

# Heat tolerance of Southern Pied Babblers in the Kalahari Desert: how will they respond to climate change?

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## Abstract

Earth will soon be faced with warmer conditions than it has experienced in the past 10,000 years, and these changes are occurring at a striking rate. Changes are predicted to impact species as natural selection will drive range shifts and adaptations, and is predicted to precipitate the extinction of some species. In an effort to understand this process, scientists use models to predict future change. Although bioclimatic envelope models accurately predict species distributions at broad scales, a more detailed understanding of model systems, developed using physiological and behavioural traits, is necessary to make the most accurate predictions about the consequences of a changing climate to biological diversity. Among the habitats predicted to experience the most rapid changes in climate are hot, subtropical deserts, including southern Africa's Kalahari Desert. Birds not only fill important niches in desert ecosystems, but they are also considered biological indicators of change. An increasing incidence of mass mortalities of birds in hot deserts suggests that birds may be appropriate candidates for assessing how natural selection, under the influence of climate change, drives adaptation. Past research highlights the importance of behaviour in determining a species' ability to survive in a given climatic region, but few empirical studies have tested the limits to this adaptability. The effects of ambient temperature on daily weight gain, foraging effort and efficiency and the presence of heat-dissipation behaviours were assessed to determine the mechanisms by which increased temperature affect babbler body condition. The effect of heat-wave duration on babbler weight gain was assessed from a long-term dataset to explore the potential consequences of prolonged high temperatures on babbler body condition. This study of Southern Pied Babblers in the Kalahari Desert identified temperature as the main driver of weight loss (LMM:  $f_{23,235} = 38.487$ ,  $P < 0.001$ ). An analysis of foraging behaviour revealed that high ambient temperatures and the resulting need to dissipate heat negatively impacts the birds' ability to obtain resources and maintain a positive energy budget (LMM:  $f_{257} = 19.777$ ,  $P < 0.001$ ;  $f_{172,090} = 9.079$ ,  $P = 0.003$ ), suggesting that the birds trade off thermoregulation against foraging. An analysis of historical weight-change data showed that babbler body condition fell steadily as the duration of heat waves increased (LMM:  $f_{126,518} = 5.527$ ,  $P = 0.02$ ). Models of future climate predict that the intensity and duration of heat-wave events in the Kalahari will increase: this analysis suggests that babblers may have limited ability to cope with such changes.

## **Literature Review**

This literature review examines present knowledge of the impacts of climate change on biodiversity, in particular impacts on the time-budget and condition of desert-dwelling birds.

### ***Predictions of a changing climate***

Earth is warming faster than it ever has before (IPCC 2001), with some researchers predicting that the earth's atmosphere will become warmer than it has been at any time in the past 40 million years in the next few decades (Overpeck et al. 2002). The planet has already warmed by an average of 0.75°C, since the early 1900s and, even if all emissions are halted today, is projected to warm by another 0.5°C overall, (IPCC 2007; Sodhi & Ehrlich 2010). Weather patterns are predicted to become more erratic, and incidences of extreme temperature and droughts are predicted to increase (IPCC 2007). Whilst a warming world may offer opportunities for some species (e.g. breeding range expansions), for others these changes may offer significant challenges to their adaptability, especially for species that already inhabit the world's hottest regions.

Wildlife from most taxonomic groups, on every continent and in every ocean, has suffered direct impacts due to anthropogenic climate change (Crick 2004; reviewed in Parmesan 2006). Climate change impacts species independently of direct human contact, making it a unique threat to biodiversity (Kearney et al. 2010; La Sorte et al. 2009; Sinervo et al. 2010). It also acts synergistically and additively with other anthropogenic effects such as habitat loss and degradation (Brooks et al. 1999; Travis 2003) and invasion by alien species (Occhipinti-Ambrogi 2007). Current projections forecast that species' distributions may need to shift ten times faster than they did during the last ice age in order to compensate for the rapidly changing environment (Wormworth & Mallon 2006). It is highly likely that these challenges will surpass the adaptability of many species, threatening one million species with extinction by the year 2050 (Crick 2004).

### ***Interactions with other drivers of change***

Climate change does not act in isolation. Habitat loss and degradation, and invasive species can work synergistically with climate change, placing species and even entire ecosystems at heightened risk of extinction (MEA 2005). Of these threats, climate change is the most complex, detrimental, and widespread (Kiker 2000; IPCC 2002; see Turpie 2003). Indeed, climate change can and will impact areas and species untouched by, and even possibly unknown, to humans (La Sorte et al. 2009; Kearney et al. 2010; Sinervo et al. 2010).

### *Responses to change*

Not all species will be affected by climate change in the same way: some will benefit and others will be negatively impacted (Fajer et al. 1989). Uneven shifts in species composition due to differing degrees of adaptability and response speeds could lead to ecosystem collapse (see Coope 1994); further complicating the impacts of climate change (Chapin et al. 2000).

At the level of the individual, there are two likely adaptive responses to climate change, namely a shift in range, or behavioural adaptation (Sinervo et al. 2010). Species that already exist at or close to their physiological limits, such as tolerance to extreme temperatures, will be at a heightened risk of extinction (Sinervo et al. 2010). For example, adult Pika *Ochotona princeps* in the western United States stop foraging in the midday heat and adults die within 30 minutes of exposure to temperatures as low as 31°C (Smith 1974; Parmesan 2006). What is becoming increasingly clear is that if we are to gain a mechanistic understanding of the biological effects of climate change, empirical studies are required to support or refute the predictions of bioclimatic envelope models (Erasmus et al. 2002).

### ***Forecasting the impacts of climate change***

#### *Understanding models*

Climate and bioclimatic envelope models are currently the tools of choice to predict future changes in climate and the abilities of species' to respond to such changes (Erasmus et al. 2002; Thomas et al. 2004). The key assumption underpinning bioclimatic envelope models is that climatic factors are the main drivers of species' geographical distributions (Pearson & Dawson 2003). Critics of these models argue that important drivers of distributions, such as biotic interactions or a species' ability

to evolve or disperse, are ignored (Brook et al. 2009): as a result, the models can be criticised as being 'devoid of biology'. Pearson & Dawson (2003) hypothesise that at a broad scale, climatic variables are the main drivers of species distributions; while, at fine scales, physiologically based mechanistic models may more accurately predict ranges (Pearson & Dawson 2003; Helmuth et al. 2005; Okes et al. 2008). This dichotomy has precipitated attempts to develop integrated models that bridge the gap between abiotic and biotic drivers of responses to climate change (Huntley et al. 2010). However, models with mechanistic components require detailed information that is difficult and costly to obtain, making it important to prioritise studies of key taxa in key climatic regions (Kearney et al. 2010). Given climate predictions for hot subtropical deserts (IPCC 2007; Moise & Hudson 2008) and the physiological and behavioural specialisations needed for existence in such environments (Clark 1987; Wolf 2000; Anava et al. 2001) deserts such as the Kalahari should be priority biotopes for such studies.

### ***Predictions for deserts in the face of climate change***

#### *Deserts*

Deserts, which comprise 25-30% of the earth's surface (Polis 1991), are among the most threatened ecosystems and require special conservation attention (Lovegrove 1993). They are the hottest places on earth with intense solar radiation. Rain falls infrequently and unpredictably, and few if any sources of open water exist (Dean 2004). Often characterised as "extreme environments", these regions experience major fluctuations in ambient temperature both daily and seasonally. Anthropogenic climate change is predicted to increase average temperatures and lead to an increasing frequency and intensity of extreme weather events in these areas (Wormworth & Mallon 2006). It follows that climate change may push deserts into environmental windows that do not presently exist and potentially beyond the current threshold for life. For instance, bird species have an upper thermal limit of approximately 47°C (Williams & Tieleman 2005): if desert temperatures rise above this limit, mass bird mortalities ensue (i.e. Finlayson 1932). At least two such mass-mortality events have happened in Western Australia since 2009 (Welbergen et al. 2008; McKechnie & Wolf 2010).

### *Future climate predictions for the Kalahari Desert*

In the Kalahari Desert climate change is predicted to have major effects, notably an increase in mean seasonal temperatures, a decrease in rainfall, and an increase in the frequency of severe weather anomalies, including heat waves (Kruger & Shongwe 2004; Christensen et al. 2007). Indeed, within southern Africa the Kalahari Desert is predicted to experience the highest level of warming, potentially placing many species at risk (Moise & Hudson 2008).

### *The effects of climate change on desert species*

The combination of climatic variables present in the desert leads to low primary productivity and hence a limited food supply (Dean 2004). Difficulties in maintaining positive energy budgets arise both from resource limitation and the high costs of thermoregulation to maintain body temperatures below lethal limits (Soobramoney 2003). As a result, desert species face strong selective pressures to optimise the use of energy and water resources (Wolf et al. 1996; Williams & Tieleman 2005), making desert species good candidates for assessing the mechanistic effects of climate change on physiology and behaviour.

Birds also are appropriate candidates for climate-change studies (Crick 2004; Simmons et al. 2004). They are mostly mobile, and by virtue of this mobility are predicted to respond rapidly to climate change compared with other taxa (Wormworth & Mallon 2006). Hence, birds are potentially sensitive bio-indicators of climate-change effects on ecosystems (Crick 2004). Desert birds are primarily diurnal and, unlike mammals, few species make use of subterranean microsites that can reduce exposure to high ambient temperatures (Wolf 2000). This makes them extremely sensitive to the effects of normal desert conditions (Wolf et al. 1996) and potentially very vulnerable to changes in climate that may increase the severity of these conditions.

