The impact of high temperatures on foraging behaviour and body condition in the Western Australian Magpie *Cracticus tibicen dorsalis*§

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High temperatures can pose significant thermoregulation challenges for endotherms, and determining how individual species respond to high temperatures will be important for predicting the impact of global warming on wild populations. Animals can adjust their behaviour or physiology to cope with higher temperatures, but the physical costs of these changes are not well known. We assessed the effect of temperature on foraging behaviour, thermoregulatory behaviour and body condition in a wild, habituated population of Western Australian Magpies *Cracticus tibicen dorsalis*. Focal observation techniques were used to record individual behaviours, and body mass change was measured across a wide range of air temperatures. We found that temperature had a significant effect on behaviour, with temperatures exceeding 27 °C resulting in a significant decline in foraging effort. Individuals increased heat dissipation behaviours as temperatures rose, leading to a trade-off between foraging and heat dissipation. Individuals lost body condition over the five-month summer period, but there was no significant difference in the daily change in body mass on cool days versus hot days. Our research reveals significant changes in daily behaviour in accordance with temperature, but did not detect a measurable cost of this change. We therefore conclude that rising temperatures are likely to impact the behaviour of individuals in wild populations, but the potential flow-on effects of these behavioural changes are unclear.

Keywords: Australian Magpie, body condition, body mass, *Cracticus tibicen dorsalis*, foraging effort, heat dissipation, high temperature, temperature dependent behaviour, trade-offs

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Introduction

Global temperatures have been steadily rising over recent decades, and this change is recognised as a potential major global threat to biodiversity (Parmesan and Yohe 2003; Şekercioğlu et al. 2012). High air temperatures can be directly responsible for animal deaths, as heat stress can culminate to the point where body temperatures cannot be maintained below fatal levels (McKechnie et al. 2012). Climate-related mass mortalities have occurred historically on a significant scale, including the deaths of hundreds of bats (Welbergen et al. 2008) and birds (McKechnie et al. 2012) during extreme heatwave events. With the continued impacts of increasing temperatures and a predicted increase in the frequency of heatwaves (Meehl and Tebaldi 2004), mass mortality events may become a more regular occurrence for temperature-sensitive species, or for those that cannot adapt to higher temperatures. Avian species in particular may be highly susceptible to changes in temperature due to their typical small body size and primarily diurnal habits (McKechnie and Wolf 2010; du Plessis et al. 2012), with reports suggesting that in areas such as the tropical north-east of Australia, avian extinction rates may reach 70% under current climate change predictions (Wormworth and Mallon 2006).

Although the risk of direct mortality due to extreme temperatures poses considerable conservation concern, there may be other, sublethal impacts on individual fitness. At high temperatures, individuals may be unable to maintain body condition in the short term (du Plessis et al. 2012), leading to possible impacts on reproductive success and longevity in the longer term. However, recent empirical research has revealed that animals can adaptively adjust their behaviour to buffer the impact of higher temperatures (Fuller et al. 2010; Hoffman and Sgrò 2011; Şekercioğlu et al. 2012; Smit et al. 2013). For example, birds may use panting, wing spreading and gular fluttering, as well as changes in their patterns of daily activity to avoid extreme temperatures (Tieleman and Williams 2002; du Plessis et al. 2012). These behavioural changes may negatively

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impact an individual by increasing energy expenditure and lowering access to food resources (Tieleman and Williams 2002). In the long term, such changes in behaviour may cause a decline in body condition, which can delay the onset of breeding, or result in early cessation of care for young (Ghalambor and Martin 2001).

Empirical evidence suggests that foraging trade-offs are commonplace among birds, and it is likely that species have a critical temperature threshold where this trade-off occurs (Cunningham et al. 2013). For example, at temperatures above 35 °C, individual Southern Pied Babblers Turdoides bicolor trade off foraging against heat dissipation, which results in lower overall foraging success and a decline in body condition (du Plessis et al. 2012). As a consequence, individuals are not able to find sufficient food to offset overnight mass loss and so may lose mass during periods of sustained high temperatures (du Plessis et al. 2012). If heatwaves become more prolonged or frequent in the future, the cost of thermoregulation and an associated loss of body condition may reach lethal levels (du Plessis et al. 2012).

