

# The costs of keeping cool in a warming world: implications of high temperatures for foraging, thermoregulation and body condition of an arid-zone bird

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## Abstract

Recent mass mortalities of bats, birds and even humans highlight the substantial threats that rising global temperatures pose for endotherms. Although less dramatic, sublethal fitness costs of high temperatures may be considerable and result in changing population demographics. Endothermic animals exposed to high environmental temperatures can adjust their behaviour (e.g. reducing activity) or physiology (e.g. elevating rates of evaporative water loss) to maintain body temperatures within tolerable limits. The fitness consequences of these adjustments, in terms of the ability to balance water and energy budgets and therefore maintain body condition, are poorly known. We investigated the effects of daily maximum temperature on foraging and thermoregulatory behaviour as well as maintenance of body condition in a wild, habituated population of Southern Pied Babblers *Turdoides bicolor*. These birds inhabit a hot, arid area of southern Africa where they commonly experience environmental temperatures exceeding optimal body temperatures. Repeated measurements of individual behaviour and body mass were taken across days varying in maximum air temperature. Contrary to expectations, foraging effort was unaffected by daily maximum temperature. Foraging efficiency, however, was lower on hotter days and this was reflected in a drop in body mass on hotter days. When maximum air temperatures exceeded 35.5 °C, individuals no longer gained sufficient weight to counter typical overnight weight loss. This reduction in foraging efficiency is likely driven, in part, by a trade-off with the need to engage in heat-dissipation behaviours. When we controlled for temperature, individuals that actively dissipated heat while continuing to forage experienced a dramatic decrease in their foraging efficiency. This study demonstrates the value of investigations of temperature-dependent behaviour in the context of impacts on body condition, and suggests that increasingly high temperatures will have negative implications for the fitness of these arid-zone birds.

**Keywords:** body condition, body mass, climate change, daily maximum temperature, foraging efficiency, foraging effort, Southern Pied Babbler, temperature-dependent behaviour, thermoregulation, trade-offs, *Turdoides bicolor*

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## Introduction

Climate can determine key biological processes that ultimately influence the abundance and distribution of species. A mechanistic understanding of these processes is increasingly used as a basis for predicting the impact of climate change on a variety of organisms (Kearney & Porter, 2009; Buckley *et al.*, 2010). Such mechanistic models are becoming progressively more sophisticated, encapsulating an ever-widening diversity of biological processes (Mitchell *et al.*, 2008; Kearney & Porter, 2009; Kearney *et al.*, 2010; Angert *et al.*, 2011). Despite the nascent success of this approach the

utility of these models will be fundamentally improved by the inclusion of empirical data on how organisms respond to environmental variation and how this relates to fitness (Angilletta & Sears, 2011).

Many animals living in hot environments are regularly exposed to conditions that have the potential to raise their body temperatures above tolerable limits (Williams & Tieleman, 2005). Prolonged exposure to high temperatures can lead to the breakdown of cellular functions (Hazel, 1995; Daniel *et al.*, 2009) and eventual death (Dawson, 1954; McKechnie & Wolf, 2010). Indeed, among endotherms, heat waves have led to mass mortalities of bats (Welbergen *et al.*, 2008), birds (Finlayson, 1932; Towie, 2009) and humans (Whitman *et al.*, 1997). To avoid lethal hyperthermia, animals adjust their physiology, e.g. increasing evaporative cooling or facultative hyperthermia, and/or behaviour, e.g. reducing activity or seeking shade (Wolf, 2000).

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These responses incur costs in terms of increased demand for and/or reduced intake rates of water and energy, making it increasingly difficult for individuals to balance daily budgets.

In arid environments, where these resources are often limited and in high demand, small increases in temperature may negatively impact body condition, potentially reducing reproductive capacity and survival probabilities. Although less dramatic than mass mortality events, these sublethal fitness costs may be sufficiently great to reduce long-term survival (Moses *et al.*, 2011), and lead to local extinctions (Sinervo *et al.*, 2010). Most scenarios of global climate change predict that hot-weather events in hot, arid environments will become more frequent and/or more protracted (e.g. Meehl & Tebaldi, 2004; Akoon *et al.*, 2011). In the absence of rapid thermal adaptation, the costs of keeping cool may increase with potentially serious consequences for the persistence of some populations (Boyles *et al.*, 2011).