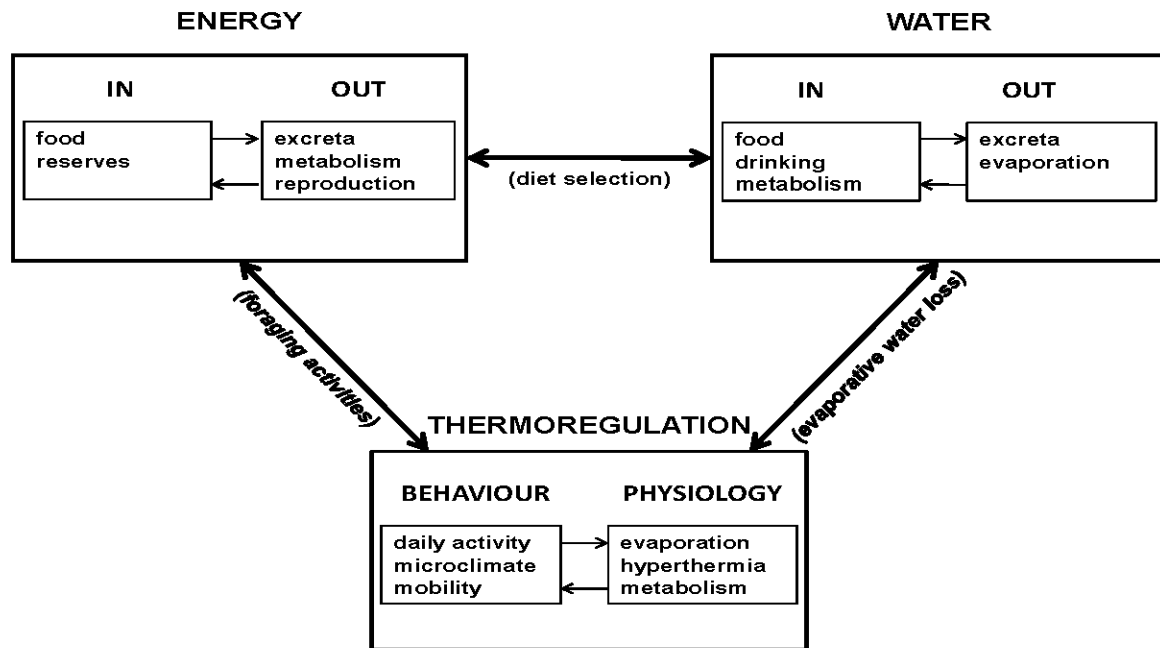
### ***The importance of behaviour and physiology in climate-change studies***

#### *Behavioural and physiological adaptations*

In the past, birds were commonly considered to possess no adaptations or physiological specialisation to desert environments (Bartholomew & Cade 1963). More recently, this wisdom has been challenged (Anava et al. 2001; Williams &

Tieleman 2005). The most important adaptations among desert birds are those that help birds maximise net energy gains, reduce water loss and increase the efficiency of thermoregulation through, for example, facultative hyperthermia (Wolf 2000; Soobramoney 2003; Williams & Tieleman 2005).

Energy, water and thermoregulation are inextricably linked in all endotherms (Figure 1), which maintain thermal homeostasis primarily through internal metabolic processes. However, endothermy also increases the cost of living for these animals by elevating energy requirements for survival and by increasing water loss (Bennett & Dawson 1976). Birds have the highest mass-specific metabolism of any vertebrate (Dean 2004). As temperatures increase or decrease beyond the thermoneutral zone, energy requirements for endotherms are increased in order to maintain their body temperatures within non-lethal limits (Williams & Tieleman 2001). In deserts, where food and water are scarce and where temperatures are extreme and variable, birds face a significant challenge in balancing energy and water budgets (Maclean 1996). Thermoregulatory adaptations in desert birds, both behavioural and physiological, act to minimise energy loss as well as water loss. For example, avian desert species have lower basal metabolic rates than species inhabiting more mesic environments (Anava et al. 2001; Tieleman et al. 2002).



**Figure 1:** A conceptual model relating energy, water and thermoregulation in desert birds (adapted from Williams & Tieleman 2001).

In terms of energy gain, foraging can be a costly activity; both in terms of energy expenditure and predation risk (Thiele et al. 2008). Maintaining a positive energy budget depends on foraging efficiency (Weathers & Sullivan 1989), which is likely to be influenced by diet. For example, a diet of insects provides a higher calorific return per unit mass than does a diet of seeds (Weathers & Sullivan 1989). Energy intake rates can also be optimised by foraging when prey activity is highest, or when the costs of foraging are the lowest. Desert birds and other animals mostly forage during the early mornings and late afternoons (crepuscular activity - Webb 1979; Carmi-Winkler et al. 1987). For instance, in the Kalahari Desert, meerkats *Suricata suricatta* have midday 'siestas' during the hot summer months (Doolan & Macdonald 1996). For granivorous birds, food availability is consistent across a given day (Maclean 1996). By contrast, insectivorous birds should, in theory, optimize energy intake rates by foraging when insect activity is at its peak (30-35°C - Kearney et al. 2009). However, foraging performance can be impacted by environmental conditions (e.g. food scarcity and/or high ambient temperatures). Poor foraging performance is likely to result in poor body condition. Individuals whose body condition is compromised may have lower reproductive success or even forego reproduction until a time when

their body condition has improved (Tieleman & Williams 2002). In terms of predicting effects of climate change on desert species, therefore, body condition may be an appropriate surrogate for potential reproductive performance (and hence the probability of persistence). For instance, protein reserves in female Red-billed Queleas *Quelea quelea* were 80% higher than normal during breeding, which suggests that some birds do not need environmental cues to breed but instead use body condition as a trigger (Jones & Ward 1976).

Hydration is a requirement of life (Bartholomew 1972), and reducing water loss is of paramount importance for desert-dwelling species (Tieleman et al. 2002a; Williams 2002). As a result, many arid-zone species have very creative ways of obtaining water. For example, in the Namib Desert, many species of tenebrionid beetle use facial appendages to precipitate water from fog (Gullan & Cranston 2005). Ecophysiologicaly, desert birds are divided into three groups: obligate drinkers, occasional drinkers, and carnivorous or insectivorous birds that do not need to drink free water because they obtain the moisture they need from their prey (Maclean 1996). Birds also gain water from catabolism and their inherently high metabolism (Williams & Tieleman 2005); however, they lose more water to evaporative cooling at high temperatures than they gain from metabolic water production (McKechnie 2008).

### *Thermoregulation*

One meteorological variable to which birds are particularly susceptible is ambient temperature. There is a range of environmental temperatures over which body temperature remains constant for most birds, where they do not have to use energy to either lose or maintain body heat (defined as the thermoneutral zone - Williams & Tieleman 2001). Outside of the thermoneutral zone animals need to regulate body temperature behaviourally or physiologically: this is costly in terms of food and water requirements (Soobramoney 2003). Above an upper critical limit, endotherms must increase their metabolic rate in order to fuel heat-dissipating mechanisms, either physiological or behavioural (Burton et al. 2008).

Birds have the highest resting metabolic rate of any taxon (Williams & Tieleman 2005). High rates of mass-specific metabolism are correlated with high body

temperature, giving birds the highest body temperature of all vertebrates, averaging about 41°C at moderate air temperatures (Williams & Tieleman 2005). Birds are also capable of facultative hyperthermia, allowing their body temperatures to increase up to 4°C. However, once core body temperature rises to 47°C, fatality becomes probable (Maclean 1996). Hyperthermia gives birds the ability to conserve water, because when their body temperature is above that of the environment, they can lose heat through conduction and radiation rather than water-costly evaporation (Wolf & Walsberg 1996).

Various options for non-evaporative heat loss available to birds include increasing the surface area by holding the wings away from the body (wing spreading); shade-seeking behaviour; bathing; and minimising activity (Maclean 1996). Mechanisms for heat-dissipation via evaporative heat loss include cutaneous water loss; panting (buccal ventilation accompanied by vigorous movements of the thoracic cage); and gular fluttering (Schleucher et al. 1991).

#### *Climate change studies*

Studies on the impacts of climate change on animal behaviour are rare, which is surprising given the frequency with which behaviour is cited as a significant factor affecting responses to climate change (Crick 2004; Simmons et al. 2004; Wormsworth & Mallon 2006; Foden et al. 2009). For example, Sinervo et al. (2010) identified behaviour, physiology and life-history traits as important factors influencing extinction risk in Mexican lizard species. Many studies highlight the importance of climate in determining foraging conditions and a bird's ability to carry out essential behaviours (Crick 2004; Simmons et al. 2004; Wormsworth & Mallon 2006; Foden et al. 2009), yet few have attempted to quantify these effects. This study, of Southern Pied Babblers *Turdoides bicolor* in the Kalahari Desert thus contributes towards rectifying this shortfall.

Good candidates for studies of the effects of climate change include those species that are long-lived and have a tendency to remain on their parental territory for extended periods (Simmons et al. 2004). Such species have long generation times and will take longer to adapt genetically to rapid climate change. Furthermore, birds that remain in their parental territories may be vulnerable to climate change because

they may lack the necessary mechanisms for dispersal to more suitable climatic regions (Simmons et al. 2004). Southern Pied Babblers satisfy both conditions for an 'appropriate' species for climate-change studies (Ridley & Raihani 2008).

#### *Concluding remarks*

It is important to understand that climate is, in essence, the outcome of a cumulative series of 'weather events'. Should those weather events change in terms of their nature, timing, duration and/or intensity, this is manifest as a change in 'climate'. Predicting species' responses to changing climate thus requires an understanding of their responses to weather events. Cumulatively, these responses will determine a species' overall response to changing climate. Understanding these responses will further enable us to make inferences about future fitness changes, because behavioural and physiological traits are the key factors that affect fitness, and adaptations are the drivers of evolution.

