How does temperature affect Fork-tailed Drongo, *Dicrurus adsimilis*, foraging effort, nestling provisioning and growth rates?

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Abstract:

Global average temperatures are predicted to increase by as much as 5^0C by 2100. Therefore, it is imperative to identify how species are affected by temperature increase to ensure that proper conservation and management of wildlife can be implemented. Species which already live in warmer climates, such as deserts, may provide the first clues to the impacts of increasing temperatures. Birds represent an ideal indicator because research has shown that rising temperatures affect their behaviour, including foraging and provisioning of young, thereby reducing reproductive success. However, it remains unclear whether this results from physiological constraints on behaviour, from declining food availability and or access to prey items at high temperatures. In this study, I aimed to identify how temperature affects the foraging and provisioning behaviour of wild Fork-tailed Drongos, *Dicrurus adsimilis*, when supplemental food is provided. Additionally, I aimed to identify how nestling growth rates change with temperature. The results of two supplemental feeding experiments indicated that as temperatures increased, adults significantly reduced their willingness to forage, reduced provisioning to offspring and exhibited increased rates of heat dissipation behaviour. Furthermore, when provisioning nestlings, adult drongos consumed a larger proportion of supplementary food at higher air temperatures, and provisioned less. This suggests that they suffer greater provisioning costs at such times. Surprisingly, despite finding several negative effects of temperatures on adults' willingness to forage and provisioning, there was only a weak and non-significant effect of temperature on nestling growth rates. This suggests that adults may be able to compensate for reduced foraging at high temperatures. My study shows that the increased thermoregulatory costs of activity at high temperatures can constrain foraging and provisioning, even when food remains abundant. However, whether this impacts the fitness of current offspring or parents future reproductive success remains unclear.

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Introduction:

Climate change: past, future, and its impacts on the environment

Overwhelming evidence indicates that the planet is undergoing a climatic shift. Evidence of this change and its impacts on the environment have been recorded on every continent (Parmesan, 2006). Rising sea levels caused by melting ice sheets in Antarctica and Greenland (Rignot et al., 2011), increased frequency of droughts in the Mediterranean during the 20th century (Hoerling et al., 2012), and increased occurrences of tropical storms, due to higher than average sea surface temperatures in the Atlantic ocean, near North America (Gillet et al., 2008), have all been attributed to global warming as a result of climate change.

Scientific evidence strongly suggests that recent climate change, since the 1950s, and increased levels of greenhouse gases (GHGs), e.g. carbon dioxide, in the atmosphere from human emissions, is primarily responsible for warming trends (Treut et al. 2007; Rosenzweig et al. 2008). The potential impacts of increased GHGs, associated with anthropogenic climate change, are so extreme that a recent study has predicted that the next ice age, modeled to begin in roughly 50,000 years, may be delayed by another 100,000 years (Ganopolski et al. 2015). Since 1951, surface temperatures have already increased between 0.5°C and 1.3°C (IPCC 2014), and climate models of the 21st century predict average surface temperatures may increase between 1.4-5.8^{0}C by 2100 (Houghton et al. 2001).

The effects of climate change will not be evenly distributed across the globe (Meehl et al., 2005) and will vary by both region and biome type. Specifically, Southern and Western Africa has showed increasing trends in daily maximum temperatures from 0.160 to 0.194^{0}C per decade from 1960-2000 (New et al. 2006). In addition, deserts, which are extensive in this region, are amongst the first biomes expected to experience rapid changes due to global warming (Loarie et al., 2009). Deserts represent the warmest regions on the planet and tend to have varying and unpredictable precipitation rates, which force their inhabitants to maximize water acquisition and retention (Dawson, 1954). Within the 21st century, deserts are expected to expand in size, and average temperatures (IPCC, 2013) and the frequency of hot days in arid environments are predicted to increase (Meehl and Tebaldi, 2004; Akoon et al., 2011). Due to the intense temperatures that desert dwelling species already experience and climate model predictions of rapid warming, it is expected that these species could become among the most vulnerable to climate change (Vale and Brito, 2015). This is because the physiological limits of these species might already be met and there may be evolutionary constraints that limit the ability of a terrestrial organism to survive under higher temperatures (Araujo et al., 2013).