Birds, because of their predominantly diurnal habits and generally small body sizes, may be particularly vulnerable to elevated temperatures (McKechnie & Wolf, 2010). Even when inactive in completely shaded microsites, small species can experience rates of evaporative water loss in excess of 5% of body mass per hour (Wolf & Walsberg, 1996). Rates of energy expenditure can also increase due to the energy required for active heat dissipation via mechanisms such as panting and gular fluttering (Calder & King, 1974). When surface water is scarce, the only way to meet these rising demands is to increase foraging rates to improve the supply of dietary water. However, elevated activity levels will increase metabolic rates and hence endogenous heat generation, and the problem could be compounded further if the act of foraging exposes birds to parts of the landscape where environmental temperatures are highest (e.g. Austin, 1976; Clark, 1987).

The degree to which individuals adjust foraging behaviour in response to rising temperatures will depend on the relative costs and benefits (Vickers *et al.*, 2011). When environmental temperatures exceed optimal body temperatures for prolonged periods, the optimal response may be to cease foraging completely, as has been observed in some species (Goldstein, 1984). As temperatures approach these extremes, a rapid increase in evaporative water loss may lead to a concomitant reduction in activity and the ability of birds to maintain body condition. Lower body condition may, in turn, compromise the ability of individuals to survive the night (Pravosudov & Grubb, 1997) or their ability to obtain breeding opportunities (Ridley & Raihani, 2007a; Ridley *et al.*, 2008). Although temperature-driven changes in foraging behaviour are well

established (Carmi-Winkler *et al.*, 1987; Clark, 1987; Wolf & Walsberg, 1996; Tieleman & Williams, 2002), variations in the pay-offs linked to foraging and the consequences for body condition have never been studied in wild birds.

We address this shortfall with a habituated population of wild Southern Pied Babblers *Turdoides bicolor* (hereafter babblers), a bird whose range is centred in the hot, arid Kalahari region of southern Africa. This region experienced a warming trend over the period 1961–2000 (New *et al.*, 2006; Kruger & Sekele, 2012) and is predicted to experience further increases in the coming decades (IPCC, 2007; Moise & Hudson, 2008; Akoon *et al.*, 2011). By comparing the behaviour of individual birds across a range of days of varying ambient temperature, we investigate the effects of temperature on the interplay of foraging effort, foraging efficiency (return per unit effort), thermoregulatory behaviour and daily body-mass change. Following Carmi-Winkler *et al.* (1987), we focused on the effects of ambient temperatures on patterns of behaviour at the scale of days. As daily variation in air temperatures follow approximately the same pattern, we used maximum daily air temperature as a measure of total daily heat stress. Maximum daily air temperature is a commonly used metric of regional climate, which allows for comparisons to be made between our data and that of other regions and future climate scenarios (see Kruger & Sekele, 2012). Specifically, we tested two predictions:

- 1 At high temperatures, babblers trade-off thermoregulatory behaviours (e.g. panting, wing spreading) against foraging.
- 2 As a consequence, high temperatures influence the ability of babblers to maintain body condition.

## Materials and methods

### *Study site and species*

The study was conducted at the 33 km<sup>2</sup> Kuruman River Reserve (KRR) in the southern Kalahari region of South Africa (26°58' S, 21°49' E), the habitat and climate of this reserve has been described previously by Clutton-Brock *et al.* (1999). The site, a sparsely treed, arid savanna, receives summer rainfall (mostly January to March) averaging 217 mm yr<sup>-1</sup> (Clutton-Brock *et al.*, 1999). Mean daily maximum and minimum temperatures in January and July are 34.7 °C and 19.5 °C, and 22.2 °C and 1.2 °C, respectively, with temperature extremes of 45.4 °C and -10.3 °C (Steenkamp *et al.*, 2008). Data were collected between 23 October and 1 December 2010, towards the end of the 6-month-long dry season, the time of lowest invertebrate abundance in seasonal desert environments (Seely & Louw, 1980; Avenant & Nel, 1992).