The ability to make correct management decisions and predict the consequences of climate change on bird species will require detailed information on the mechanisms that drive population change during extreme weather events (McKechnie & Wolf 2010). Filling the behavioural and physiological gap in climate-change science will refine our ability to predict future changes in species' distributions. This information will also inform policy-making for the development of future conservation-planning scenarios (Erasmus et al. 2002).

This study aims to contribute to filling the ecological gap in climate-change science by highlighting the importance of physiological and behavioural studies in the understanding of impacts of climate change on species. Specifically, the study aims to determine the extent to which climate variables, primarily temperature, influence the behaviour and performance of a medium-sized passerine, the Southern Pied Babbler, whose range is centred on southern Africa's Kalahari Desert.

## Introduction

Wildlife from most taxonomic groups, in all of the oceans and from every continent have shown distributional or behavioural responses to anthropogenic climate change (Hoegh-Guldberg 1998; Simmons et al. 2004; Parmesan 2006; Sinervo et al. 2010). Adaptation, range change, population decrease and possibly even extinction are all climate-change related scenarios that are predicted for species globally (Harley et al. 2006; Sinervo et al. 2010). Both independently and in combination, these responses will lead to changes in the community structure of ecosystems due to the disproportionate responses of species (Pearson & Dawson 2003; Huntley 2006).

Limited empirical support exists for range changes and extinctions (Sinervo et al. 2010) predicted by bioclimatic envelope models (Erasmus et al. 2002; Thomas et al. 2004). This may be due to a lack of appropriate biological inputs (see Huntley et al. 2010). Recently, scientists have increasingly attempted to develop a better mechanistic understanding of organismal responses to anthropogenic climate change in an effort to make accurate predictions about future impacts on biodiversity (Helmuth et al. 2005; Okes et al. 2008).

Climatic models predict that the Kalahari Desert will undergo a disproportionately large change in temperature in the coming century (IPCC 2007; Moise & Hudson 2008). Many desert animals already live at temperatures that are near their upper thermal limit for survival (Heatwole 1970; Wolf & Walsberg 1996; Stillman 2003; Robinson et al. 2007). Increasing temperatures in deserts may therefore rapidly exceed the physiological thermal limits of species living in these areas (Bolger et al. 2005; Thuiller et al. 2006), forcing them to move (Wilson et al. 2005; Sinervo et al. 2010). Species that do not move may face costs in terms of physiological functions, directly impacting body condition and hence reproductive capacity (Porter et al. 1973; Clark, 1987; Wolf & Walsberg 1996; Tieleman 2002; Crick 2004). For instance, Webb (1980) hypothesised that heat stress negatively impacted juvenile Yellow-bellied marmots *Marmota flaviventris* by decreasing their foraging time.

Many species of desert animal show a bimodal rhythm of behaviour, foraging in the early mornings and late afternoons and resting in the shade during the heat of the day (Wolf 2000; Tieleman & Williams 2002; McKechnie & Wolf 2010). This pattern

may either be driven by a trade-off between foraging and thermoregulation (Sinervo et al. 2010), changes in satiation levels, changes in food availability or predation risk (Tieleman & Williams 2002). Most scenarios of global climate change predict hot weather events in hot, subtropical deserts will become more frequent and/or more protracted (Erasmus et al. 2002; Meehl & Tebaldi 2004; McKechnie & Wolf 2010). If these changes in climate affect the behaviour or physiology of birds such that foraging is compromised by the need to devote time to thermoregulation and/or heat dissipation, then there may be fitness consequences stemming from the resultant lowered body condition (McKechnie & Wolf 2010).

Southern Pied Babblers *Turdoides bicolor* are an excellent study species for assessing the impacts of climate change on birds. They are locally common residents of the Kalahari Desert (Hockey et al. 2005). These birds rarely drink as they obtain the moisture they need from their food (Maclean 1996), are diurnal and do not use below-ground microsites. Consequently, they may be vulnerable to increases in daily temperature maximum (McKechnie & Wolf 2010). Furthermore, terrestrially foraging birds, like babblers, may experience higher ambient temperatures due to reflected solar radiation (Kotzen 2003) and are more likely to become heat stressed. Although the social behaviour of these birds is well studied (Radford & Ridley 2006; Ridley & Raihani 2006, 2007; Ridley et al. 2007; Raihani & Ridley 2007, 2008; Bell et al. 2009, 2010; Raihani et al. 2010a,b), no studies have addressed how they respond to or are affected by changes in their environment (but see Thiele et al. 2008). The Pied Babbler Research Project, with its population of habituated babblers, presents an excellent opportunity for bird studies because detailed behaviour and weight data can be obtained (Ridley & Raihani 2007).

The aim of this thesis is to investigate the effects of ambient air temperature on body condition and explore the extent to which this effect is mediated by thermoregulatory trade-offs in the Southern Pied Babbler. Ultimately, we intend to predict the consequences of future, hotter climates, and the incidence of extreme weather conditions for these birds.

Specifically I aim to test the following predictions:

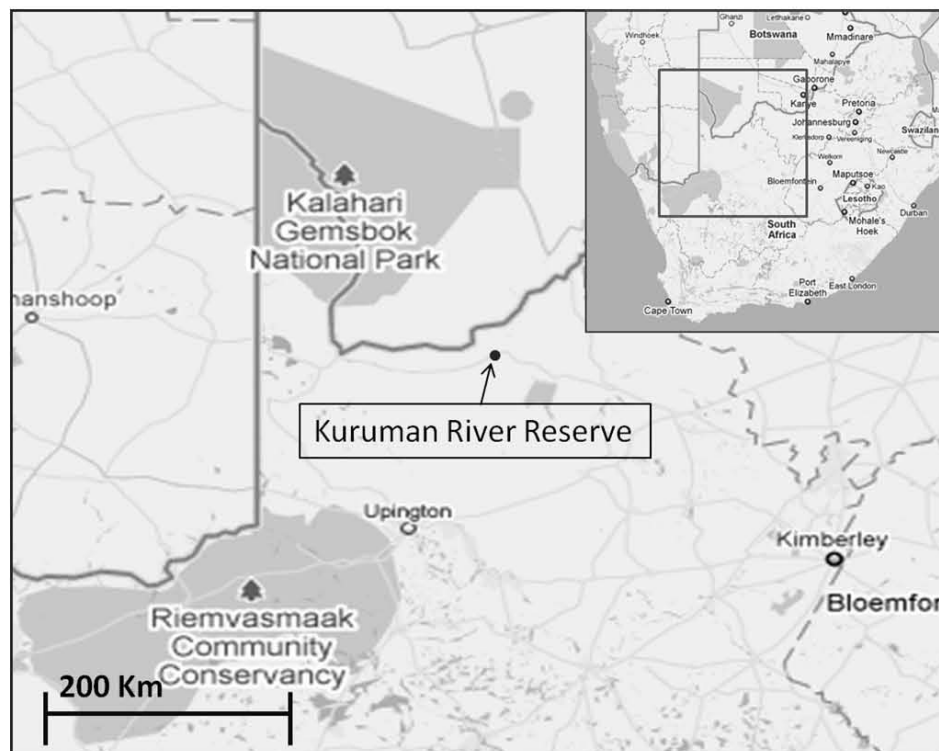
1. On hot days, trade-offs between foraging and thermoregulation and/or the effects of higher temperatures on food availability will result in babblers gaining less weight than they do on cooler days, or possibly losing weight.
2. As ambient temperature increases, babblers will forage less, and foraging efficiency will decrease as reflected in reduced intake rates.
3. Heat-dissipation (thermoregulation) behaviour will increase with ambient air temperature and will negatively influence foraging behaviour.
4. Prolonged periods of high ambient temperatures (heat waves) will lead to a progressive loss of body condition.

This study will aid in the development of a detailed and mechanistic understanding of species responses to climate change, which can guide management decisions through more accurate predictions of the future (Helmuth et al. 2005; Kearney 2009).

## Research Design and Methods

### Study site

The study was conducted at the Kuruman River Reserve, in South Africa's southern Kalahari (12 km<sup>2</sup>), (26°58'S, 21°49'E) between 23 October and 1 December 2010 (Figure 2). Major habitat types at the Reserve include semi-arid grassland, shrubland and dune habitat dominated by Camelthorn (*Acacia erioloba*) trees and Blackthorn (*A. mellifera*) bushes (see Raihani & Ridley 2007 for a detailed description of the study area). The site experiences summer rainfall (mostly Jan-Mar), which averages 217 mm/year (Clutton-Brock et al. 1999). This study took place towards the end of the dry season, when no rain had fallen in the previous six months.



**Figure 2:** A map of southern Africa showing the location of the Kuruman River Reserve.

Climatically, the semi-arid Kalahari Desert is characterised by extreme variation in temperature, both seasonally and daily. In January, the hottest month of the year, the mean maximum daily temperature is 34.7°C, and the mean daily minimum temperature is 19.5°C, with temperatures reaching up to 45.4°C. In July, the coldest month of the year, the mean daily maximum and minimum temperatures are 22.2°C and 1.2 °C respectively, although the temperature can fall as low as -10.3°C (Steenkamp et al. 2008).

### *Study species*

Southern Pied Babblers (hereafter babblers) are medium-sized (75-95 g) passerines (Hockey 2005) that are territorial year-round and breed cooperatively (Ridley & Raihani 2007). Groups comprise a dominant breeding pair and up to 12 non-breeding subordinate helpers (Ridley & Raihani 2008). They forage primarily terrestrially (more than 95% of foraging time - Ridley & Raihani 2007), eating mainly arthropods and their larvae (Raihani & Ridley 2008). Babblers not only glean prey from the ground surface, but also dig to obtain larger, buried items such as scorpions and beetle larvae.