The effects of higher average temperatures associated with climate change may cause additional physical stress to organisms, as temperature is a fundamental driver of physiological processes, e.g. energy acquisition (Angilletta et al., 2010) and retention (Geraert, Padilha and Guillaumin, 1996). High temperatures can cause a reduction in the efficiency of these processes (Huey and Stevenson, 1979) and have been shown to have numerous impacts on plants and animals. For example, high temperatures can create a gender bias among temperature-dependent sexual determinant species, e.g. crocodiles and turtles (Mitchell and Janzen, 2010; Ospina-Álvarez and Piferrer, 2008). Additionally, higher temperatures can affect species survival by increasing plant and animal diseases (Harvell et al., 2002), or decreasing reproductive potential through tradeoffs between thermoregulatory behaviour and foraging (Tieleman and Williams, 2002; Du Plessis et al., 2012). In extreme cases, prolonged temperature increases i.e. heat waves, have caused catastrophic mammal (Welbergen et al., 2007) and avian mortality events (McKechnie and Wolf, 2009). On several occasions, these mass mortality events associated with heat waves have taken place in desert environments. Such events have been documented in the deserts of Western Australia during the 1930s (Finlayson, 1932) and more recently in 2009 (Towie, 2009) when, thousands of small birds were found dead following extreme heat waves. The precise cause of these mass mortality events may have been unsustainable rates of evaporative water loss and or dehydration (McKechnie and Wolf, 2009). As water requirements increase with temperature, desert dwelling organisms, which typically have less access to water than other species, may suffer reduced survival rates during the hot summer months (McKechnie and Wolf, 2009). Therefore, research on the effects of higher temperatures, and specifically higher maximum temperatures, on behavior is needed to explore what mechanisms can lead to mortality.

Behavioural responses to high temperatures

Although the impacts of increasing temperatures associated with climate change have been well documented with respect to the phenology and timing of migratory birds (Both et al., 2006; Møller, Rubolini, and Lehikoinen 2008) comparatively little research has been done on the mechanistic link between temperature and behavioural patterns, specifically foraging and provisioning habits. Research has shown that high temperatures can alter adult to chick provisioning rates and adult foraging success (Ricklefs and Hainsworth, 1968; Austin, 1976; Cunningham et al., 2013; Wiley and Ridley, 2016). For example, Verdins, *Auriparus flaviceps*, of the Sonoran Desert in the United States, primarily forage at air temperatures below 35^{0}C, and decrease activity above this temperature (Austin, 1976). Similarly, Cactus wrens, *Campylorhynchus brunneicapillus*, of the Sonoran Desert, decrease their nest visits and provisioning, when temperatures exceeds 35^{0}C (Ricklefs and Hainsworth, 1968). Recently, in the Kalahari Desert of South Africa, researchers have honed in on more specific behavioural responses to high maximum air temperatures. Wiley and Ridley (2016), found that adult southern pied babblers, *Turdoides bicolor*, decreased provisioning rates to nestlings when air temperature exceeded 35.5^{0}C. This decrease in provisioning rates is believed to be the result of a thermoregulatory parental tradeoff as it may be more difficult to maintain body condition on days above 35.5^{0}C (du Plessis et al., 2012; Wiley and Ridley, 2016). Therefore, parents may choose to limit the number of flights back and forth to the nest as the risk of overheating from flying could be higher on hotter days (Wiley and Ridley, 2016). Moreover foraging and provisioning may also become less efficient under higher temperatures because individuals adjust their foraging behaviour. Research by Cunningham et al. (2015) found that Common fiscals, *Lanius collaris*, had a 50%

decrease in foraging success when air temperatures exceeded 35^{0}C. This decrease was attributed to shifts in male fiscals from their preferred exposed and unobstructed foraging perches to cooler shaded and somewhat obstructed ones at higher temperatures (Cunningham et al., 2015).