Southern Pied Babblers are medium-sized passerines (75–95 g; Dean, 2005) that breed cooperatively and maintain year-round territories (Ridley & Raihani, 2007b). They forage primarily terrestrially, gleaning and digging for arthropods and their larvae (Ridley & Raihani, 2007b; Ridley & Child, 2009). At KRR, multiple groups comprising individually colour-ringed birds have been habituated to the close (2–3 m) presence of humans (since 2003), and in response to a very small food reward the birds hop onto a top-pan, digital Ohaus scale for weighing, removing the need for repeated capture to monitor body condition (for details on the habituation process, see Ridley & Raihani, 2007b). No food rewards were offered at any other time and the presence of an observer did not influence foraging behaviour (Ridley & Raihani, 2007b). All babbler groups had access to water throughout the study period due to farming activities at the study site. There was thus no significant variability between groups in access to this resource.

### Behavioural observations

To investigate the effect of temperature on the behaviour and body mass of babblers, we made repeated focal observations and weight measurements of individuals in five social groups. We observed only groups without dependent young to avoid confounding the potential effects of breeding activity on behaviour and body condition (Tieleman & Williams, 2002; Ridley & Raihani, 2007a). Within groups, we focused on subordinate birds (individuals >6 months old but not the dominant pair) to reduce variation that may stem from the effects of dominance rank (e.g. Raihani, 2008). In southern Africa, *Turdoides* babblers undergo postbreeding moult (Hockey *et al.*, 2005), so the birds were not experiencing additional energy costs associated with moult. Groups ranged in size from four to seven individuals (average  $5.4 \pm 0.5$ ), each containing two or more subordinates. Focal observations were made on 14 individuals (an average of  $2.80 \pm 0.37$  individuals per group) on days when maximum temperature ( $T_{\max}$ ) ranged from 31.7 to 40.6 °C.

Due to the unpredictable nature of  $T_{\max}$ , the group to be observed each day was determined the previous evening using the forecast  $T_{\max}$  for the nearby airstrip at Van Zylsrus. Groups and days were selected to ensure that individuals in each group were observed across a range of  $T_{\max}$  values. The daily  $T_{\max}$  at the study site was obtained from a Campbell Scientific ET107 Weather/ETo Station. Focal observations (as described by Altmann, 1974) involved continuously recording (to the nearest second) the behaviour of a single individual for a period of ~10 min (average  $10.35 \pm 1.10$  min) using a Dell Axim PDA (Personal Digital Assistant) and CyberTracker software (<http://www.cybertracker.org>).

Focal sessions, where each focal bird within the group was observed consecutively, were conducted every 2 h starting at 07:00 hours, with the last observation period beginning at 17:00 hours, resulting in six focals per bird per day (total  $n = 260$ ). The order in which individuals were observed was randomized between sessions following the protocol of Quené & van den Bergh (2008). Each bird was focalled once per session. If normal foraging and resting routines were inter-

rupted by intergroup interactions or the presence of predators, or the focal bird was out of the observer's view for more than a minute, the focal was abandoned. An overall daily measure of each behaviour (i.e. heat dissipation, foraging effort and foraging efficiency) was calculated as the mean of the six focals made on each individual over each day.

'Foraging effort' was defined as the proportion of a focal that a bird spent actively foraging. Individuals were considered to be 'foraging' if they were searching or scanning for prey, gleaning, probing or digging in the substratum, or handling prey.

'Foraging efficiency' was defined as the biomass intake rate per unit foraging time, measured in g per min (Ridley & Raihani, 2007a). Type, number and sizes of prey captured and then handled successfully were estimated and converted to prey biomass (wet g) following the calculations of Ridley & Raihani (2007b). The biomass of prey consumed during each focal was summed and divided by the number of minutes spent foraging. To achieve the desired degree of accuracy, calculations of foraging efficiency were made only from focals during which birds spent 5 min or more actively foraging (Ridley & Raihani, 2007a). This is unlikely to have substantially biased estimates of the relationship between foraging efficiency and temperature because the proportion of observations in which birds spent five minutes or more actively foraging did not vary with  $T_{\max}$  (GLMM,  $n = 229$  observations,  $\chi^2 = 1.01$ ,  $df = 1$ ,  $P = 0.38$ ).