Data were collected on five babbler groups that are fully habituated to the presence of humans. Each babbler is uniquely marked with three coloured rings and one metal ring. They are observable from distances of two to three metres and are trained to hop onto a scale so that weight data can be collected. Non-breeding groups (groups that were not feeding chicks) containing two or more subordinate adults were chosen in order to maximise the number of birds that could be observed and to avoid confounding the effects of temperature on weight changes with those of raising young (Tieleman 2002; Ridley & Raihani 2007). The five groups ranged in size from four to seven individuals (average  $5.4 \pm 0.5$  birds), including adult and immature (6-12 months) birds. Each group was observed at a variety of daily maximum temperatures in an attempt to identify the effects of temperature on behaviour and body condition. There are eight years of life-history data including daily weight data available for Southern Pied Babbler groups found at the Kuruman River Reserve.

### ***Factors affecting changes in weight***

In this study a number of factors were hypothesised to affect the daily weight change of babblers, which was used as a proxy for body condition (i.e. birds experiencing weight loss were considered to be experiencing negative energy budgets). These factors included those that directly impacted weight (ultimate factors) such as daily maximum temperature. It was hypothesised that proximate factors, including biomass intake rate, the proportion of time spent dissipating heat, foraging effort, biomass intake rate and foraging efficiency might be affected by temperature with knock-on effects for body condition. Through a combination of both ultimate and

proximate influences of temperature on weight it was further hypothesised that during extended periods of heat-wave conditions (as defined by the results of this study), babblers increasingly lose body condition. All data except daily maximum temperature and age were recorded using a Dell Axim Personal Digital Assistant (PDA) running Cybertracker 3.0 (Cybertracker Conservation 2005).

#### *Daily weight gain*

Body mass was used as a proxy for body condition and was obtained several times during the day from babblers trained to hop onto a scale. Each day, once the focal group was located, crumbed boiled egg was placed on a top-pan Ohaus scale (400 +/- 0.1 g) in a sheltered location on the ground near the babblers. When a babbler hopped on the scale its weight was recorded, and then to maintain habituation, the babbler was rewarded with a small food item, which had a negligible effect on weight. Weights were taken four times daily: as near as possible to first light (before daily foraging had begun) and then routinely at 10h00, 14h00 and 18h00.

Weights obtained at dawn ( $w_1$ ) were compared with those measured at 18h00 ( $w_2$ ) and were standardised as the proportion of grams lost or gained per hour ( $t_2 - t_1$ ) and then converted into a daily weight loss value.

Proportional weight change per 12-hour-foraging-day =

$$((w_2 - w_1) / w_1) / (t_2 - t_1) * 12$$

At temperatures around 30°C, many desert birds are at or near the lower limit of their thermoneutral zone (Carmi-Winkler et al. 1987; Anava et al. 2001; Tieleman et al. 2002a,b). Also, insect activity diminishes at temperatures below this threshold (Kearney et al. 2009). As temperatures decrease below 30°C, it is probable that both of these factors negatively impact weight gain. Therefore, weights obtained on days where the daily maximum temperature was below 30°C were excluded from analyses in order to avoid the confounding effects of cool temperatures on babbler weight changes.

#### ***Ultimate factors affecting daily weight change***

Daily maximum temperature was predicted to be the ultimate factor influencing changes in weight over the day. It has been shown that other factors, such as age, influence foraging efficiency of babblers (Ridley & Raihani 2008). To control for other factors that might ultimately influence weight: rainfall, habitat type, group size, age and average biomass intake were included in analyses of weight changes. Age data were obtained from the historical database. Weather-related conditions, including daily maximum temperature (°C) and rainfall (mm) were recorded using an ET107 Weather/ETo Station with a CR200 Series Datalogger (Campbell Scientific 2006) located within the reserve.

#### *Rainfall as a proxy for insect abundance*

Rainfall correlates strongly with insect abundance and was therefore hypothesised to have a potential effect on weight change. Although arthropod abundance was not measured directly during the study, it was important to establish a surrogate measure because arthropods make up the bulk of the babblers' diet (Hockey 2005). Cumming & Bernard (1997) found a strong and protracted correlation between precipitation and insect abundance over different latitudes in South Africa that showed insect abundance increases for up to a month after rain falls. Thus, the total amount of rainfall that fell in the 30 days prior to the day of observation was used as a proxy for insect abundance.

#### *Habitat type*

Habitat type can affect both babbler behaviour as well as their responses to other variables considered in this study. For example, habitat type may affect the distribution of food resources and the ease of extracting food from the substratum (Ridley pers. comm.). Different habitats also provide different levels of protection from predators (Thiele et al. 2008).

Habitats were defined as: blackthorn thicket (characterised by dense stands of Blackthorn *Acacia mellifera* trees, dune (sparsely vegetated, sandy areas), shrubland (predominantly grass or shrubs such as Drie Doring *Rhigozum trichotomum*, and open acacia savanna (riverbed and other areas with a relatively high density of Camelthorn *Acacia erioloba* trees).

#### *Group size*

Group size has been shown to affect the food intake rates of babblers, with individuals in larger groups having more foraging time available because of reduced time spent in anti-predator vigilance (Ridley & Raihani 2008). Because group size could fluctuate as birds leave and rejoin the group during incubation periods, the average group size found throughout the day was assessed.

### *Age*

Age (days since hatching) was included in all analyses because biomass intake rate (and hence potential weight gain) are age-dependent due to differences in foraging ability (Ridley & Raihani 2008) and efficiency in thermoregulation (Maclean 1996). All individuals observed in this study were at least six months old, which decreased variation due to age because all of the babblers were either immature or adults (with no juveniles). For individuals who entered the population as immigrants, age was estimated using plumage characteristics (see Ridley & Raihani 2007 for further details).

### *Average biomass intake rate*

Average biomass intake rate was used as an estimate of the amount of food the babbler had eaten over the day. This was hypothesised to influence weight because the only way that these birds can gain weight is through ingesting food and water. Biomass intake can be seen as both a proximate and an ultimate controller of weight change and is discussed in more detail below.

### ***Proximate factors affecting daily weight change***

Proximate factors are those factors that are affected by temperature which themselves have knock-on effects on weight gain. They include the proportion of time spent dissipating heat, biomass intake rate, foraging effort and foraging efficiency. It was further hypothesised that foraging efficiency would be negatively impacted by heat-dissipation behaviour.

### *Behavioural observations*

Behavioural data were collected by carrying out focal observations (focals) on individuals. This method was used instead of the scan-sampling technique to decrease sampling bias caused by the conspicuousness of certain birds or activities

(Altmann 1974). To reduce variation in behaviour and weight that may occur due to dominance, only subordinate birds (non-breeding individuals) were observed. Fourteen birds from five groups were observed during 260 focal observations, each for a period of  $10.35 \pm 1.10$  minutes. Focals were defined as continuously recording the behaviour of a single individual to the nearest second (Martin & Bateson 1986) and were paused as the bird moved out of sight to ensure that all foraging bouts and successes were recorded and during group disturbances (e.g. inter-group interactions or predator events) to avoid biasing the data toward rare events. Focal sessions, where each bird in the group was observed consecutively, were conducted every two hours starting at 07h00, with the last observation period beginning at 17h00. To avoid repetition effects, the order was randomised during each session and each bird was only observed once per observation period as per the protocol of Quené & van den Bergh (2008).

Data recorded included ambient air temperature (measured in the shade at the time of observation) using an omega k-type thermocouple [model HH21A] fitted with a polystyrene shield to block direct solar and soil-surface radiation [accuracy  $\pm 0.1^\circ\text{C}$ ], observed behaviour, and prey capture information (including prey type and size). Behavioural characteristics recorded included time spent foraging and in Heat-dissipation (wing spreading and/or panting). A babbler was considered to be foraging if it was hopping or standing while visually searching, using its beak to search in the substratum or handling a prey item. Heat-dissipation behaviours were recorded as secondary behaviours; in other words, a bird could be foraging, panting and wing spreading at the same time.

#### *Biomass intake rate, foraging effort and foraging efficiency*

Foraging effort was defined as the amount of time a babbler spent foraging per focal observation. The total time spent foraging per focal was divided by the total time of the focal to obtain the proportion of time spent foraging. Type, number and size of prey consumed were recorded during each focal. Prey items were assigned to one of five size categories and were converted to a biomass value (grams) using data from Raihani & Ridley (2007). Biomass intake rate per minute of observation was obtained by dividing the total biomass intake for the focal by the number of minutes that the focal lasted (Bell et al. 2009). Foraging efficiency (success-to-effort ratio)

was calculated by dividing biomass intake by the amount of time spent foraging to assess biomass intake per unit effort (Ridley & Raihani 2007). In order to assess this parameter accurately, foraging efficiency was only analysed if the focal bird spent five or more minutes actively foraging (Ridley & Raihani 2007). Thus, if a bird was foraging for five minutes of a ten-minute observation period and consumed a total of 2 g of food, its foraging efficiency rate would be 0.4 g/minute spent foraging.

#### *Heat-dissipation behaviour*

Observed heat-dissipation behaviours included wing spreading and panting. If a babbler had its beak open and was not calling or foraging at the time, it was considered to be panting. If the bird's wings were held away from the body so that a noticeable gap appeared between the leading edge of the wing and the feathers on the body it was considered wing spreading (Maclean 1996). Babblers also frequently held their wings open while grooming. If wing spreading was initiated before grooming (either autopreening or allopreening) began, it was considered an effort to dissipate heat. If wing spreading occurred during grooming and ended at the time that the grooming session ended, it was not considered Heat-dissipation behaviour. There was much variation in the degree of wing spreading, from a minor gap between wing and body to wings dangling down towards the feet, this action was not recorded in degree but merely as either present or absent.