Although previous research indicates that the physiological costs of activity at high temperatures cause declines in foraging and provisioning behaviour, these patterns could also be the result of a reduction in food availability. As temperatures increase, available terrestrial prey may move into cooler shaded areas, or over the longer term, decline in abundance (Cunningham et al., 2013; Gullan and Cranston, 2005; Kearney et al., 2009). Feeding experiments provide a means to determine whether food availability, or tradeoffs between foraging and thermoregulation, result in decreased foraging success and offspring investment at high temperatures. Previously, feeding experiments on Hoopoe-larks, *Alaemon alaudipes*, in the Arabian Desert, found that they decrease overall foraging time and increase thermoregulatory behaviour during the heat of the day, on days when food and water were provided compared to unsupplemented periods (Tieleman and Williams, 2002). However, it remains unclear whether the behavioural shift at high temperatures results in lower foraging payoffs, or how this might affect individual fitness (Tieleman and Williams, 2002; Stearns, 1992). Consequently, there is a need to further explore how temperature affects foraging and offspring provisioning when food access and availability is controlled in wild animals.

Physiological responses to high temperatures

Breeding birds adjust their behaviour in response to high temperatures which can impose physiological costs on both parents and offspring. For example, adult provisioning rates have been shown to affect chick mass and growth rates (Huin, Prince, and Briggs, 2000). Therefore, if higher temperatures cause a behavioural shift, such as a decrease in provisioning rates to reduce physiological costs to provisioning adults, the response may be that chicks gain less body mass. Nestling body mass is a good indicator of a bird's overall fitness (Cresswell, 2009), and is typically linked to juvenile survival and adult mass (Mumme et al., 2015). Evidence of this link has been shown in southern pied babblers, where provisioning rates decreased when air temperature exceeded 35.5^{0}C and nestlings which were raised above this threshold had a lower body mass than those raised under cooler temperatures (Wiley and Ridley, 2016). Additionally, when the frequency of days over 35^{0}C increased, a similar pattern was found in common fiscal nestlings, which acquired a lower body mass and shorter tarsus length compared to nestlings raised during periods with fewer days over 35^{0}C (Cunningham et al., 2013). It is important to note, that the decrease in common fiscal nestling mass on hotter days could not be entirely attributed to a decreased rate of provisioning alone, but was also likely to partly result from additional energy expenditure and increased rates of water loss by nestlings on days over 35^{0}C (Cunningham et al., 2013). Nevertheless, parental provisioning is a key factor in offspring growth and evidence suggests provisioning declines with increasing temperatures (Wiley and Ridley 2016). What remains unclear is whether this results from a decrease in parental foraging investment/success, and/or from parents eating a greater proportion of foraged food, in order to meet the physiological costs of foraging at higher temperatures.

Rationale for my study:

Numerous studies have shown that foraging, provisioning, and nestling growth rates in arid zone birds decrease when temperatures exceed 35^{0}C (Cunningham et al., 2013; Du Plessis et al., 2012; Wiley and Ridley 2016). The mechanism behind reduced nestling growth rates under high temperatures is believed to be partially linked to decreased provisioning rates from adults (Cunningham et al., 2013). However, why provisioning rates decrease above 35^{0}C and how willingness to forage changes with temperature remains unknown. Research by Du Plessis et al. (2012) suggests that there may be thermoregulatory tradeoffs; for example if birds spend greater time panting or wing drooping under high temperatures to maintain a stable body temperature, this could affect their foraging efficiency and effort. This may cause parents to consume a greater proportion of food themselves and curtail investment in foraging, reducing the total amount of food available to provision.

Alternatively, provisioning patterns may solely result from decreased food availability at higher temperatures.

