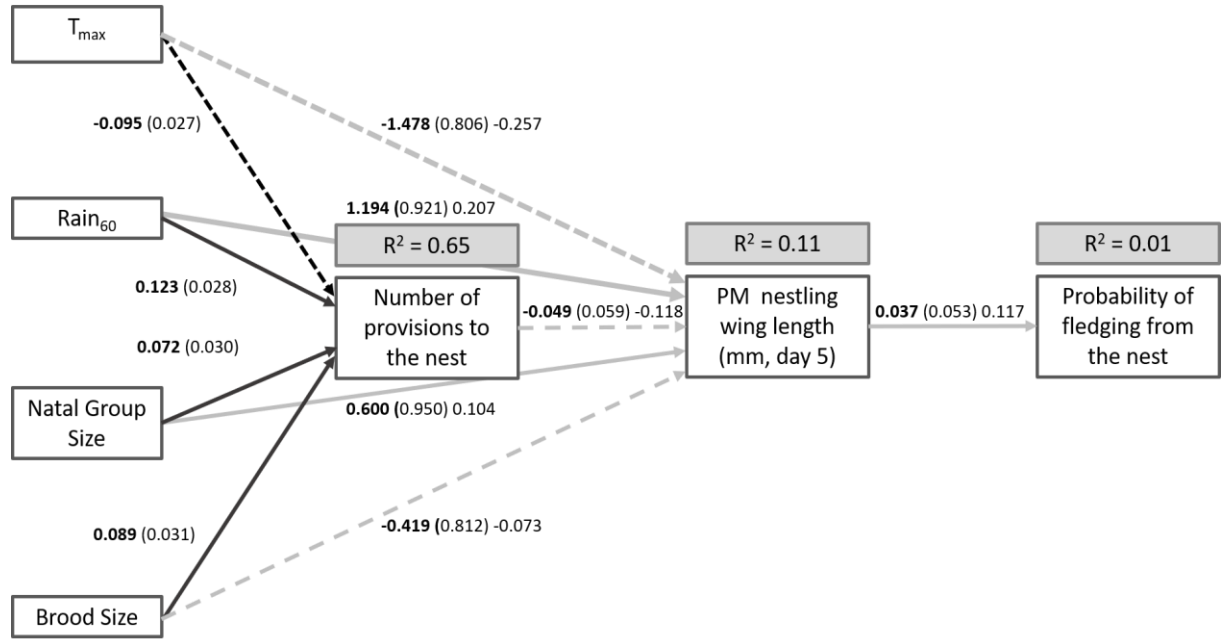

Figure 5.2: Path analysis exploring the effects of environmental factors (temperature and rainfall), group size, and brood size on individual probabilities of fledging via number of provisions and nestling wing length (evening) 5 days after hatching. Boxes represent measured variables. Arrows represent unidirectional relationships among variables. Solid arrows denote positive relationships, dashed arrows negative relationships. Unstandardised path coefficients are shown in bold, followed by standard errors in parentheses, and standardised estimates. Standardised Poisson effects could not be calculated in piecewiseSEM. Non-significant paths are grey. Path thickness has been scaled relative to the absolute magnitude of the standardised estimates, such that stronger effects have thicker arrows. R2 for component models are given in the grey boxes above response variables. Model fit: X2 = 15.08, df = 10, p = 0.129.