#### ***Effects of heat-wave length on weight changes***

It was hypothesised that as the number of days in a heat-wave event increased, babbler body condition would decline, potentially leading to loss of weight over the heat-wave period. Heat-wave conditions were defined as the daily maximum temperature at which babblers were negatively affected by warm temperatures. Babblers showed an increase in heat-dissipation at temperatures above 35°C, so days on which the maximum temperature equalled or exceeded 35°C were classified as 'heat-wave days'. This temperature is in accordance with the temperature at which other desert birds exhibit increases in heat-dissipation behaviours (Austin 1976; Wolf 2000).

#### *Historical weight data*

Historical weight data were used to assess the impacts of heat-wave length on the

proportional weight change that occurred during heat waves of different durations. Only morning weight values were used in the analysis to minimize weight increases from recent foraging events and to approximate change in weight over a consistent time period. Only weight data from groups who were breeding at the time (the bulk of the data set) were included in the analysis. Chick-ringing records were used to assess the breeding status of a group during the event. Weight change data from heat-wave events were compared with those from non-heat-wave events to control for the affects of breeding.

Proportional weight change over a heat wave period lasting  $x$  days was calculated as follows:

$$\text{Proportional weight change} = (W_{(\text{day } x)} - W_{(\text{day } 0)}) / W_{(\text{day } 0)}$$

\* where  $w$  = weight at dawn

## Data analyses

Data were analysed using linear mixed models (LMMs) specified as having normal distributions and identity link functions. Individual and group identity were included as random factors to account for variation caused by repeatedly sampling the same groups and individuals (pseudoreplication). Maximum-likelihood estimates were used for all LMM analyses (Bolker et al. 2009). A binomial generalised linear model (GLM) with a logit link function was used to assess the effects of ambient air temperature on heat-dissipation behaviour. Given that group and individual identity accounted for an insignificant amount of the variation in an LMM of temperature effects on Heat-dissipation behaviour the GLM analysis was considered acceptable (Garson 2011). A paired-sample t-test between individuals was used to evaluate the effect of heat-dissipation behaviour on foraging efficiency. SPSS 19.0 (SPSS 2011) was used for statistical analyses and the threshold for statistical significance was set at 0.05.

### *Factors affecting weight changes*

To assess the effects of environmental variables as well as individual, group and behavioural characteristics on weight changes, LMMs were compared using the Akaike's Information Criterion corrected for small data sets (AICc) (Burnham &

Anderson 2002; see Ridley & Raihani 2008 for more details). First, an LMM was run using the 'basic model', including only random terms (i.e. bird and group identity), to obtain baseline data. Each explanatory variable was added to the basic model and AICc values and Akaike weights, which are used to determine the relative support for each model, were calculated (Burnham & Anderson 2004). Support for a given model increases as the Akaike weight increases and the AICc value decreases. The model with the lowest AICc value and the highest Akaike weight was considered the best-fit model, but only significantly so if its AICc value differed by at least two units from the next-best model (Burnham & Anderson 2002).

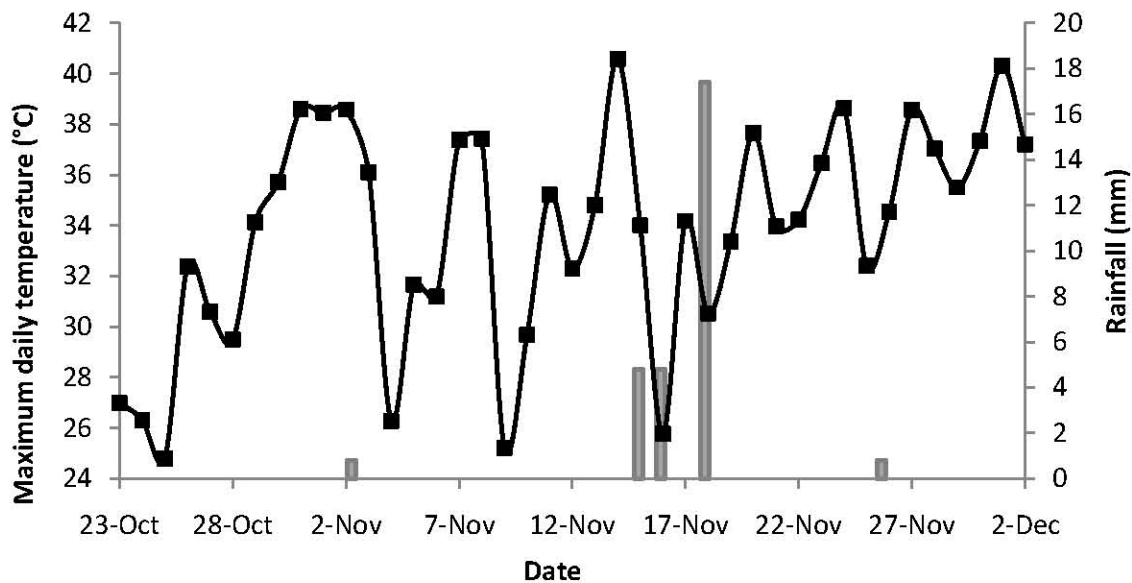
To determine what terms affected changes in body mass, the proportional weight change over a 12-hour day was specified as the response term in an LMM with a normal distribution and an identity link function. Because there is only one weight-change value per individual per day, averages were taken of the behavioural and group characteristics which were measured routinely throughout the day during the focal observations. Potential explanatory terms were environmental terms (daily maximum temperature, prior month's rainfall, habitat type), individual and group characteristics (age, average group size), and behavioural characteristics (average proportion of time spent dissipating heat, average biomass intake rate). Due to small sample sizes, habitat type was only differentiated at the scale of non-acacia savanna vs. acacia savanna.

The LMM including temperature as the explanatory variable converged when individual identity was selected as a random term. Due to non-convergence of the Hessian matrix (potentially caused by a small sample size, uneven sampling at the group level, or the small effect of random terms on the response), results for all other effects on proportional weight change over a 12-hour-day were uncertain. Models were therefore re-run with individual identity and group identity included as fixed factors (Garson 2011).

## Results

### *Climate*

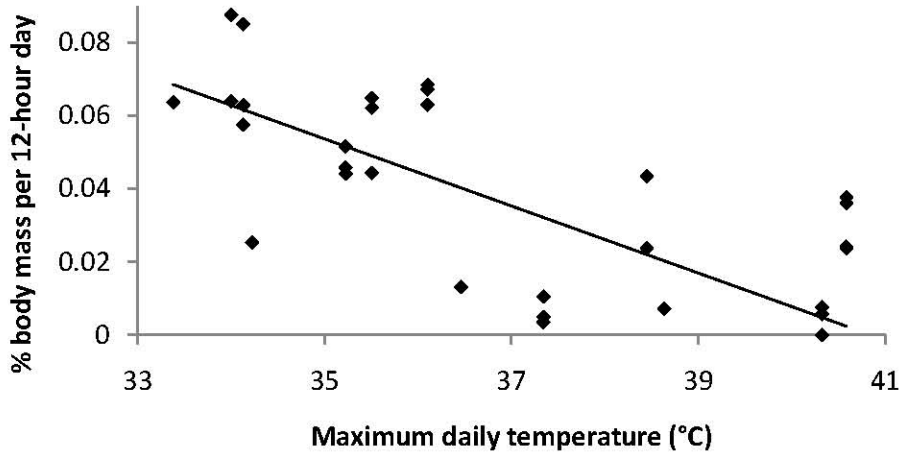
During the study period, daily temperature maxima varied between 24.8 and 40.6°C. Daily maximum temperature was highly variable at the end of October and the beginning of November, but by mid-November there was an upward trend (Figure 3). Only 28.6 mm of rain fell during the study period, of which 17.4 mm fell on one day, 18 November.



**Figure 3:** Daily maximum air temperature (°C, solid squares) and daily rainfall (mm, bars) for the Kuruman River Reserve between 23 October and 2 December 2010.

### ***Factors affecting proportional weight gain***

The proportional change in weight over a 12-hour day was best explained by the model that contained daily maximum temperature as the explanatory variable (Table 1; LMM:  $f_{23,235} = 38.487$ ,  $P < 0.001$ ). As daily maximum temperature increased above 33°C, the proportional body weight gained over a 12-hour period decreased (Figure 4). There was no significant effect of biomass intake rate on daily weight gain (LMM:  $f_{29} = 0.025$ ,  $P = 0.876$ ).



**Figure 4:** The percentage of weight gained over a 12-hour period for Southern Pied Babblers as a function of daily maximum temperature (°C). The line of best fit was generated from the prediction of the LMM with the largest Akaike weight ( $n = 29$  weight change measurements from nine birds) (Table 1).