In this study, I will investigate the potential impacts of high temperatures associated with climate change on the foraging behaviour and reproduction of Fork-tailed Drongos, *Dicrurus adsimilis,* in the Kalahari Desert of South Africa. Since the 1960s, there has been a significant increase in the number of hot days > 35^0C, in the Kalahari Desert (Kruger and Shongwe, 2004). More specifically, the Kalahari Desert has experienced the strongest warming trend within South Africa (Kruger and Sekele, 2013). Furthermore, climate models predict an increase in the mean annual temperature of the region by up to 4^0C within the 21st century (Moise and Hudson, 2008). With such predictions, it is essential to identify how increasing temperatures may affect avian inhabitants of the Kalahari Desert. Therefore, I performed two supplemental feeding experiments to identify how willingness to forage and provisioning rates of drongos change under varying temperatures at constant food availability, and how temperature affects nestling growth rates and fledgling size.

Experiment one focuses on how temperature affects willingness to forage (costs of foraging). By experimentally providing mealworms at a constant rate to non-provisioning drongos (i.e. drongos without nestlings to feed), we can identify whether the likelihood that drongos fly to capture a mealworm changes with temperature. Additionally, by recording heat dissipation behaviours, we can identify the physiological costs of foraging in terms of evaporative water loss (EWL) rates via panting.

Experiment two will look at the effects of temperature on provisioning rates. By providing mealworms to breeding drongos, food availability will be held constant during the experiment and we can identify whether adults alter the amount of prey they capture, the proportion they consume themselves versus provision to the nest and thus their provisioning rates, under varying temperatures. This will provide insight into the thermoregulatory tradeoffs drongos may make as temperatures increase. Under higher temperatures drongos may choose to consume prey for themselves, obtaining that energy and water and maintaining a minimum rate of EWL. Alternatively, drongos may provision, forfeiting the prey item and the energy and water expended when flying to the nest, which could lead to an unsustainable rate of EWL. Additionally, if drongos decrease provisioning rates under increasing temperatures then I will identify the temperature threshold where this trend begins.

My final aim is to assess whether temperature has an effect on nestling growth rates and fledgling size (mass and tarsus length), which has been shown in several other species (Cunningham et al., 2013; Rodríguez and Bustamante, 2003; Wiley and Ridley 2016) but remains unknown for drongos. Specifically, I seek to identify temperature thresholds that may cause a reduction in nestling growth rates. Additionally, if high temperatures do have an effect on nestling and fledgling growth rates then I will identify whether the average temperature during the nesting period or the number of days over 35^{0}C have a greater impact.

Methods:

Ethics

All field methods used in this study, including experiments and chick handling techniques, were approved by the University of Cape Town Animal Ethics Committee (2016/v16/TF). Access to the Kuruman River Reserve was kindly provided by the Kalahari Research Trust.

Study Site

From September 23rd to December 9th 2016, fieldwork was conducted at the Kuruman River Reserve (KRR), a 3500 ha area situated 17 km south of the South Africa/Botswana border and 30 km west of the small settlement of Van Zylsrus in the Northern Cape (26^{0}58’S, 21^{0}49’E). Located in the southern Kalahari Desert the KRR consists primarily of sparsely vegetated duneveld composed of Camelthorn (*Acacia erioloba*) and semi-arid grasslands (for a more detailed description of the KRR habitats see Ridley and Thompson, 2011).

Temperature and rainfall

All temperature and rainfall data was collected using an onsite weather station (Vantage Pro2, Davis Instruments, Hayward, California, USA), logging at ten-minute increments. From the data, accumulated daily maximum air temperatures and rainfall were calculated for the duration of this study. From October 5th to December 5th, 2016 the highest recorded temperature was 42.4^{0}C. However, daily maximum temperatures at the KRR have been recorded as high as 45.4^{0}C (Steenkamp et al. 2008) with average summer temperatures of 34.7^{0}C (Steenkamp et al. 2008). Annually, the KRR region receives 197 mm of rainfall (Kong et al. 2015). However, during the study period only 11 mm of rain fell over four separate days.