'Heat dissipation' was defined as the proportion of time that a focal babbler exhibited any heat-dissipation behaviour (i.e. panting or wing spreading). Birds were considered wing spreading if they were holding the wings away from the body and/or wings drooped down towards the feet. These behaviours did not preclude foraging because birds simultaneously panted and wing drooped while they searched and gleaned for prey.

### Daytime mass gain

Body masses of focal individuals were measured as close as possible to first light (before foraging had begun;  $t_1$ ) and again as close as possible to 18:00 hours (just prior to going to roost;  $t_2$ ). Body-mass measures were recorded only once the scale had stabilized for more than 3 s.

The diurnal change in body mass ( $\Delta_m$ ) was calculated as a percentage of body mass at sunrise ( $t_1$ ) and standardized for differences in the timings of the weighing sessions to generate a daily percentage mass change using the equation:

$$\Delta_m = 100[(w_2 - w_1)/w_1]/[\Delta_t/12]$$

where  $t_1$  = time weighed prior to start of behavioural observations, i.e. ~sunrise;  $t_2$  = time weighed at the end of the day's behavioural observations, i.e. ~sunset;  $\Delta_t$  = number of hours between  $t_2$  and  $t_1$ ;  $w_1$  = mass at  $t_1$  and  $w_2$  = mass at  $t_2$ .

### Overnight mass loss

Data available from a long-term (8-year) database (Ridley unpubl.) were used to estimate typical overnight mass loss

of babblers. To be consistent with the birds included in the observational component of this study we only included weights of subordinate birds that were weighed during the period between October and December. Overnight mass loss was determined from weight measurements that were taken in the evening (post-foraging) and the next morning (prior to foraging), following a day on which  $T_{\max} \geq 30$  °C. When more than one measurement was available for a single individual ( $n = 12$ ) the mean value for those measurements was used. We assessed overnight percentage mass loss of 44 individuals on 60 nights.

### Statistical analysis

The effects of  $T_{\max}$  on foraging behaviour, heat dissipation and body-mass change were investigated with generalized linear mixed models (GLMMs) using the lme4 package (Bates *et al.*, 2011) within the R statistical environment (R Development Core Team, 2011). Separate models, with appropriate error structures (details below), were fitted for each behaviour. The sole predictor term in all models was  $T_{\max}$ , and a random term of individual nested within group was fitted to account for variance that may be attributable to differences between individuals or groups on which repeated measures were made.

For the foraging efficiency model, visual examination of residual plots confirmed that the assumptions of a normal error distribution with an identity link function were met. For the foraging effort and heat-dissipation analyses, response data were proportional and therefore binomial error structures with logit link functions were used. For the foraging effort model, the total time spent foraging was set as the response variable and the total time observed as the binomial total. For the heat-dissipation model, the total time observed displaying heat-dissipation behaviour was set as the response variable, with total time observed as the binomial total. To account for overdispersion in the binomial models, an observation-level random effect was also included. We report effect size estimates (correlation coefficients and odds ratios) and standard errors for the effect of  $T_{\max}$ , and  $P$ -values and chi-squared test statistics from likelihood-ratio tests.

To investigate whether babblers were able to maintain foraging efficiency while concurrently heat dissipating, focal observations were filtered to leave only those in which an individual was observed to spend at least 2 min foraging while heat dissipating (mean  $\pm$  SE =  $4.46 \pm 0.86$  min) and at least 2 min foraging while not heat dissipating (mean  $\pm$  SE =  $4.32 \pm 0.71$  min) within the same focal. Twelve focals from eight individuals met these criteria: all were made between 11:00 and 17:00 hours on days when  $T_{\max}$  exceeded 33.4 °C. When more than one focal was available for a single individual ( $n = 4$ ), the mean value for those focals was used. Foraging efficiencies with and without concurrent heat dissipation were compared using a paired  $t$ -test.

Unless otherwise stated, data are presented as mean  $\pm$  SE.