Tarsus length, d11

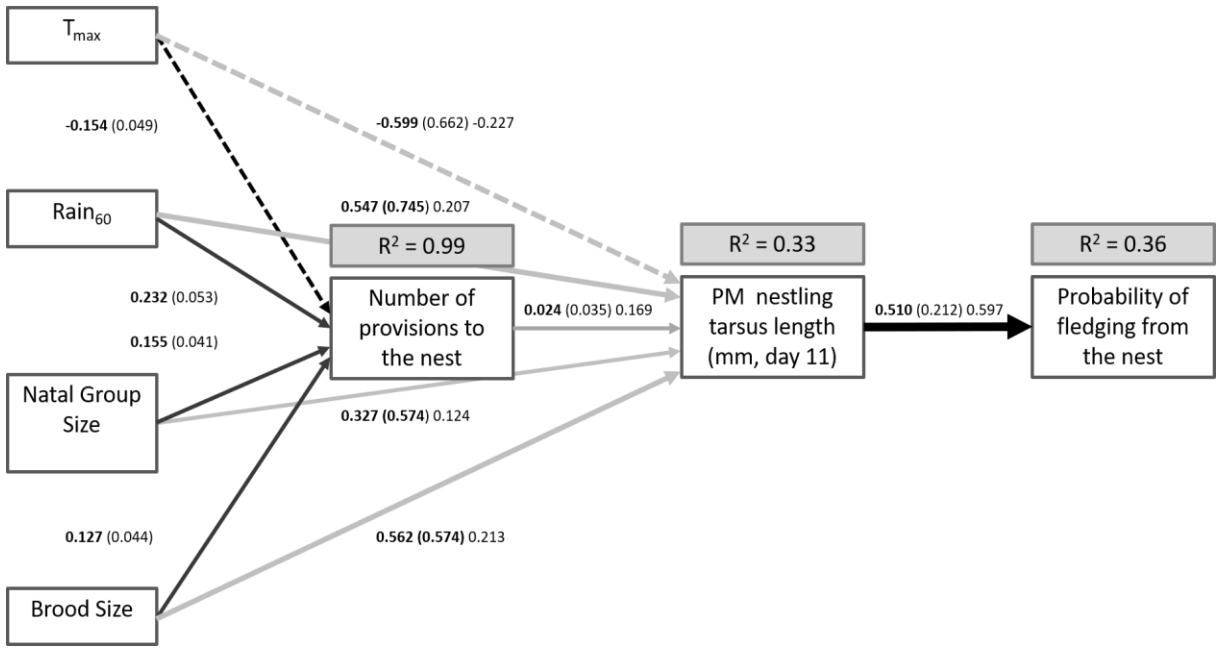

Figure 5.3: Path analysis exploring the effects of environmental factors (temperature and rainfall), group size, and brood size on individual probabilities of fledging via number of provisions and nestling tarsus length (evening) 11 days after hatching. Boxes represent measured variables. Arrows represent unidirectional relationships among variables. Solid arrows denote positive relationships, dashed arrows negative relationships. Unstandardised path coefficients are shown in bold, followed by standard errors in parentheses, and standardised estimates. Standardised Poisson effects could not be calculated in piecewiseSEM. *Non-significant paths are grey. Path thickness has been scaled relative to the absolute magnitude of the standardised estimates, such that stronger effects have thicker arrows.* R^2 *for component models are given in the grey boxes above response variables. Model fit:* $X^2 = 10.13$, $df = 10$, $p = 0.429$.