Although behavioural changes in response to high temperatures have been well studied in birds (Wolf and Walsberg 1996; Tieleman and Williams 2002), few studies have looked at the impacts of behavioural changes on body condition (du Plessis et al. 2012; McKechnie et al. 2012). Gaining an understanding of the trade-off between heat dissipation and other behaviours will be important for predicting survival rates as air temperatures continue to rise, as well as for determining the impact on reproductive activity. This follows the prediction that under certain conditions parents will trade off their own survival against investment in their young (Ghalambor and Martin 2001). We examined the effect of fluctuating daily maximum temperature on foraging and heat dissipation behaviours and subsequent changes in body condition in the Western Australian Magpie Cracticus tibicen dorsalis. behaviours were compared across a range of spring and summer temperatures to determine (1) at what temperature individuals trade-off foraging behaviour with heat dissipation behaviours and (2) the relationship between air temperature, foraging effort, foraging efficiency (return per unit effort) and body mass. We hypothesised that foraging efficiency and the proportion of time spent foraging would decrease as temperatures rose, while heat dissipation behaviours would concomitantly increase. As a consequence of this predicted trade-off, we hypothesised that body condition would decline following consecutive days of high temperatures. Determining critical temperature thresholds adds to our currently limited insights into the potential effects of climate change on wild bird populations.

Methods

Study species

The Western Australian subspecies of the Australian Magpie Cracticus tibicen is a common, medium-sized (250–370 g) passerine bird inhabiting the south-west of Western Australia (Kaplan 2004). It is highly territorial, living in groups that range in size from 3 to 16 individuals, with group members aggressively defending their territory from both neighbouring groups and invaders (Kaplan 2004). Magpies begin nest construction in late August to September, and chicks typically fledge 1–2 months later (Kaplan 2004). Each female can initiate several broods per season, with breeding activity (including the provisioning of young) continuing until April each year. Magpies are primarily terrestrial foragers, and their acute hearing allows them to locate subterranean prey, including a wide variety of arthropods. Individuals gain full adult plumage at approximately three years of age (Kaplan 2004), and are sexually dichromatic, with males possessing a full white back, and females a scalloped black and white back (Johnstone and Storr 1998). Magpies are long-lived, with individuals surviving for over 20 years in the wild (Kaplan 2004).

Since 1993 groups of magpies within our study area have been habituated to the presence of humans by Professor Ian Rowley and Dr Eleanor Russell, allowing the birds to be observed from within 5 m without affecting daily activity patterns (for details of observation of habituated animals, see Ridley and Raihani 2007). Individuals within these groups have been ringed with unique coloured leg bands, allowing for easy identification. Ringing occurred between 1993 and 2005, and resumed in 2013 by one of the authors (ARR). Individuals from seven magpie groups, with an average group size of 7.4 ± 1.3 adults, were studied between 30 September 2013 and 3 March 2014 (austral spring to late summer).

Study area

Our study took place in the suburbs of Guildford and Bassendean, approximately 15 km north-east of Perth city, Western Australia, during a typical dry spring and summer period. The study site had a mean daily maximum and minimum temperature of 20.1 °C and 8.9 °C in September and 31.9 °C and 17.5 °C in March, respectively (Bureau of Meteorology 2014; see also Supplementary Figures S1 and S2). The area is mainly residential, with sparse bushland scattered around several parks within the urban matrix. Magpies inhabited the open, irrigated grassland areas at the study site where they normally foraged. Each group had access to both open and shaded areas. Shade was primarily provided by mature eucalyptus trees. All magpie groups were surrounded by residential properties and thus had some access to artificial food and water sources, either directly or indirectly.