## Results

### Influence of $T_{\max}$ and time of day on foraging and heat dissipation

Overall, there was no evidence that daily foraging effort was affected by  $T_{\max}$  (GLMM, odds ratio = 1.04 (1.02–1.07),  $n = 36$  bird days,  $\chi^2 = 2.38$ ,  $df = 1$ ,  $P = 0.12$ ). A negligible effect of air temperature on foraging effort was also supported by an absence of variation in the proportion of time babblers spent foraging with time of day (GLMM,  $\chi^2 = 3.34$ ,  $n = 229$  observations,  $df = 5$ ,  $P = 0.65$ ; Fig. 1), despite mean focal-period air temperatures ranging from  $17.93 \pm 1.49$  °C to  $34.36 \pm 0.66$  °C.

In contrast to foraging effort, daily foraging efficiency was negatively affected by increasing temperature (GLMM, estimate =  $-0.011 \pm 0.01$  g  $\text{min}^{-1}$  °C $^{-1}$ ,  $n = 36$  bird days,  $\chi^2 = 5.42$ ,  $df = 1$ ,  $P = 0.02$ ; Fig. 3). Comparisons of foraging efficiency between focal periods also supported a negative effect of air temperature. Foraging efficiency peaked ( $0.27 \pm 0.06$  g  $\text{min}^{-1}$ ) between 06:00 and 10:00 hours when temperatures were relatively low (mean  $21.54 \pm 1.13$  °C) and was at its lowest ( $0.10 \pm 0.02$  g  $\text{min}^{-1}$ ) between 14:00 and 18:00 hours when air temperatures were highest (mean  $34.15 \pm 0.75$  °C) (GLMM,  $n = 229$  observations,  $\chi^2 = 18.62$ ,  $df = 5$ ,  $P < 0.01$ ; Fig. 1).

Overall, the daily proportion of time spent heat dissipating increased with  $T_{\max}$  (GLMM, odds ratio = 1.61

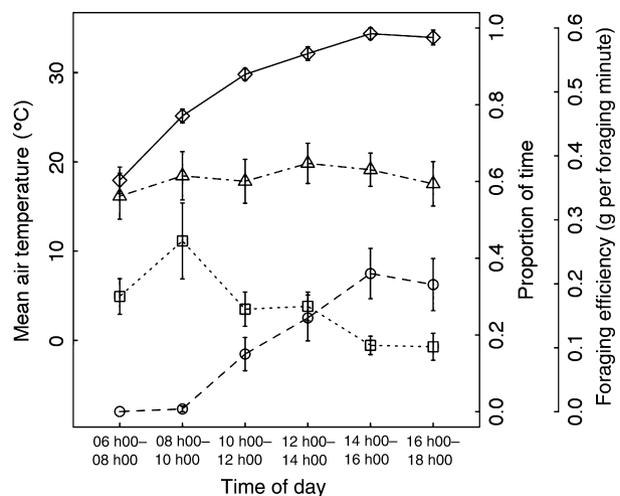
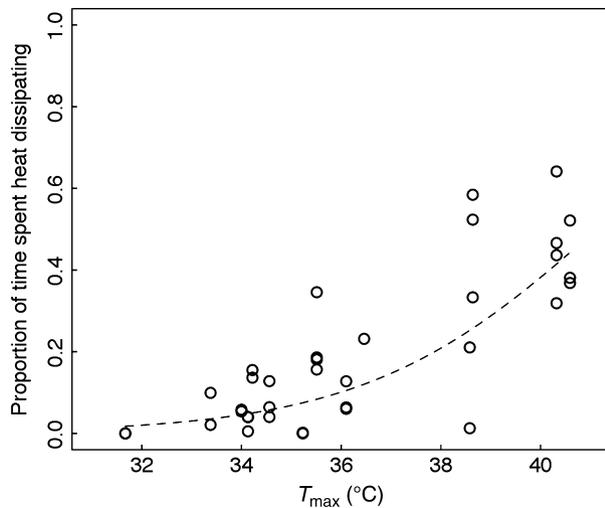
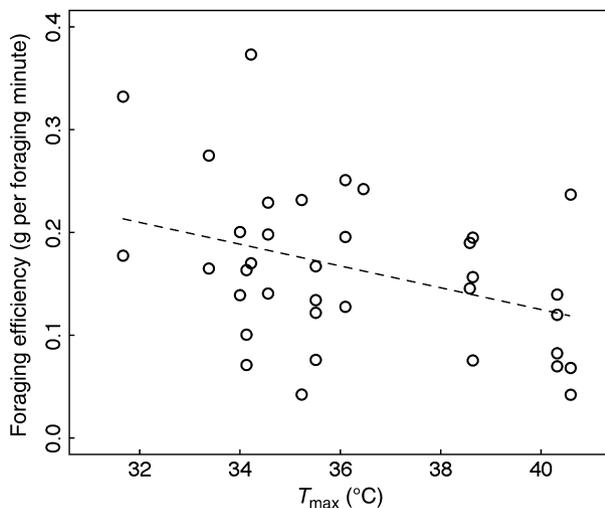