Wing length, d11

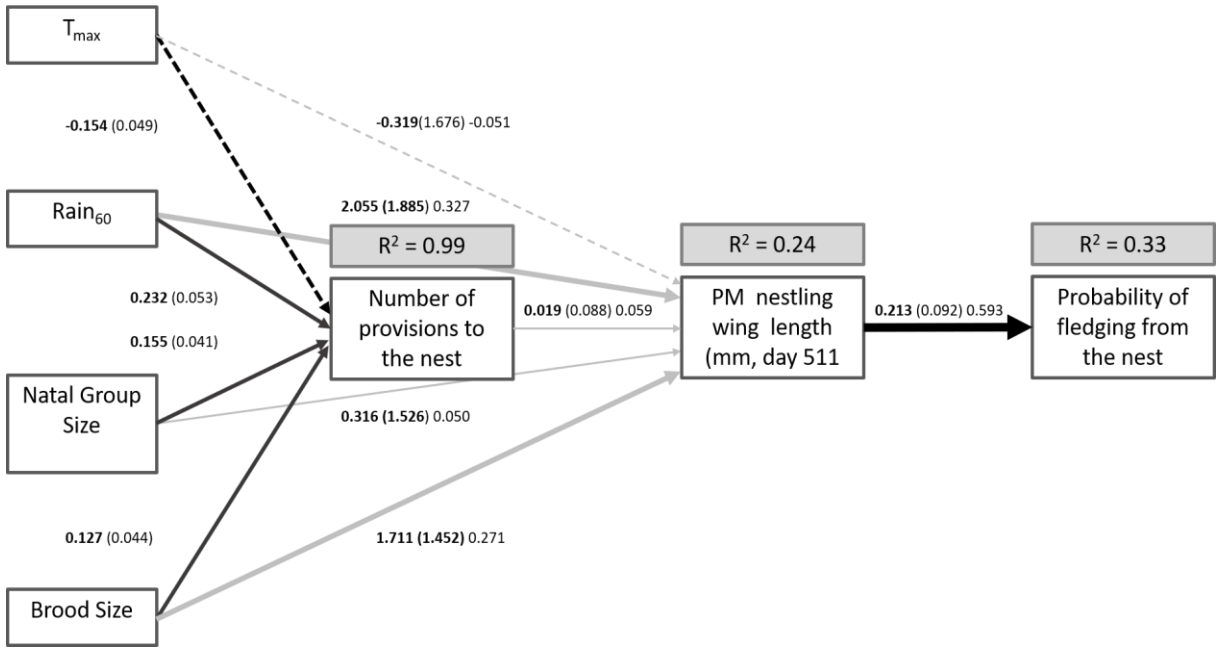

Figure 5.4: Path analysis exploring the effects of environmental factors (temperature and rainfall), group size, and brood size on individual probabilities of fledging via number of provisions and nestling wing length (evening) 11 days after hatching. Boxes represent measured variables. Arrows represent unidirectional relationships among variables. Solid arrows denote positive relationships, dashed arrows negative relationships. Unstandardised path coefficients are shown in bold, followed by standard errors in parentheses, and standardised estimates. Standardised Poisson effects could not be calculated in piecewiseSEM*. Non-significant paths are grey. Path thickness has been scaled relative to the absolute magnitude of the standardised estimates, such that stronger effects have thicker arrows.* R^2 *for component models are given in the grey boxes above response variables. Model fit:* $X^2 = 13.45$, $df = 10$, $p = 0.200$.

Model output tables

Table 5.1: Full LMM model outputs for analyses of nestling daily mass change at 5 days old. Data from 93 nestlings weighed am and pm at 5 days old, from 37 breeding attempts by 19 different groups over 3 breeding seasons. Random terms: Brood identity.

Model Term	***AICc***	***ΔAICc***	***weight***
Null model	*726.9*	*5.03*	*0.052*
Brood size	725.6	3.7	0.102
T_{max}	721.9	0	0.645
$Rain_{60}$	725.4	3.56	0.109
Group size	725.8	3.88	0.092
Top models	***AICc***	***ΔAICc***	***weight***
Null model	726.9	5	0
T_{max}	721.9	0	1
Effect size of explanatory terms after model averaging	Estimate	SE	95% CI
Intercept	23.737	1.944	19.927/27.534
T_{max}	**-4.043**	**1.986**	**-7.922/-0.151**

Table 5.2: Full LMM model outputs for analyses of nestling daily mass change at 11 days old. Data from 77 nestlings weighed am and pm at 11 days old, from 34 breeding attempts by 18 different groups over 3 breeding seasons. Random terms: Brood identity.

Model Term	***AICc***	***ΔAICc***	***weight***
Null model	540.2	29.84	0
Brood size	539.4	29.08	0
T_{max}	510.4	0	1
$Rain_{60}$	539.8	29.42	0
Group size	539.3	28.95	0
Top models	***AICc***	***ΔAICc***	***weight***
Null model	540.2	29.8	0
T_{max}	510.4	0	1
Effect size of explanatory terms after model averaging	Estimate	SE	95% CI
Intercept	6.697	1.077	4.590/8/806
T_{max}	**-7.028**	**1.122**	**-9.316/-4.834**

Table 5.3: Full LMM model outputs for analyses of nestling daily tarsus length change at 11 days old. Data from 77 nestlings weighed am and pm at 11 days old, from 34 breeding attempts by 18 different groups over 3 breeding seasons. Random terms: Brood identity.