Focal observations

The effects of temperature on the foraging behaviour and body mass of individual birds was determined by making repeated focal observations on 21 magpies within the seven territorial groups. Three birds were selected randomly from each group, with 11 females and 10 males in the total sample. Two focal birds in one group died early in the study and were replaced with two alternative birds from the same group. Observations were made over 70 d within five two-week periods, spread evenly throughout the study, which allowed observations to be made over a range of air temperatures from 4.8 °C to 43.4 °C. Different groups were observed on each day and the behaviours of the three focal birds were recorded during each of three focal periods throughout the day from dawn until dusk (06:00–08:00, 12:00–14:00 and 16:30–18:30). During the study, the earliest sunrise was 05:03 and the latest sunset at 19:26, therefore...
all morning focal observations were made less than 3 h after sunrise. Similarly, all evening focal observations were made before sunset. The air temperature for each focal observation was obtained from an online database of half-hourly temperature records available from the Bureau of Meteorology (http://www.bom.gov.au) for Perth Airport, 3.2 km from the study site. The closest half-hour recorded temperature to the time of each focal observation was used for analysis. These temperatures were considered to accurately represent temperatures at the study site, as historical records from the now closed Guildford Post Office weather station indicate a similar temperature profile between the two areas (Bureau of Meteorology 2014).

Each focal observation consisted of a 20-minute time-activity period per bird, where all behaviours were recorded, including foraging, vocalising, heat dissipation, preening and vigilance. An individual was recorded as being engaged in a particular behaviour if the behaviour lasted for more than 10 s, otherwise the behaviour was not recorded, and would remain as the previous behaviour. The only exception to this was when a bird made a quick, but successful foraging attempt that lasted less than 10 s, in which case a foraging attempt was recorded. Changes in behaviour were recorded to the nearest second with a Google Nexus 7 tablet, using the CyberTracker Program developed by CyberTracker Conservation, with a specific focal programme created for the magpies. If a focal bird could not be located within each two-hour period, or it flew away and could not be relocated within 10 min, then the focal was abandoned. Similarly, foci were paused if the bird was out of sight and did not resume unless the bird was relocated within the next 10 min.

The foraging behaviours recorded during each focal included gleaning substrates, digging for and handling prey, with the combined focal time spent in these behaviours defined as foraging effort. When a successful foraging attempt was made, the approximate size of the prey item was recorded using size categories shown in Table 1, based on a previous study by Raihani and Ridley (2007). Where possible, prey items were classified into broad taxonomic groups (e.g. Coleoptera, Orthoptera and Lepidoptera) and life stages (larvae, pupae or adult). Samples of various arthropods and other prey items were collected from the Perth Metropolitan area and weighed to determine a typical mass for each size category. Several representatives of each size were weighed in the laboratory on an analytical balance (Mettler AC 100 ± 0.001 g) and the average prey biomass was calculated following the methods of Raihani and Ridley (2007).

Foraging efficiency was defined as the biomass intake per unit of foraging time, measured in grams per minute. It was calculated by determining the total prey biomass consumed by a bird during a focal period and dividing it by the time spent foraging. Heat dissipation was defined as the proportion of focal time a bird spent engaged in any heat dissipation behaviour such as bill-gaping or wing-spread (sensu du Plessis et al. 2012). A bird was considered to be bill-gaping if it held its beak open for more than 10 s (without vocalising or foraging), and was considered to be wing-spread if it held its wings away from the body or drooped towards the feet for more than 10 s.

| Size class | Definition | Wet biomass (g) |
|------------|------------|----------------|
| Tiny       | Food not visible in bill, but bird has clearly captured and consumed an item | 0.014 |
| Small      | Food visible in bill, but no part of food item hangs out of bill | 0.09 |
| Medium     | Less than 50% of food item hangs out of bill | 0.18 |
| Large      | Between 50% and 75% of food item hangs out of bill | 0.38 |
| Extra Large | More than 75% of food item hangs out of bill | 0.89 |