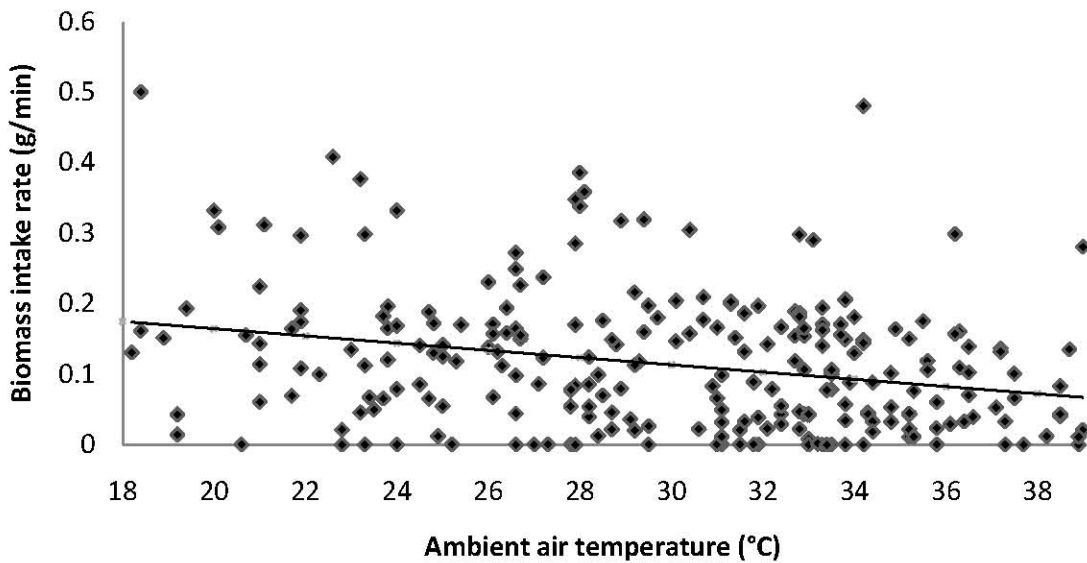
Rank	Model	Deviance	K	AICc	$\Delta$ AICc	Akaike weight	Effect $\pm$ SE
3	Basic	91.7	4	99.0	15.6	4.061E-04	3.491 $\pm$ 0.391
<b>1</b>	<b>Daily maximum temperature(°C)</b>	<b>73.1</b>	<b>5</b>	<b>83.4</b>	<b>0.0</b>	<b>9.982E-01</b>	<b>-0.737 <math>\pm</math> 0.119</b>
4	Total rain over the previous month (mm)	91.4	5	101.7	18.3	1.053E-04	-0.014 $\pm$ 0.027
7	Habitat type (open acacia savanna)	86.5	5	96.8	13.4	1.206E-03	-1.07 $\pm$ 0.683
	Habitat type (non-open acacia savanna)						0 $\pm$ 0
5	Age (days)	91.6	5	101.9	18.5	9.461E-05	2.2E-04 $\pm$ 1.0E-03
6	Average group size	85.4	5	95.7	12.3	2.118E-03	-0.689 $\pm$ 0.253
2	Average proportion of time spent dissipating heat	84.3	5	94.5	11.2	3.776E-03	-5.265 $\pm$ 1.659
8	Average biomass intake rate	113.1	5	120.1	36.7	1.058E-08	10.481 $\pm$ 7.769

**Table 1: LMM output of the factors affecting daily rates of weight change in Southern Pied Babblers.** The table lists all candidate models tested (see Methods for description of predictor terms). The basic model includes the constant and the random terms (group and individual identity). Deviance presents the  $-2$  log-likelihood output of each model. K is the number of factors included in each model. AICc is for small data sets, which assesses the parsimony of each model.  $\Delta$ AICc is the difference between that particular model and the one defined as the model of best fit (in bold). Akaike weight denotes the relative support for each model in relation to the other models. Analysis was conducted on nine individuals from five groups with a total of 29 weight change observations.

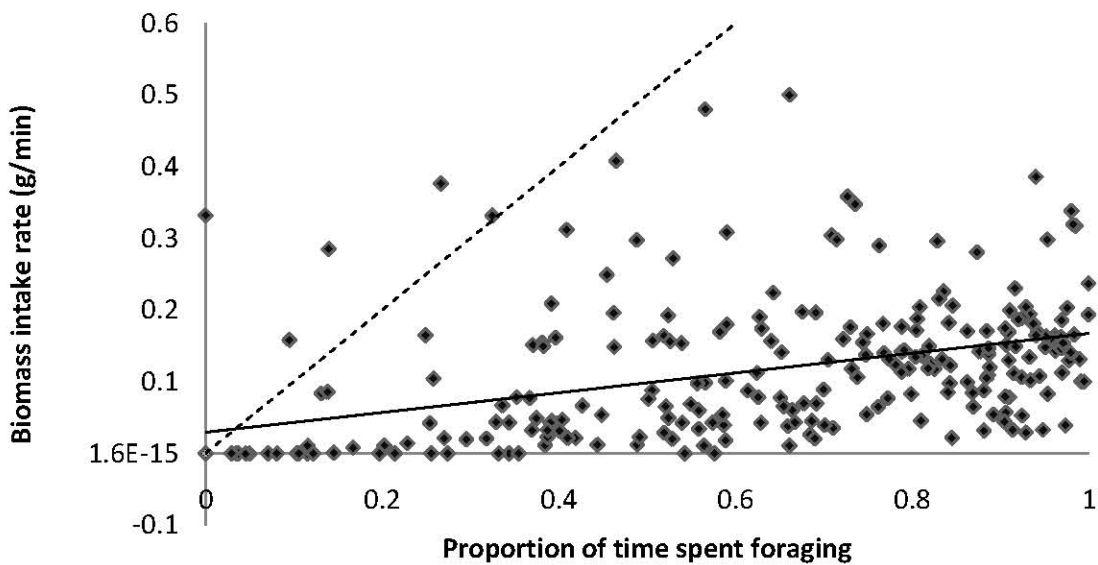
### **Effects of temperature on foraging**

Both foraging effort and ambient air temperature significantly affected biomass intake rate (LMM: foraging effort:  $f_{256,232} = 58.163$ ,  $P < 0.001$ ; temperature  $f_{257} = 19.777$ ,  $P < 0.001$ ). Biomass intake increased with increased proportion of time spent foraging (foraging effort) and decreased as ambient air temperature rose (Figures 5, 6). Temperature had no significant effect on babbler foraging effort, which averaged  $60.5 \pm 1.88$  % of time observed (Figure 7, LMM:  $f_{257} = 0.492$ ,  $P = 0.484$ ). Ambient air temperature significantly affected biomass intake per minute spent foraging (foraging

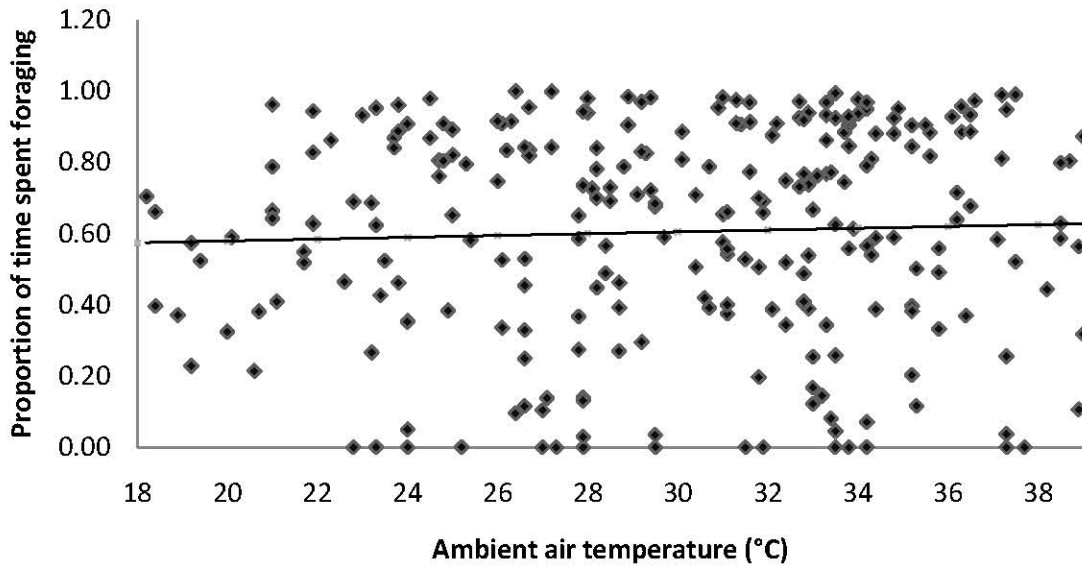
efficiency): as temperature increased, foraging efficiency decreased (Figure 8, LMM:  $f_{170,922} = 15.317$ ,  $P < 0.001$ ).



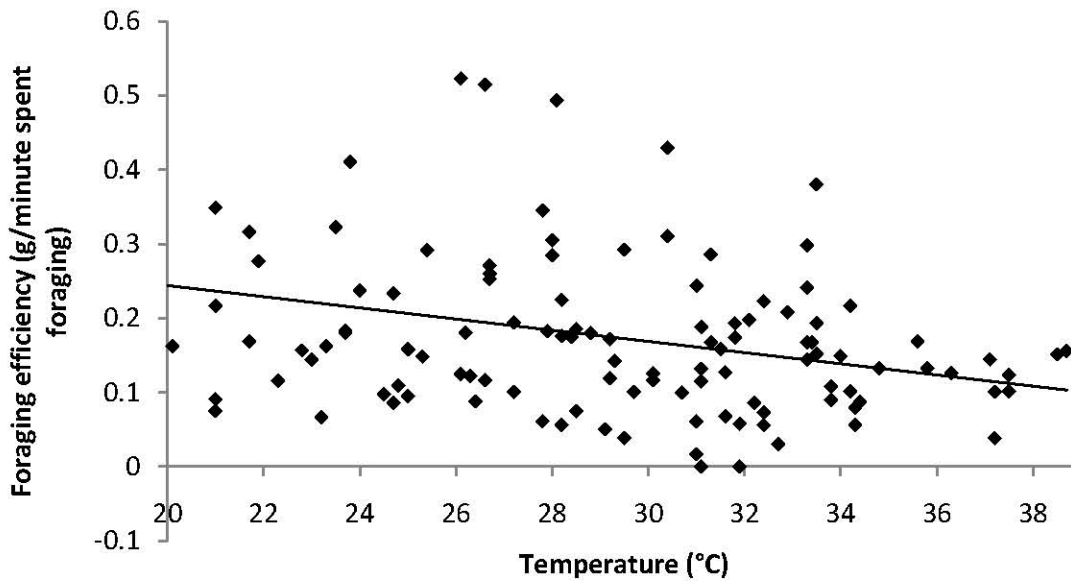
**Figure 5:** Biomass intake rate (g/min) of Southern Pied Babblers as a function of ambient air temperature (°C) at the time of observation. The line of best fit is generated from the prediction of the LMM ( $n = 257$  focal observations of 17 birds).