Fig. 1 Diurnal patterns of air temperature and behaviour of babblers. Diurnal patterns of air temperature (average during focal period; diamonds), heat dissipation (proportion of time spent exhibiting panting and/or wing-spreading behaviours; circles), foraging effort (proportion of time spent foraging; triangles) and foraging efficiency (grams of biomass consumed per foraging minute; squares) for each 2 h focal observation session. Data presented are means  $\pm$  1 SE.

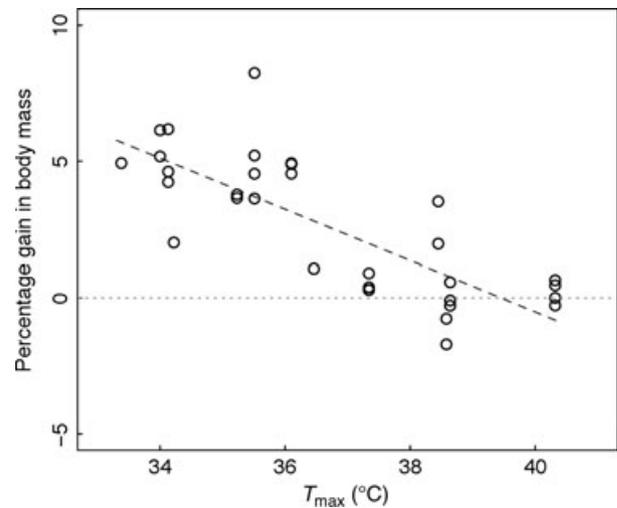


**Fig. 2** Proportion of time babblers exhibited heat-dissipation behaviour as a function of  $T_{\max}$ . Heat-dissipation behaviour includes 'panting' and/or 'wing-spreading' behaviours. Each point represents an average across a single day for a single individual. Dashed line of best fit was generated from predictions of a GLMM (see Methods for details of model specification).



**Fig. 3** Average foraging efficiency per day of individual babblers as a function of  $T_{\max}$ . The dashed line of best fit is generated from predictions of a GLMM (see Methods for details of model specification).

(1.52–1.70),  $n = 36$  bird days,  $\chi^2 = 47.6$ ,  $df = 1$ ,  $P < 0.001$ ; Fig. 2). Patterns of heat dissipation at different times of day broadly mirrored those of foraging efficiency (Fig. 1). No heat dissipation was observed when air temperatures were lowest between 06:00 and 08:00 hours, and peaked at  $36.00 \pm 6.56\%$  of observation time between 14:00 and 16:00 hours when air temperatures were highest ( $34.36 \pm 0.66$  °C) (GLMM,  $n = 229$  focal observations,  $\chi^2 = 138.59$ ,  $df = 5$ ,  $P < 0.001$ ; Fig. 1).



**Fig. 4** Daily change in body mass of babblers as a function of  $T_{\max}$ . Each point represents a single individual on a single day. The dashed line of best fit is generated from predictions of a GLMM (see Methods for details of model specification).

The potential causal link between heat dissipation and foraging efficiency, independent of temperature effects, was examined using within-focal comparisons. Foraging efficiency while simultaneously engaging in heat-dissipation behaviours was lower than foraging efficiency while not (while heat dissipating,  $0.063 \pm 0.03$  g min<sup>-1</sup>; while not heat dissipating,  $0.24 \pm 0.05$  g min<sup>-1</sup>;  $t = 2.50$ ,  $n = 8$  birds,  $P = 0.041$ ), even though air temperatures changed little during the 10-min focal period.