Change in body mass of focal birds
Daily changes in body mass were measured by enticing individuals onto a top-pan balance (Ohaus Challenger series 1 000 ± 1 g) for a small food reward (c. 1 g of cheese). Each focal bird was weighed within a half-hour period before each focal observation. The change in body mass from morning to afternoon and morning to evening for each individual was calculated from these measurements, using the change in body mass divided by the number of hours between the two measures. For seasonal changes in body mass, spring measurements were taken as the average morning body mass measurement for each individual during the first two-week observation period (30 September to 14 October), while late-summer body mass was taken as the average morning body mass of each individual in the final two-week observation period (10 February to 2 March).

Data analysis
The effect of temperature on the foraging and heat dissipation behaviours of individual magpies was investigated using model selection with generalised estimating equations for binomial models, using the statistical program IBM SPSS 20 (IBM Corporation, Armonk, NY, USA). Using individual identity (nested in group identity) as random terms to account for the potential influence of repeated measures on the distribution of the data, a series of models were tested, with each model representing a biological hypothesis (Burnham et al. 2011).

For the analysis of both foraging effort and heat dissipation, the response data were proportional, so therefore a binomial model was used, with the response variable as seconds invested in (a) foraging (model 1) or (b) heat dissipation (model 2), and the total time of the observed focal as the binomial denominator (using a numerator/denominator model rather than a traditional 1,0 binomial model). For the analysis of foraging efficiency a normally distributed generalised linear mixed model was used. The predictor terms tested in each model included sex, temperature at the time of focal, time of day, group size (number of adults), Julian date (taken as the number of days since the beginning of spring, 1 September), and the age of any chicks present in the group, categorised as either nestlings or fledglings.

Models of greatest parsimony were selected using Akaike’s information criterion (AIC) for normally distributed
data and the quasi-likelihood information criterion (QIC) for binomial data. Using model selection, a series of models were analysed and the AIC/QIC value of each model was noted. A null model containing no predictors was also included in the model selection process. If the AIC/QIC of the predictor models were not more than 5 AIC/QIC points smaller than the null model, then it was considered that none of the models were a good predictor of the distribution of the data. A top model set was determined by taking all significant models that were within 5 AIC/QIC points of the best model. These models were then carefully scrutinised; any terms with a confidence interval that did not intersect zero were considered to have a significant influence on the data (sensu Grueber et al. 2011).

A series of paired $t$-tests were used to test for the effect of temperature on individual changes in body mass, as we had insufficient data for multiple regression analysis. Daily mass gain from morning to evening and morning to midday was compared for individual birds on cool days (defined as days less than 25 °C: this temperature was chosen as the upper limit for ‘cool’ days, as it was the average temperature recorded during all focal periods) and ‘hot days’ (defined as days with a maximum temperature >32 °C) to determine if birds either lost or gained less body mass on hot days relative to cool days. The change in body mass for each focal bird during summer heatwave periods (three or more consecutive days above 35 °C; Bureau of Meteorology 2014) was also compared to the change in mass over non-heatwave periods in summer. There were four heatwaves during the study period, and birds focalled during these times were compared to a focal taken during the closest non-heatwave period, to reduce any influence of other factors on changes in mass. Finally, paired $t$-tests were conducted to determine whether birds lost body mass over the entire study period. In these cases, the morning masses of birds during the first two-week observation period in spring were compared to the morning masses of the same birds during the final two-week observation period at the end of summer. This was done three times: first, for all study birds; second, for each sex; and third, for birds that raised young and birds that did not raise young. In this final case, although all groups attempted to breed during the study period, the regular focal observations of each study bird meant it was easy to separate birds that regularly invested in young from birds that did not.