**Figure 6:** Biomass intake rate (g/min) of Southern Pied Babblers as a function of foraging effort (the proportion of time spent foraging per minute observed). The dashed line is the line predicted for a one-to-one relationship. The solid line represents the line of best fit generated from the prediction of the LMM ( $n = 257$  focal observations of 17 birds).



**Figure 7:** The proportion of time Southern Pied Babblers spent foraging (foraging effort) as a function of ambient temperature at the time of observation. The line of best fit is generated from the prediction of the LMM ( $n = 257$  focal observations of 17 birds).

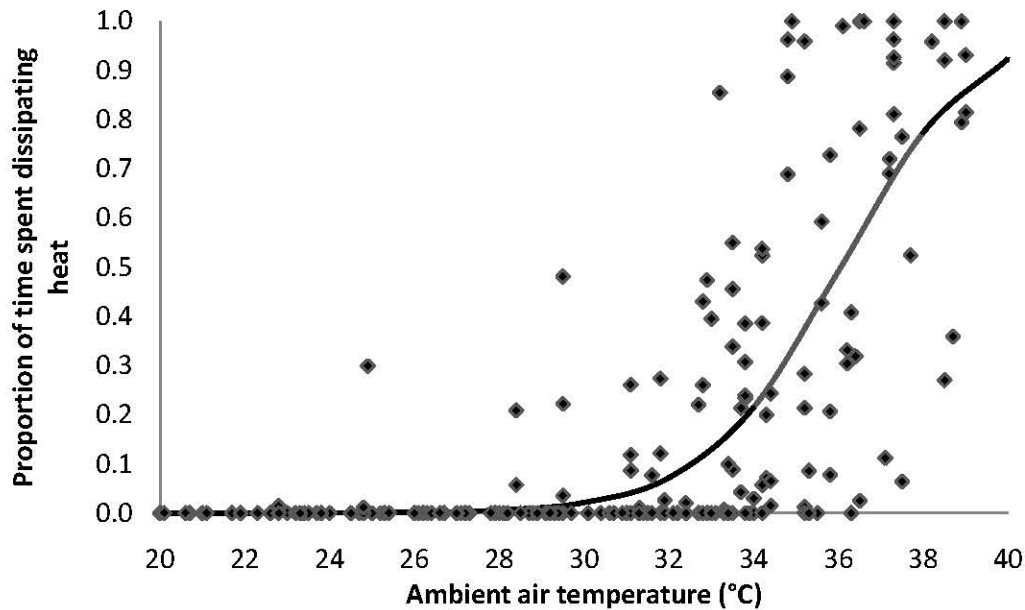


**Figure 8:** Southern Pied Babbler foraging efficiency (g/minute spent foraging) as a function of ambient temperature at the time of observation. The line of best fit is generated from prediction of the LMM with the largest Akaike weight ( $n = 171$  focal observations of 15 birds).

### ***Effects of Heat-dissipation on foraging***

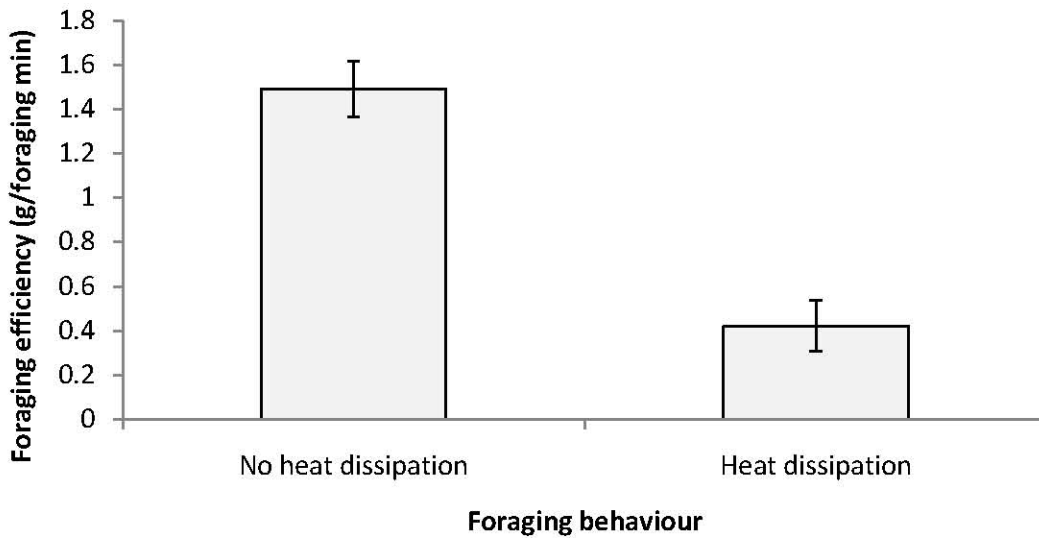
#### *Effects of temperature on thermoregulation*

The incidence of Heat-dissipation behaviour was strongly influenced by ambient air temperature: as temperature increased, so did the proportion of time spent in Heat-dissipation (Figure 9, binomial GLM;  $t_9 = 5.521$ ,  $p < 0.001$ ).



**Figure 9:** The proportion of time Southern Pied Babblers spent in Heat-dissipation behaviour of as a function of ambient air temperature (°C) at the time of observation. The line of best fit was generated from the prediction of a binomial GLM ( $n = 257$  focal observations of 17 birds).

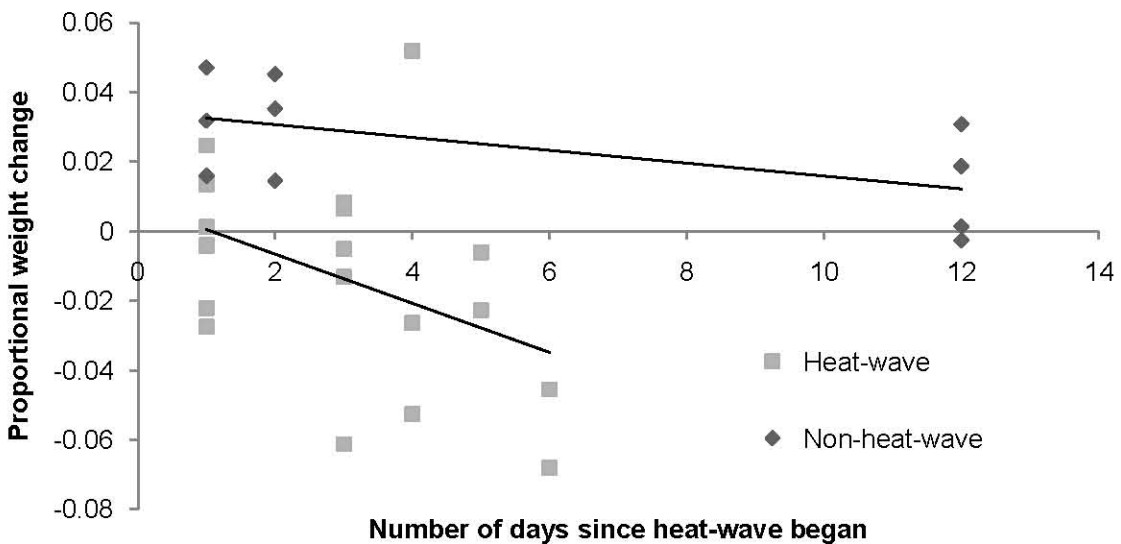
A paired-samples t-test between individuals revealed a significant difference between foraging efficiency while dissipating heat ( $0.42 \pm 0.115$  g/minute spent foraging) and foraging efficiency while not dissipating heat ( $1.49 \pm 0.126$  g/minute spent foraging) ( $t_9 = 5.521$ ;  $p < 0.001$ ) (Figure 10).



**Figure 10:** Mean foraging efficiency (g/minute spent foraging) of Southern Pied Babblers while dissipating heat and not dissipating heat, with standard errors predicted from the paired-sample t-test.

### ***Effects of heat-wave duration on weight changes***

Average proportional weight change was correlated with the number of days they spent in heat-wave conditions. As the duration of the heat-wave increased the body condition of babblers decreased (Figure 11).



**Figure 11:** Proportional weight change of Southern Pied Babblers as a function of the number of days during heatwave conditions and non-heatwave conditions. The trend line was generated using the line of best fit in excel.

## Discussion

This study represents one of the first analyses of the existence of the trade-offs between foraging and thermoregulation as well as the potential consequences of this trade-off. Ambient air temperature affects foraging efficiency, and hence biomass intake rates, and also determines the amount of time that has to be devoted to thermoregulatory behaviour. Both of these effects have the potential to influence body condition and therefore individual fitness.

### *Effects of temperatures on thermoregulation*

As ambient air temperature increases, the proportion of time that babblers spend in Heat-dissipation behaviour (active thermoregulation) also increases. Support for this comes from Carmi-Winkler (1987), who showed Wild Chukar Partridges *Alectoris chukar* increased resting thermoregulatory behaviour by 25% between summer and winter time-budgets.