#### *T<sub>max</sub> and body-mass change*

Rates of mass gain by individuals between dawn and dusk ( $\Delta_m$ , expressed as a percentage of mass at dawn) decreased with increasing  $T_{\max}$  (GLMM,  $-0.93 \pm 0.14\%/^{\circ}\text{C}$ ,  $n = 32$ ,  $\chi^2 = 29.13$ ,  $df = 1$ ,  $P < 0.001$ ; Fig. 4). On days when  $T_{\max}$  exceeded 38.5 °C, several individuals failed to gain any mass, and in some instances lost mass between dawn and dusk (Fig. 4). Typical overnight rates of mass loss, based on a long-term database of mass measurements that followed days with  $T_{\max} \geq 30$  °C, averaged  $3.82 \pm 0.58\%$  ( $n = 44$  measures). According to our model of daytime mass gain, when  $T_{\max}$  exceeded 35.5 °C, babblers struggled to regain enough mass over the daytime period to replace the amount typically lost overnight (Fig. 4).

#### **Discussion**

We found that high  $T_{\max}$  has the potential to compromise the ability of babblers to maintain body condition.

Contrary to expectations, this pattern was not driven by a reduction in foraging effort at high air temperatures, suggesting that the thermoregulatory costs of continuing to forage did not outweigh the benefits in terms of energy and/or water gain. The return per unit foraging effort did, however, decrease considerably: this was in part driven by birds actively thermoregulating at the same time as foraging. Although such short-term losses of body condition may have limited consequences, the longer energy and water balances remain negative, the greater the probability that individual fitness and survival will be compromised (Baldwin & Kendeigh, 1938).

The absence of a discernible effect of temperature on foraging effort contrasts with the findings of several other studies in which birds living in hot, arid environments have been observed to reduce foraging effort during the hottest hours of the day (Calder, 1968; Ricklefs & Hainsworth, 1968; Austin & Miller, 1982; Goldstein, 1984; Carmi-Winkler *et al.*, 1987; Williams, 2001; Tieleman & Williams, 2002). This suppression of activity is often considered to be driven primarily by thermal constraints (Carmi-Winkler *et al.*, 1987; Wolf, 2000), an idea supported by studies of captive birds in which increasing environmental temperature has driven reductions in activity regardless of time of day (Calder, 1968; Ricklefs & Hainsworth, 1968).

As well as heat balance considerations, patterns of foraging activity may also be driven by energetic and other requirements. In the absence of thermal constraints, many birds follow bimodal foraging patterns (with a decrease in activity in the middle of the day), and a reduction in bimodality or a lack of bimodality (this study) may only be optimal when food is scarce and unpredictable, and demand is high (Bednekoff & Houston, 1994; McNamara & Houston, 1994; Polo & Bautista, 2006). A similar absence of bimodality in foraging effort has been reported in birds living in harsh winter climates in the northern hemisphere (Pulliainen, 1980). In terms of energetic stress, such cold conditions may be akin to those experienced by babblers at the time of this study, which took place towards the end of the long, dry winter when availability of arthropod prey is low (Seely & Louw, 1980; Avenant & Nel, 1992).

Babblers may continue to forage through the middle of the day if the risks of dehydration and heat stress are outweighed by the costs of failing to obtain adequate energy over the day. Our data indicate that babblers typically lose ~4% of their body mass overnight. Failure to gain at least that amount during the day may result in a gradual deterioration in body condition. In babblers, body condition is an important determinant of breeding potential (Ridley & Raihani, 2007a), and by extension fitness, as has been proposed for other

species (Wauters & Dhondt, 1989; Russell *et al.*, 2002). Individuals may be able to offset low daytime mass gain by facultatively downregulating metabolic rates overnight (Reinertsen & Haftorn, 1984; McKechnie & Mzilikazi, 2011), but this in turn may incur costs, such as increased vulnerability to predation (Grubb & Pravosudov, 1994).