**Results**

A total of 568 twenty-minute focals were collected from 23 birds from seven groups over the course of the study, with an average of 25 focals per Magpie. Air temperature increased from a maximum of 26.9 °C in October to a maximum of 43.4 °C in January, and declined slightly in February, where the maximum temperature was 36.8 °C. Magpies experienced an average daily variation in temperature of 9 °C during the first observation period (spring), to an average daily variation of 13 °C in the final observation period (late summer).

**Factors influencing heat dissipation and foraging**

As temperatures rose there was a significant increase in the proportion of focal time spent engaged in heat dissipation behaviours, in a pattern associated with the time of day (Table 2). Parameter weights revealed that temperature alone explained 15% of the variation in the data, while the interaction between temperature and time of day explained 85%. During cooler mornings between 06:00 and 08:00, when the average temperature across all focals was 18.2 °C, no heat dissipation behaviours were observed (Figure 1). In contrast, during the afternoon focals between 12:00 and 14:00, heat dissipation peaked at a mean of 14.8% of focal time across all afternoon periods from spring to summer. The average air temperature during afternoon focals was 28.7 °C. Finally, during evening focals (16:30–18:30) from spring to summer, magpies spent on average 9.7% of their time heat dissipating when the average temperature was 28.0 °C (see Supplementary Figure S3 for the maximum and minimum temperatures during each focal time period).

There appeared to be a critical temperature threshold of 27 °C where magpies began to heat dissipate (Figure 1). Below this temperature, during afternoon focals, individuals spent less than 0.68% of time heat dissipating, but 22.3% of time above this temperature was spent displaying heat

![Figure 1: Proportion of time focal individuals spent heat dissipating during morning, afternoon and evening focal periods. No heat dissipation was recorded during morning focals. Data were based on 568 twenty-minute focals from 23 individuals from seven groups. CI = confidence interval](image)

Table 2: The top model set for the terms associated with the time spent heat dissipating (for a full list of models tested refer to Supplementary Table S1). No heat dissipatation was recorded during morning focals. Data were based on 568 twenty-minute focals from 23 individuals from seven groups. CI = confidence interval

| Parameter | Estimate | SE | CI |
|-----------|----------|----|----|
| Temperature | 0.479 | 0.0642 | 0.355, 0.605 |
| Temperature*Time of day | 0.463 | 0.0617 | 0.342, 0.584 |
| Temperature*Time of day | 0.479 | 0.0591 | 0.363, 0.0595 |
dissipation behaviours. During evening focus periods, heat dissipation increased from 0.23% to 21.8% once the temperature rose above 27 °C. There was no effect of sex, nor level of investment in young on the amount of time that magpies spent heat dissipating (Supplementary Table S1).

Foraging effort was also influenced by temperature variation (Table 3). Foraging effort declined more sharply during afternoon and evening focus periods compared with morning observations, where the proportion of time spent foraging was relatively constant (Figure 2). During the morning, magpies spent on average 27.2% of their time foraging, compared to 9.9% and 22.1% of their time during afternoon and evening focus periods, respectively. However, above the critical temperature threshold of 27 °C when magpies began to heat dissipate, the frequency of foraging behaviour declined more rapidly. For example, when air temperature was less than 27 °C, foraging behaviours comprised 16.6% (afternoon) to 32.2% (evening) of total focal time. Once air temperatures exceeded 27 °C, foraging effort declined to 6.2% and 14.0%, respectively.

Foraging efficiency, unlike foraging effort, was not affected by temperature (Supplementary Table S3). The interaction between foraging effort and the time of day was the best predictor of foraging efficiency, explaining 76% of the variation (Table 4). The longer a bird spent foraging the less efficient it was, with birds observed during afternoon focals showing the largest decline in efficiency (Figure 3).