Study species

The Fork-tailed Drongo, *Dicrurus adsimilis,* hereafter ‘drongo’, is an insectivorous passerine in the Dicruridae family. Drongo body mass ranges from 38-55g and they are typically 23-26cm in length (Sinclair et al., 2014). Drongos are a common species in southern Africa, found in a wide variety of habitats, from arid grasslands to woodlands. They principally hawk invertebrate prey from a perch, but also glean invertebrate and small vertebrate prey from the ground or kleptoparasitise prey from other species (Flower et al., 2013). Drongos live in territorial pairs throughout the year and are capable of having multiple broods per breeding season (Hockey et al., 2005; T. Flower *pers. obs.*). All individuals observed in this study were identifiable by unique color ring combinations and were well habituated to the presence of humans within five meters (Flower and Gribble, 2012). Additionally, all adult drongos used in this study are trained to come to a human call, in response to which they receive a mealworm. The gender of individual drongos was known from genetic testing (undertaken by T. Flower), or by both examination of the vent feathers, where white tips indicate female sex (22 individuals sexed through vent feathers and behaviour were all subsequently found to have been correctly sexed following genetic sexing), and through observations of nest building which is undertaken by females alone. A total of 27 adults (n = 10 males and 17 females) were used in two experiments to identify how temperature affects drongos' willingness to forage and the rate at which adults provision their chicks. Within each experiment both sexes were sampled and all birds were adults >2 years old, while the oldest individual was at least 10 years old. Moreover, data was collected from 49 nestlings to understand the link between maximum daily temperature and chick growth rates/fledgling size.

Nesting status

The nesting status of all experimental birds was determined by visual observation. This consisted of a maximum one hour focal where the drongo pair was observed via binoculars from over 60 meters away, to identify if the female was nest building or to see if one member of the pair would return to an active nest. Following the discovery of a nest, I used a collapsible flag pole which could extend up to 10 meters in length, with a video camera (HTC Wildfire phone) attached to the top of the pole so that it could be extended above the nest and record whether the nest was active, i.e. eggs or chicks present, or inactive, i.e. empty. All inactive but completed nests were checked every three days to ensure an accurate laying date was recorded. All active incubating nests were checked at three-five day intervals from the time the first egg was laid, and daily after day 15 to ensure an accurate hatching date was recorded. After the first egg hatched, the nest was checked on alternate days to identify if brood size changed or if the nest was depredated. Additionally, all non-breeding birds' territories were checked on a weekly basis to identify when nest building began. Experimental birds were assigned to one of three nesting states. They were considered to be non-breeding/building, laying/incubating or feeding (i.e. feeding nestlings). Individuals that were considered non-breeding and or nest building were grouped together, as nest building may start in multiple locations and continue over extended periods of time before egg-laying is initiated. Thus non-breeding/nest building was identified if the experimental bird was found carrying nesting material, visiting a partially built nest within their territory, or not undertaking any breeding activities. An individual was considered to be laying after a single egg was found in the nest and continued 24 hours past when the third egg was laid, to ensure the clutch was complete. After the final egg was laid and or an adult was observed incubating the eggs, the incubation state began. For analysis purposes, due to short period of time from the first egg being laid to incubation and a relatively small sample size, laying and incubation were combined. Following the incubation period and after hatching had been confirmed, and or provisioning was observed, the nest state was changed to feeding. All experimental birds were considered to be non-provisioning adults until the first chick hatched.