Model Term	***AICc***	***ΔAICc***	***weight***
Null model	346.6	4.52	0.081
Brood size	347.3	5.26	0.056
T_{max}	342.1	0	0.772
$Rain_{60}$	349.3	7.25	0.021
Group size	346.8	4.77	0.071
Top models	***AICc***	***ΔAICc***	***weight***
Null model	346.6	4.5	0
T_{max}	342.1	0	1
Effect size of explanatory terms after model averaging	Estimate	SE	95% CI
Intercept	2.945	0.279	2.401/3.501
T_{max}	**-0.804**	**0.287**	**-1.381/-0.245**

Table 5.4: Full GLMM model outputs for analyses of total biomass caught. Data from 84 focal days collected on 56 different individuals at 22 breeding attempts by 13 different groups over 3 breeding seasons. Random terms: Brood identity.

Model Term	***AICc***	***ΔAICc***	***weight***
Null model	438.7	17.33	0
Sex	438.6	17.16	0
Rank	440.9	19.45	0
Brood size	434.6	13.21	0.001
T_{max}	438.6	17.17	0
T_{max} ^ 2	426.3	4.84	0.038
$Rain_{60}$	435.6	14.17	0
Group size	438.8	17.4	0
Group size ^ 2	435.7	14.26	0
Brood size + $Rain_{60}$	431.7	10.25	0.003
T_{max} ^ 2 + Brood size	427	5.58	0.026
Group size ^ 2 + $Rain_{60}$	435.3	13.92	0
T_{max} ^ 2 + $Rain_{60}$	427.9	6.44	0.017
T_{max} ^2 + Group size ^ 2	421.4	0	0.43
Group size ^ 2 + Brood size	430	8.61	0.006
T_{max} ^ 2 + $Rain_{60}$ + Brood size	428.3	6.85	0.014
T_{max} ^ 2 + Brood size + Group size ^2	421.8	0.39	0.354
T_{max} ^ 2 + $Rain_{60}$ + Brood size + Group size ^2	424.2	2.74	0.11

Table 5.5: Full GLMM model outputs for analyses of total biomass provisioned. Data from 84 focal days collected on 56 different individuals at 22 breeding attempts by 13 different groups over 3 breeding seasons. Random terms: Brood identity.

Model Term	***AICc***	***ΔAICc***	***weight***
Null model	237.1	5.61	0.036
Sex	239.1	7.66	0.013
Rank	233.8	2.36	0.181
Brood size	238.5	7.01	0.018
T_{max}	239.2	7.72	0.012
$Rain_{60}$	238.7	7.24	0.016
Group size	234.4	2.95	0.135
Group size + Rank	231.5	0	0.59
Top models	***AICc***	***ΔAICc***	***weight***
Basic (1 + (1|NestCode)	237.1	5.6	0
Group size + Rank	231.5	0	1
Effect size of explanatory terms after model averaging	Estimate	SE	95% CI
Intercept	0.223	0.177	-0.184/0.539
Rank	**-0.468**	**0.210**	**-0.690/-0.029**
Group size	**-0.334**	**0.157**	**-0.890/-0.063**

APPENDIX to CHAPTER 6

Model output tables

Table 6.1: Full LMM model outputs for analyses of body mass change between fledging and independence in juveniles. Data from 129 individuals from 78 nests by 25 groups over 14 breeding seasons. Random terms: Nest identity nested within Group identity.