**Change in body mass**

Paired comparisons revealed that magpies did not lose more body mass from morning to midday (paired t-test, \( T = -0.39 \), \( n = 19 \), \( p = 0.70 \)), nor from morning to evening (\( T = -0.13 \), \( n = 20 \), \( p = 0.90 \)) during hot days (\( >32 °C \)) compared to cooler days (\( <25 °C \)). Although foraging effort decreased with increasing temperature, magpies were typically able to maintain body mass throughout the day. Similarly, body mass changes during heatwave periods were similar to changes during non-heatwave periods (morning to midday, paired t-test, \( T = -1.30 \), \( n = 7 \), \( p = 0.24 \); morning to evening, \( T = -0.82 \), \( n = 8 \), \( p = 0.44 \)). However, magpies lost body mass over the entire study period (\( T = 2.86 \), \( n = 31 \), \( p = 0.008 \)). This change appeared to be driven by investment in young, as birds that did not spend heat dissipating (Supplementary Table S1).

**Table 3:** The top model set (all significant models less than 5 QICc from the best model) for the terms associated with the foraging effort of individual Magpies (for a full list of models tested refer to Supplementary Table S2). Data were based on 568 twenty-minute focal periods from 23 individuals from seven groups. CI = confidence interval

| Model                     | Weight QICc | ΔQIC |
|---------------------------|-------------|------|
| Basic                     | –           | 328.84, 46.82 |
| Temperature*Time of day   | 1           | 282.02, 0 |
| Parameter                 | Estimate    | SE   | CI   |
| Temperature*Time of day   |             |       |      |
| Morning                   | –0.059      | 0.0238, –0.106, –0.013 |
| Afternoon                 | –0.088      | 0.0145, –0.0116, –0.059 |
| Evening                   | –0.053      | 0.0144, –0.081, –0.0025 |

**Table 4:** The top model set (all significant models less than 5 QICc from the best model) for the terms associated with the foraging efficiency of magpies (for a full list of models tested refer to Supplementary Table S3). Only those birds were seen foraging during focal periods were included in the analysis of foraging efficiency. Data were based on 342 twenty-minute focal periods from 23 individuals from seven groups. CI = confidence interval

| Model | Weight QICc | ΔQIC |
|-------|-------------|------|
| Null  | –           | 263.53, 5.89 |
| Time of day*Proportion foraging | 0.76 | 257.64, 0 |
| Proportion foraging | 0.20 | 260.30, 2.66 |
| Parameter | Estimate | SE | CI   |
| Proportion foraging | –0.219 | 0.087, –0.390, –0.049 |
| Time of day*Proportion foraging | –0.115 | 0.094, –0.300, 0.070 |
| Morning | –0.363 | 0.166, –0.690, –0.037 |
| Afternoon | –0.387 | 0.110, –0.602, –0.171 |

**Figure 2:** Proportion of time spent foraging during morning, afternoon and evening focal periods as a function of temperature. Trend lines are generated from the predictions of the model of greatest parsimony presented in Table 3

**Figure 3:** Foraging efficiencies of magpies as a function of the proportion of time spent foraging during morning, afternoon and evening focal periods. Trend lines are generated from the predictions of the model of greatest parsimony presented in Table 4
raise young did not lose body mass over the study period (paired t-test, \( T = 0.76, n = 17, p = 0.46 \)). In contrast, there was a significant loss in body mass for birds that were raising young (paired t-test, \( T = 2.48, n = 16, p = 0.03 \)). Both males and females that were raising young lost body mass over the study period (females, paired t-test, \( T = 2.34, n = 15, p = 0.03 \); males, paired t-test, \( T = 5.43, n = 16, p < 0.001 \)).