To keep cool during the hottest times of day, babblers elevated rates of heat loss by panting and wing spreading. On numerous occasions babblers continued to forage while simultaneously engaging in these heat-dissipation behaviours; attempting to 'multi-task' in this manner immediately reduced the efficiency with which babblers could forage. Precisely how foraging efficiency is compromised by heat-dissipation behaviours is open to conjecture, but there are obvious mechanical constraints on attempting to use a beak to dig while simultaneously holding it open to pant. Trade-offs with heat-dissipation behaviour and foraging efficiency may not be the only processes driving reduced rates of food intake on hotter days. Babblers feed primarily on arthropods, the activity of which can be strongly temperature dependent (Holm & Edney, 1973; Gullan & Cranston, 2000). At high temperatures, prey may become inactive and so harder to detect. From a previous study, adult babblers were found to spend roughly 34% of foraging time digging, which resulted in the capture of larger prey items than other forms of foraging (Ridley unpubl.). If prey species retreat deeper as temperatures rise then babblers may have to work considerably harder to find food. Very little rain fell during the study (rain fell on only 5 days with only one rainfall event exceeding 5 mm), so variation in soil moisture content is unlikely to have had a significant effect on foraging efficiency. Investigations of the impacts of temperature and rainfall on prey activity, energy expenditure and foraging mode may provide further insight into the mechanisms that drive changes in foraging effort as well as efficiency.

Regardless of the mechanisms underpinning the reduction in foraging efficiency, the observation that babblers continued to forage at high ambient temperatures despite reduced returns and high thermal costs suggests that the birds may have been close to a resource bottleneck during this study. Whether this reduced ability of babblers to maintain body mass on hotter days was the result of a failure to balance water budgets, energy budgets or a combination of the two, remains unclear. This question could potentially be resolved with a series of field experiments involving the provision of supplementary food and/or water.

It is striking that even under the range of climatic conditions currently experienced in the Kalahari, babblers are sometimes unable to maintain body mass

during the course of the day. Considering the link between body mass and breeding potential (Ridley & Raihani, 2007a; Ridley *et al.*, 2008), it is easy to imagine that during breeding attempts, when energetic demands are even greater, the fitness costs of high temperatures could be considerable. The frequency of heat waves in the southern Kalahari has increased since the 1960s (Kruger & Sekele, 2012) and further increases are predicted (Kruger & Shongwe, 2004; IPCC, 2007; Moise & Hudson, 2008; Akoon *et al.*, 2011). Extreme heat events elsewhere have already resulted in mass breeding failures (Bolger *et al.*, 2005) and mortalities of birds (McKechnie & Wolf, 2010). The sublethal effects of temperature described here may already be impacting local populations of Southern Pied Babblers and could be a harbinger of catastrophic future effects of climate change on arid-zone birds globally.

The concept of the foraging or activity 'window' – the period of time when prevailing conditions permit activity – is often invoked to explain or predict species' responses to climate change (Kearney *et al.*, 2009; Sinervo *et al.*, 2010). This concept is underpinned by the idea that animals trade-off thermoregulatory requirements against time spent engaged in other activities such as foraging, and that these trade-offs result in mutually exclusive behaviours. Although potentially valid for ectotherms, in which body temperatures are determined by environmental temperatures, our results suggest that this concept may need refining for endotherms. Thermoregulatory trade-offs in some desert birds are not necessarily played out in terms of a reduction in the time available for foraging. Rather, thermoregulatory trade-offs may be manifested as a reduction in foraging efficiency while simultaneously attempting to dissipate heat behaviourally.

Mechanistic models, based on biophysical principles, aim to predict the effects of different climatic conditions by modelling energy, water and mass fluxes to predict fitness consequences for animals (Porter & Mitchell, 2006; Kearney & Porter, 2009; Kearney *et al.*, 2009). Our study illustrates that, for a diurnal endotherm, the link between a single climatic variable (temperature) and a proxy measure of fitness (body mass) is potentially complex. In the quest for realism such modelling frameworks may need to consider a variety of ways in which thermoregulation may be traded off with foraging behaviour and in turn impact energy and water fluxes. We explored only a subset of a larger suite of behavioural, physiological and reproductive variables that are needed for convincing species-specific models. Predictions of the impact of climate change on species will be improved by further empirical studies that exploit natural environmental variation and experimental manipulations to explore these causal pathways in

focal species. In short, mechanistic models will be fundamentally improved by a greater understanding of the processes through which climatic variables affect the fitness of individuals (Angilletta & Sears, 2011).

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