At temperatures above 35°C, birds spend more than 50% of the time dissipating heat, potentially signifying a switch from activities aimed at increasing fitness to those focused on maintaining body temperatures below lethal limits. Austin (1976) found that, as temperatures exceeded 35°C, the foraging effort of Verdins *Auriparus flaviceps* decreased significantly. In addition, Schleucher et al. (1991) showed that above 35°C the respiratory evaporative water loss of the Australian Diamond Dove *Geopelia cuneata* increased exponentially. Panting increases respiratory evaporative water loss (Maclean 1996), and wing spreading increases the surface area of a bird, facilitating cutaneous water loss (Wolf & Walsberg 1996a). However, each of these forms of behavioural thermoregulation carries with it the risks associated with elevated rates of water loss. Above 35°C, evaporative water loss increases exponentially (Wolf & Walsberg 1996a). At high temperatures that are still below body temperature (ca 41°C) some desert birds use facultative hyperthermia to drive non-evaporative heat loss, which aids conservation of water resources (Soobramoney 2003). This highlights the costs of thermoregulation at high temperatures and provides support for the idea that birds will only actively dissipate heat if they have no alternative.

*Effects of temperature on foraging behaviour*

In general, desert birds rest during the hottest part of the day (Clark 1987; Wolf et al. 1996; Williams et al. 1999; Tieleman 2002; McKechnie & Wolf 2010) but this was not the case for the babblers, which continued to forage even during the hottest parts of the hottest days, even though foraging efficiency was negatively impacted by rising temperatures. The decrease in foraging efficiency of babblers as temperatures increase could be due to a decrease in food availability (Gullan & Cranston 2005; Kearney et al. 2009), an increase in time devoted to thermoregulatory processes, or both. When babblers use behavioural thermoregulation at the same time as they are foraging, their foraging efficiency decreases significantly. However, results do not provide strong support for babblers trading off foraging time (effort) against time spent thermoregulating (see Carmi-Winkler et al. 1987, who found a genuine trade-off between thermoregulation and other activities in Chukar Partridges *Alectoris chukar*). Rather, the act of thermoregulation compromises their foraging performance. This study was conducted at the end of the dry season (no rain for six months) when resources levels were probably close to their annual minimum (e.g. Dean 2004). The ways in which desert-dwelling Hoopoe Larks *Alaemon alaudipes* trade off foraging and thermoregulation is determined by their physiological state at the time (Tieleman 2002). When birds have limited energy stores during times of resource scarcity, they – like babblers – continue to forage at the same time as actively thermoregulating. It is almost certain that foraging or thermoregulating alone would be more efficient (in terms of energy intake or body temperature regulation) than attempting to perform both behaviours simultaneously. The fact that they seemingly compromise both behaviours suggests that food is a potentially limiting resource: even in the heat of the day, babblers periodically fight over food items.

Increases in babbler foraging effort correlate positively with biomass intake rate. It could be predicted that effort and reward should be directly proportional, with a doubling of effort resulting in a doubling of return. However, the relationship between foraging effort and biomass intake rate indicates that as birds put more effort into foraging, their additional returns diminish. This may be because of an increased need to thermoregulate, but at the same time reduced prey availability may negatively influence foraging efficiency.

*Effects of food availability on foraging behaviour*

Food availability is likely to influence both foraging effort and foraging efficiency. For example, high food availability to seals results in a decrease in foraging effort and an increase in returns (Costa et al. 1989). Insects are active at temperatures between 20 and 40°C with a peak in activity from 30 to 35°C (Kearney et al. 2009). Above and below this temperature range, there should be a reduction in the food readily available to babblers, because many desert insects retreat underground to thermoregulate during the hottest and coldest parts of the day (Gullan & Cranston 2005). Babblers are able to obtain buried prey items by digging, but digging is likely more energetically costly than gleaning in terms of both metabolism and heat production. Also, as temperatures increase, insects presumably dig deeper into the substratum to avoid rising sand temperatures. This could further lower intake rates of babblers at high temperatures, over and above the costs associated with thermoregulating while foraging.

*Effects of temperature on food intake rate and body condition*

Biomass intake rate, a function of foraging effort and foraging efficiency, was negatively influenced by increasing ambient temperature. Desert systems are characterised by scarce food resources due to low productivity (McKechnie & Wolf 2010). Situations under which birds lose body condition (as measured using body mass as a surrogate) indicate a loss of energy and/or water suggesting that body condition may be sacrificed to the demands of thermoregulation (Soobramoney 2003). Loss of water may seem trivial when compared to losses of energy; however, it is difficult to regain those losses, especially at high temperatures (McKechnie & Wolf 2010). The primary way for babblers to rehydrate is through their diet selection of arthropods (Maclean 1996), because accessible water sources in the Kalahari are seasonal, limited and uncommon. However, if climate change leads (as predicted) to rising temperatures, the risks associated with increased water demand escalate concomitantly (McKechnie & Wolf 2010). Species that previously derived most or all of their daily water requirements from their diet may be forced to seek free water in an attempt to counter elevated water-loss rates due to increased temperatures. T

Individuals of those species that are territorial or have limited daily ranges may be more at risk should this scenario arise and should they lack open water sources within their territory/home range.

On days when the maximum temperature exceeds 33°C, proportional daily mass gain by babblers starts to decrease: the significance of this relationship was robust to slight changes in LMM specifications. Direct effects of temperature on weight gain could include dehydration (Wolf & Walsberg 1996a) or reduced energy intake resulting from time allocated to thermoregulation (Maclean 1996). Whilst short-term losses of body condition may have limited consequences, the longer that negative energy or water balances persist, the greater the probability that individual fitness will be compromised.

#### *Effects of biomass intake rate on body condition*

One may expect the average biomass intake rate of a bird to influence daily weight gain. The absence of a significant relationship between intake rate and weight gain is potentially a product of sampling technique and/or the complex relationship between energy gain and energy expenditure (including the high cost of thermoregulation). Because sampling occurred every two hours for a period of roughly ten minutes the majority of intake events were unrecorded which could lead to sampling bias. Also,

#### *Effects of heat-wave duration*

It is clear that ambient temperature can affect body condition over time scales of at least a single day. At temperatures above 35°C, babblers seem to switch from the normal daily activities aimed at maximizing fitness to survival activities directed at maintaining their body temperatures below the lethal limit. However, it appears that a net daily (between dawn and dusk) loss of body condition occurs once daily maximum temperature peaks between 40 and 41°C. Heat-waves of an increasing frequency and duration are predicted for the Kalahari Desert due to climate change (Kruger & Shongwe 2004; Christensen et al. 2007). Analysis of body condition during such heat-wave conditions indicated convincingly that the impact of heat waves (daily maximum temperatures of 35°C or more) was proportional to their duration, with heat waves lasting three or more days causing cumulative decreases in condition. This observation provides one mechanism to explain mass mortalities of

birds elsewhere under heat-wave conditions (Welbergen et al. 2008; McKechnie & Wolf 2010; Sinervo et al. 2010). This link provides compelling support for the need to understand the responses of individuals to environmental stressors when attempting to make population-level predictions. In this case, the key response variable measured was body mass as a proxy for condition (and ergo a likely proxy for survival probability - Baldwin & Kendeigh 1938).

## Conclusion

On days in the Kalahari Desert when the maximum temperature exceeds ca 33°C, the foraging performance of Southern Pied Babblers is compromised by the birds' need to perform thermoregulatory behaviours, such as panting. However, rather than making a binary trade-off between e.g. foraging and thermoregulation, the birds continue to forage at the same time as thermoregulating. This results in lowered foraging efficiency (and probably reduced thermoregulatory efficiency). That the birds 'multi-task' in this fashion suggests that their energy budgets are tenuous and that the costs of ceasing to forage altogether while thermoregulating exceed the benefits (however small) derived from continuing to forage.

The Kalahari Desert is a place of extreme weather conditions: scant erratic rainfall, highly variable daily and seasonal temperatures and frequent heat-wave and drought events. Climate-change models for this region predict that heat-waves and droughts will become more severe and more frequent (Kruger & Shongwe 2004; Christensen et al. 2007). Under current conditions, babblers already face trade-offs when attempting to balance energy and water budgets while maintaining their body temperature below lethal limits

On days when maximum temperature in the Kalahari Desert exceed 35°C, there is a negative relationship between temperature and the body condition of Southern Pied Babblers. In the time frame of a single day, babblers lose condition if the maximum temperature exceeds 40-41°C. However, heat waves (maximum temperature >35°C) of three days or more lead to progressive decreases in body condition: there are thus already demonstrable effects stemming from both the intensity and duration of hot weather events. This suggests that, at least in early summer, babblers in this region of the Kalahari may already be close to the limits of their physiological tolerance.

## Future Research

Babblers make good candidates for future climate-change research for many reasons. There are detailed life-history data for the Kuruman River Reserve population of this species dating back eight years. Future studies thus have the potential to assess changes in fitness as a function of environmental conditions and determine whether temperature or rainfall is the limiting factor for reproduction and, ultimately, fitness.

At the broader scale, it is possible to exploit the fact that Southern Pied Babblers have a patchy distribution within the Kalahari. They are, for example, rare in the (very hot) regions of the western Kalahari. It should now be possible to determine whether gaps in the species' distribution correlate with climatic conditions or environmental features such as the presence or absence of large trees (used for breeding) in the landscape. The patchy distribution also lends itself to a study of gene flow: if climate models can be used to predict landscape-level directions of movement, models of gene flow should provide insight as to whether these movements are or are not likely to happen.

## Acknowledgements

To my husband (the best friend, cook and jack of all trades a girl could find): I could not have done this without you!

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