**Discussion**

We showed that high air temperatures can negatively impact the foraging effort of magpies. Focal birds significantly increased the time spent employing heat dissipation behaviours in the middle of the day when temperatures were highest, and spent less time foraging as a consequence. Despite an increase in heat dissipation and a decrease in foraging effort at high temperatures, individuals generally maintained their body condition throughout the day, with no cost to body mass from the lower foraging effort on hot days. This raises the possibility that individual birds focused primarily on self-preservation at the expense of their own offspring, distributing less food to their young and consuming more themselves at high temperatures. This trade-off has been observed in a number of bird species (Tveraa and Christensen 2002; Bleecker et al. 2005; Schultner et al. 2013), with studies by Erikstad et al. (1998) and Ghalambor and Martin (2001) suggesting that long-lived bird species such as magpies are more likely to prioritise their own survival ahead of their young when faced with harsh environments. This has important ramifications for understanding the potential effects of long-term increases in air temperatures due to climate change; if parents reduce investment in young at high temperatures, then declines in reproductive success are likely.

The negative effect of temperature on foraging effort as found in this study has also been identified by other researchers (Ricklefs and Hainsworth 1968; Williams 2001; Tielman and Williams 2002; Smit et al. 2013), and is typically considered to be a response to thermoregulatory constraints (Smit et al. 2013). The concept of a critical temperature threshold above which certain behaviours increase while others decrease has been investigated in several species, with temperatures in the mid-30s °C appearing potentially harmful (expressed through an exponential increase in heat dissipation behaviours), requiring individuals to trade-off heat dissipation against other behaviours in which they would normally invest (du Plessis et al. 2012; Cunningham et al. 2013). For magpies, this critical temperature appeared to be lower at around 27 °C. Above this critical point rates of heat dissipation behaviour increased rapidly, while foraging effort decreased at similar rates. However, as maintenance of good body condition is important for survival, in some cases it may not be feasible to avoid foraging altogether. For example, if the energetic costs of not foraging outweigh the risk of dehydration and heat stress, then birds may not show a decrease in foraging effort (sensu du Plessis et al. 2012). As magpies typically did not forage during the hottest part of the day, it suggested that they were able to avoid the energetic costs of foraging when temperatures were not ideal. Further, given that magpies typically feed on arthropods, foraging effort could decline at very high temperatures because prey is less active at extreme temperatures (Holm and Edney 1973; Flower et al. 2013).

Many species of birds exhibit a bimodal foraging pattern, where they forage mostly in the mornings and evenings and decrease activity in the middle of the day (e.g. Santiago-Quesada et al. 2012). The level of foraging effort magpies exhibited during morning focals did not seem to be affected by temperature, but effort decreased significantly as temperatures rose during the day. This pattern suggests that high temperatures may affect daily foraging patterns, with a preference for foraging in the cooler hours of the morning. Furthermore, birds typically lose mass overnight, and so the initial morning foraging bout is required to recoup overnight mass loss, regardless of adverse conditions (Polo and Bautista 2006).

While no evidence was found of temperature-related mass loss (as was found by du Plessis et al. 2012), high temperatures can increase the length of the midday resting period in birds (Jacquet and Launay 1997). Birds must eventually forage again or risk not being able to gain enough energy to maintain body condition overnight (Polo and Bautista 2006). The two peaks in foraging activity normally result in two corresponding peaks in rates of body mass gain (Polo and Bautista 2006), and if birds do not forage sufficiently during the evening, this second peak may not occur. Typically in Perth, the hottest part of the day is around 14:00 (Bureau of Meteorology 2014), and if afternoon and evening temperatures exceed the critical temperature threshold of magpies, as occurred several times throughout the study period, then magpies may delay foraging until air temperatures decline sufficiently. With projected regional temperature increases of 2–4 °C by 2070 due to global warming (IPCC 2007), such scenarios will become more frequent and birds thus may find it increasingly difficult to regain overnight mass loss.