Experiment one: Willingness to forage

Experiment one was designed to test how temperature affects a bird's willingness to forage (cost of foraging) and heat dissipation behaviour. Experimental trials were undertaken between the hours of 13:00 and 15:30. In total, 27 non-provisioning adult drongos, 17 females and 10 males, were sampled a minimum of three separate times across a variety of temperatures. To begin an experimental trial, non-provisioning adult drongos were first approached without reward (mealworms) and a 10-minute control observational focal was performed to record a baseline of natural behaviours under current temperature conditions. Immediately after the control focal was completed, a 10 minute feeding focal (experimental focal) was performed. During the feeding focal a single mealworm was flicked eight to 10 meters from and perpendicular to the focal drongo's chosen perch, starting the experiment. This was repeated every 60 seconds for a total experimental duration of 10 minutes. During both control and feeding focals, the duration (seconds) of any heat dissipation behaviour was recorded as: (i) none, (ii) wing drooping, where wings are held away from the body; (iii) panting, where the beak is held open for > 1 second; and or (iv) both panting and wing drooping. The location of the bird was recorded as on the ground or perched (any form of vegetation higher than 10 cm). Additionally, the number of foraging attempts was recorded and categorized as: in response to provisioned mealworms or natural prey; successful in the air, or on the ground; unsuccessful; and, whether any foraging attempt was made in response to an offered mealworm.

Experiment two: provisioning rate

Experiment two was designed to identify how parental care changes with temperature, by investigating if provisioning rates differ at higher temperatures. Experimental trials were undertaken between the hours of 15:00 and 17:00. In total, 17 provisioning adult drongos, 12 males and five females, were sampled. Each individual was sampled a minimum of three separate times during the chick provisioning period with resulting variation in the temperature during experimental trials. Provisioning trials were initiated by approaching the nest of a drongo pair with chicks whereupon the focal drongo either approached, or was called to, a perch on the shaded side of a tree 60-80 meters away from the nest. A single mealworm was then flicked within two meters directly perpendicular to the drongo and whether the worm was consumed by the drongo; provisioned to its chicks; or ignored was recorded. After one minute had passed and the drongo returned from its provisioning flight, or remained on its selected perch, another mealworm was flicked. This was repeated until a total of 20 mealworms were presented. However, trials were stopped if the drongo did not return from the nest within three minutes of worm presentation, or otherwise moved away. Trials were performed on as many consecutive days as possible starting two days after the last chick in a brood hatched and ending at day eleven. Any gaps in this data set were due to predation events or the result of morning and evening chick mass being collected on that day (see later), when trials were not undertaken.

Chick mass and tarsus

Mass (Ecotone digital scale) and tarsus length (Vernier Caliper [same set throughout]) were both collected within the first hour of sunrise and the last hour before sunset, on days 3, 6, 9, and 12. Day one began 24 hours after the first chick in the brood hatched; due to observed asynchronized hatching of one to two days between nestlings in the same brood, all mass and tarsus measurements were grouped into four categories. Day 3 mass and tarsus measurements range from actual nestling age 2-4; day 6 from 5-7; day 9 from 8-10; and, day 12 from 11-13. To ensure accurate data was collected for broods of more than one chick, nail polish was applied to the toes of nestlings, each nestling within a single brood received only one of three shades of nail polish (blue, purple, cream) to mark and distinguish it from other nestlings in the brood. Measurements were taken until day 12 (from 13 nests of 26 individuals) unless the nest failed by predation, abandonment or for unknown reasons (total 49 chicks from 23 nests by 23 drongo pairs). The title of pre-fledgling was given to chicks that were 12 days old as drongo nestlings typically fledge around day 14. Broods where a parent was undergoing provisioning experiments, which could provide supplementary food to chicks, were noted and identified within our analysis.

Statistical analysis

All data were analysed in the R statistical environment (R Core Team 2016). The package lme4 version 1.1-12 (Bates et al., 2015) was used for mixed-effects modeling; model selection and averaging were carried out using MuMIn version 1.15.6 (Barton, 2016) to compare models. Proportion data (experiment one and two) were modeled using generalised linear mixed models (GLMMs) with binomial error distribution and a logit link function. Therefore, no units were presented for average models, because effect size estimates are not back transformed. Nestling growth data were normally distributed and modeled using linear mixed models (LMMs) with Gaussian error distribution and an identity link function. All global models (see below) with a binomial or Poisson distribution were checked for overdispersion by comparing the residual deviance to the residual degrees of freedom. If a model was overdispersed an observation level random effect, where each observation is assigned a unique code, was used to reduce any bias in parameter estimates or standard errors (Hilbe, 2011; Harrison, 2014). Finally, residuals were checked for normality, and visual checks for heteroscedasticity, using the mcp.fnc function in the LMERConvenience package, version 2.10 (Tremblay, 2015).