Model Term	AICc	ΔAICc
Null model	829.0	18.29
Brood size	818.8	7.99
$Drought_{BrSeas}$	825.7	14.92
$G.Size_{90}$	829.4	18.60
Mean T_{max90}	828.8	18.05
$Rain_{60}$	822.9	12.11
$Rain_{90}$	820.9	10.13
Sex	826.7	15.94
Brood size + $Rain_{60}$	815.6	4.81
Brood size + $Rain_{90}$	813.8	3.06
Brood size + $Rain_{60}$ + $Rain_{90}$	810.8	0.00
$Rain_{60}$ + $Rain_{90}$	815.4	4.65
$G.Size_{90}$ + Mean T_{max90} + $Rain_{90}$	821.7	10.96
$G.Size_{90}$ + Mean T_{max90} + $G.Size_{90}$ * Mean T_{max90}	825.8	15.09
$G.Size_{90}$ + $Rain_{60}$ + $G.Size_{90}$ * $Rain_{60}$	823.5	12.75
$G.Size_{90}$ + $Rain_{90}$ + $G.Size_{90}$ * $Rain_{90}$	822.3	11.49
$G.Size_{90}$ + $Drought_{BrSeas}$ + $G.Size_{90}$ * $Drought_{BrSeas}$	825.3	14.52

Table 6.2: Full LMM model outputs for analyses of body mass change between the start and the end of the breeding season in dominant individuals. Data from 74 measurements of 46 different individuals at 20 groups over 10 breeding seasons. Random terms: Bird identity nested within Group identity.

Model Term	**AICc**	**ΔAICc**
Null model	409.6	12.72
$Drought_{BrSeas}$	406.6	9.72
$G.Size_{BrSeas}$	410.3	13.49
Mean T_{max}	405.7	8.83
$Rain_{BrSeas}$	406.6	9.76
Sex	409.3	12.40
Mean T_{max} + $Rain_{BrSeas}$	396.9	0.00
$G.Size_{BrSeas}$ + Mean T_{max} + $Rain_{BrSeas}$	399.1	2.26
$G.Size_{BrSeas}$ + Mean T_{max} + $G.Size_{BrSeas}$ * Mean T_{max}	408.7	11.81
$G.Size_{BrSeas}$ + $Rain_{BrSeas}$ + $Rain_{BrSeas}$ * $G.Size_{BrSeas}$	407.6	10.74
$G.Size_{BrSeas}$ + $Drought_{BrSeas}$ + $Drought_{BrSeas}$ * $G.Size_{BrSeas}$	407.9	11.05

Table 6.3: Full GLMM model outputs for analyses of interannual survival of juveniles considering the influence of conditions in the nest. Data from 247 known juvenile individuals still present in the population at nutritional independence (90 days of age) from 143 broods by 30 distinct groups over 14 breeding seasons. Random terms: Nest identity nested within Group identity.

Model Term	**AICc**	**ΔAICc**
Null model	315.5	10.17
Brood size	315.0	9.70
$Drought_{BrSeas}$	315.6	10.23
$G.Size_{Brood}$	317.3	11.98
$Mass_{11}$	315.7	10.32
Mean $T_{maxBrood}$	313.2	7.88
$Rain_{60}$	310.1	4.77
Sex	315.8	10.50
$Rain_{60}$ + Mean $T_{maxBrood}$	307.8	2.45
$G.Size_{Brood}$ + $Rain_{60}$ + Mean $T_{maxBrood}$	309.8	4.52
$G.Size_{Brood}$ + Mean $T_{maxBrood}$ + $G.Size_{Brood}$ * Mean $T_{maxBrood}$	315.6	10.32
$G.Size_{Brood}$ + $Rain_{60}$ + $G.Size_{Brood}$ * $Rain_{60}$	314.2	8.86
$G.Size_{Brood}$ + $Drought_{BrSeas}$ + $G.Size_{Brood}$ * $Drought_{BrSeas}$	316.1	10.72
$Rain_{60}$ + Mean $T_{maxBrood}$ + $Rain_{60}$ * Mean $T_{maxBrood}$	305.3	0.00
$Drought_{BrSeas}$ + Mean $T_{maxBrood}$ + $Drought_{BrSeas}$ * Mean $T_{maxBrood}$	315.1	9.77

Table 6.4: Full GLMM model outputs for analyses of interannual survival of juveniles considering the influence of conditions between fledging and independence. Data from 229 known juvenile individuals still present in the population at nutritional independence (90 days of age) from 133 broods by 30 groups over 14 breeding seasons. Random terms: Nest identity nested within Group identity.