Contrary to our hypothesis, foraging efficiency was not affected by temperature, as magpies foraged at similar efficiencies over the entire air temperature range in this study. Our result differs to that found by du Plessis et al. (2012) in Southern Pied Babblers, and may in part explain why individuals did not lose body mass on hot days. Two potential reasons can be proposed; first, unlike Babblers who both glean and dig for prey, magpies are primarily subterranean foragers, and prey abundance is less likely to be affected by temperature. Second, magpies expend very little foraging effort at high temperatures, thus making it difficult to quantify foraging efficiency during these times. More data on foraging efficiency at higher temperatures may have allowed us to demonstrate a direct impact of temperature on this aspect of foraging behaviour; currently, we can only conclude that temperature indirectly affects foraging efficiency via its negative impact on foraging effort. However, if magpies are able to maintain foraging efficiency at higher temperatures, they may benefit from ceasing to forage sooner and thereby decreasing their exposure to high temperatures (Tielman and Williams 2002).

To avoid hyperthermia, magpies pant and spread their wings to elevate rates of heat loss. The proportion of time spent engaged in this behaviour increased appreciably as
temperatures rose, with some birds employing heat dissipation behaviours for the entire focal period on hot days. Magpies that were heat dissipating rarely foraged at the same time, in contrast to other species that can perform both activities simultaneously (du Plessis et al. 2012; Smit et al. 2013). Thermoregulatory behaviour requires an input of energy, which must be satisfied before birds can allocate collected energy to the maintenance of body condition (Speakman and Król 2010). If individuals forage while simultaneously heat dissipating, the energy gained from foraging may be insufficient to avoid hyperthermia (Speakman and Król 2010). In contrast, heat dissipation while resting incurs no trade-off with other activities, therefore allowing more efficient reductions in body temperature (Smit et al. 2013). The fact that magpies do not heat dissipate and forage simultaneously suggests that further increases in temperature would reduce the time available for foraging, potentially having a negative impact on body condition in the short term, and on long-term fitness.

Although magpies maintained body mass on hotter days (above 32 °C) and cooler days (below 25 °C), focal birds did lose body condition over the study period. This loss of body condition was likely due to the fact that it was the breeding season, rather than being an effect of high temperatures. As there was considerable variation in the investment of young during the study period, we were able to show that breeders and non-breeders differed significantly in body mass loss, with only breeding birds showed a significant decline in body mass. This suggests that parental care, and not temperature, was the cause of the observed body mass loss, presumably because resources that parents would typically use for themselves are instead invested in young (sensu Lindén and Mäller 1989).

The short-term changes in behaviour in relation to temperature observed during this study suggest that future climate change could impact foraging behaviours of magpies. Foraging effort declined sharply at high temperatures (due to magpies trading-off foraging activity with heat dissipation) and if such declines are exacerbated by increasing temperatures, or by an increase in heatwave events, then future body condition, longevity and reproductive success may all be affected, even more so if future reproduction depends on the maintenance of body condition from previous years (Nilsson and Svensson 1996). Developing single-taxon models that improve our understanding of behavioural patterns when temperatures are high may improve our ability to accurately predict the impact of future climate change more generally on avian species (McKechnie et al. 2012).

In conclusion, this study of magpies provides a useful indication of how short-term influences of temperature affect individual behaviour. While we examined only a single abiotic variable known to influence foraging behaviours, our empirical data can be used as a basis for modelling the potential influence of global warming on avian populations, as it is one of only a few studies that has directly measured a decline in foraging effort and body mass change in a wild population. Importantly, we showed that (1) temperature has a strong effect on foraging effort and (2) above a critical temperature threshold of 27 °C magpies display increased heat stress and reduce their foraging behaviours. Taken together, these results indicate that although magpies appear to cope with current conditions, their relatively low heat dissipation threshold means they are potentially vulnerable to higher temperatures in the future. Long-term studies of trade-offs between thermoregulation and reproduction would be a valuable avenue for future research.

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Ghalambor CK, Martin TE. 2001. Fecundity-survival trade-offs and reproductive success and if such declines are exacerbated by increasing temperatures, or by an increase in heatwave events, then future body mass loss. This suggests that parental care, and not temperature, was the cause of the observed body mass loss, presumably because resources that parents would typically use for themselves are instead invested in young (sensu Lindén and Mäller 1989).

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