Model Term	**AICc**	**ΔAICc**
Null model	300.6	17.52
Brood size	300.2	17.12
$Drought_{BrSeas}$	301.7	18.68
$G.Size_{90}$	302.3	19.23
$Mass_{11}$	300.5	17.49
Mean T_{max90}	292.3	9.27
$Rain_{90}$	301.9	18.90
Sex	301.4	18.37
$G.Size_{90}$+ $Rain_{90}$ + Mean T_{max90}	296.2	13.17
$G.Size_{90}$+ Mean T_{max90} + $G.Size_{90}$ * Mean T_{max90}	293.5	10.49
$G.Size_{90}$ + $Rain_{90}$ + $G.Size_{90}$ * $Rain_{90}$	303.2	20.13
$G.Size_{90}$+ $Drought_{BrSeas}$ + $G.Size_{90}$ * $Drought_{BrSeas}$	301.9	18.82
$Drought_{BrSeas}$ + Mean T_{max90} + $Drought_{BrSeas}$ * Mean T_{max90}	283.0	0.00
$Rain_{90}$ + Mean T_{max90} + $Rain_{90}$ * Mean T_{max90}	295.3	12.22

Table 6.5: Full GLMM model outputs for analyses of interannual survival of breeding adults considering the influence of conditions during the breeding season. Data from 352 measurements of interannual survival from 136 different individuals who were dominant for at least one whole breeding season Sept to March, from 37 distinct groups over 14 breeding seasons. Random terms: Bird identity nested within Group identity.

Model Term	**AICc**	**ΔAICc**
Null model	391.0	33.73
$Drought_{BrSeas}$	367.8	10.54
$G.Size_{BrSeas}$	392.6	35.39
Mean T_{max}	384.7	27.52
$Rain_{BrSeas}$	368.5	11.31
Sex	393.0	35.78
Mean T_{max} + $Drought_{BrSeas}$	368.9	11.69
Mean T_{max} + $Rain_{BrSeas}$	367.5	10.25
$G.Size_{BrSeas}$ + Mean T_{max} + $Rain_{BrSeas}$	367.4	10.21
$G.Size_{BrSeas}$ + Mean T_{max} + $G.Size_{BrSeas}$ * Mean T_{max}	386.0	28.83
$G.Size_{BrSeas}$ + $Rain_{BrSeas}$ + $G.Size_{BrSeas}$ * $Rain_{BrSeas}$	371.1	13.84
$G.Size_{BrSeas}$ + $Drought_{BrSeas}$ + $G.Size_{BrSeas}$ * $Drought_{BrSeas}$	371.0	13.78
$Drought_{BrSeas}$ + Mean T_{max} + $Drought_{BrSeas}$ * Mean T_{max}	357.2	0.00
$Rain_{BrSeas}$ + Mean T_{max} + $Rain_{BrSeas}$ * Mean T_{max}	366.4	9.21

Table 6.6: Full GLMM model outputs for analyses of the number of breeding attempts undertaken by each social group. Data from 177 group-seasons from 38 groups over 14 breeding seasons. Random terms: Group identity.

Model Term	**AICc**	**ΔAICc**
Null model	701.7	68.64
Mean $T_{maxBrSeas}$	699.2	66.10
Mean $T_{maxBrSeas-1}$	673.0	39.95
$G.Size_{BrSeas}$	703.7	70.68
$Drought_{BrSeas}$	653.8	20.77
$Drought_{BrSeas-1}$	672.7	39.67
$Rain_{BrSeas}$	654.3	21.26
$Rain_{BrSeas-1}$	692.5	59.48
$Rain_{BrSeas}$ + Mean $T_{maxBrSeas-1}$	652.8	19.71
$Rain_{BrSeas}$ + $Drought_{BrSeas-1}$	633.1	0.00
$Rain_{BrSeas}$ + $Drought_{BrSeas-1}$ + Mean $T_{maxBrSeas-1}$	634.4	1.35
$Drought_{BrSeas-1}$ + Mean $T_{maxBrSeas-1}$	654.0	1.26
$G.Size_{BrSeas}$ + Mean $T_{maxBrSeas-1}$ + $G.Size_{BrSeas}$ * Mean $T_{maxBrSeas-1}$	697.5	64.45
$G.Size_{BrSeas}$ + Mean $T_{maxBrSeas}$ + $G.Size_{BrSeas}$ * Mean $T_{maxBrSeas}$	676.5	43.45
$Drought_{BrSeas-1}$ + $G.Size_{BrSeas}$ + $Drought_{BrSeas-1}$ * $G.Size_{BrSeas}$	675.4	42.36
$Rain_{BrSeas}$ + $G.Size_{BrSeas}$ + $Rain_{BrSeas}$ * $G.Size_{BrSeas}$	656.6	23.56

Table 6.7: Full GLMM model outputs for analyses of the number of surviving young (90 days) produced by each social group. Data from 144 group-seasons from 32 groups over 14 breeding seasons. Random terms: Group identity.

Model Term	**AICc**	**ΔAICc**
Null model	501.0	53.46
Mean $T_{maxBrSeas}$	502.9	55.36
Mean $T_{maxBrSeas-1}$	484.4	36.82
$G.Size_{BrSeas}$	499.1	51.53
$Drought_{BrSeas}$	486.3	38.72
$Drought_{BrSeas-1}$	491.8	44.21
$Rain_{BrSeas}$	455.6	8.01
$Rain_{BrSeas-1}$	500.3	52.74
$Rain_{BrSeas}$ + Mean $T_{maxBrSeas-1}$	457.5	9.93
$Rain_{BrSeas}$ + $G.Size_{BrSeas}$	452.1	4.55
$Rain_{BrSeas}$ + $Drought_{BrSeas-1}$	452.8	5.21
$Rain_{BrSeas}$ + Mean $T_{maxBrSeas-1}$ + $Drought_{BrSeas-1}$	454.8	7.26
$Rain_{BrSeas}$ + $G.Size_{BrSeas}$ + Mean $T_{maxBrSeas-1}$	454.2	6.67
$Rain_{BrSeas}$ + $Drought_{BrSeas-1}$+ $G.Size_{BrSeas}$	447.6	0.00
$Rain_{BrSeas}$ + $Drought_{BrSeas-1}$+ $G.Size_{BrSeas}$ + Mean $T_{maxBrSeas-1}$	449.0	1.45
Mean $T_{maxBrSeas-1}$ + $G.Size_{BrSeas}$	483.3	35.78
Mean $T_{maxBrSeas-1}$ + $Drought_{BrSeas-1}$	481.9	34.39
$Drought_{BrSeas-1}$ + $G.Size_{BrSeas}$	486.5	38.97
$Drought_{BrSeas-1}$ + $G.Size_{BrSeas}$ + Mean $T_{maxBrSeas-1}$	479.1	31.60
$G.Size_{BrSeas}$ + Mean $T_{maxBrSeas}$ + $G.Size_{BrSeas}$ * Mean $T_{maxBrSeas}$	502.6	55.00
$G.Size_{BrSeas}$ + Mean $T_{maxBrSeas-1}$+ $G.Size_{BrSeas}$ * Mean $T_{maxBrSeas-1}$	484.0	36.48
$Drought_{BrSeas-1}$ + $G.Size_{BrSeas}$ + $Drought_{BrSeas-1}$ * $G.Size_{BrSeas}$	488.4	40.84
$Rain_{BrSeas}$ + $G.Size_{BrSeas}$ + $Rain_{BrSeas}$ * $G.Size_{BrSeas}$	454.1	6.54

The End