Global models were created for both GLMMs and LMMs and were fitted with all measured variables and their interactions. For every model individual ID and or nest identity were included as random terms to control for pseudo-replication. I used the dredge function in R package MuMin (Barton, 2016) to model all possible nested models (i.e., models containing all possible subsets of variables) within the global model. Top model sets were defined as all models per analysis that were within 2 AICc points of the top-ranked model (defined as the model with the lowest AICc value). Parameter estimates and the significance of each independent variable (z-value) were determined using these top model sets. When there was more than one competing model in a top model set, significance of each independent variable was reported from the full average of the model-averaged coefficients. In the case when only one top model (AICc < 2) was found, the summary of this model was used to identify the significance of each independent variable. Estimates for which 95% confidence intervals did not cross zero were considered significant. The model was run with a Binomial error structure and logit-link function. Effect size estimates are not backtransformed, therefore no units are presented.

How does temperature affect heat dissipation behaviour:

To identify how temperature affected heat dissipation behaviour, I ran a binomial GLMM, with the proportion of total focal time that an individual spent panting during a control or feeding focal period as the dependent variable (coded as a combined vector of time spent panting/time spent not panting using the 'cbind' function in R; 113 trials on 28 birds). An observation level random effect was added to control for overdispersion and explanatory terms in the global model included the average temperature over the entire observation period (temperature), focal period (control or feeding), and the interaction between temperature and focal period. Additionally, the proportion of time an individual spent wing drooping, or panting and wingdrooping during focals was analysed using the same method as above.

How does temperature affect foraging behaviour:

To determine whether temperature affected natural foraging, I ran a Poisson GLMM, with the number of natural foraging attempts recorded during control focals (115 control focals on 28 birds) and experiments (113 feeding focals on 28 birds) as the dependent variables. A single model was run which included both focal periods. Temperature was the only explanatory term and the interaction between focal periods and other variables were not used as this prevented the model from converging. To determine whether temperature affected non-provisioning adults' willingness to forage (or refusal to fly for prey) I ran a binomial GLMM with the proportion of offered worms for which an individual made a foraging attempt during the feeding focal (modeled as combined vector of the number of times the bird did not fly for the worm/flew for the worm; 113 trials on 28 birds) as the dependent variable. Temperature was included as an explanatory term.

How does temperature affect provisioning:

To identify whether high temperatures reduced parental provisioning behaviour I ran a binomial generalized linear mixed model (GLMM) on the proportion of worms provisioned by an adult to its nestlings during a feeding experiment (modeled as combined vector of the number of worms the bird provisioned to the nest/did not provision; 67 trials on 27 birds). The total number of worms provided to an adult during each trial ranged from one to twenty, with all 20 worms provided in 50/67 trials. In the other 17 trials, birds did not return from the nest within three minutes or otherwise moved away before the trial was complete. The experimental bird's identity was included as a random term. Explanatory terms included: sex (of experimental adult), chick age (number of days since hatching), brood size (number of chicks in each nest), average temperature (mean temperature during each trial), and all 2-way variable interactions. Additionally, the proportion of worms ignored (proportion refused) and the proportion of worms consumed was analysed using the same method as above.

How does temperature affect nestling mass, growth rates, and tarsus length:

To determine the effects of temperature on nestling growth I ran LMMs on (i) daily body mass and (ii) daily tarsus length change as a proportion of morning body mass and tarsus length respectively (113 experiments from 28 nestlings). Chick identity was included as a random term in global and subsequent models. Explanatory terms were daily maximum temperature, chick age, brood size, whether the parents of the chick measured were part of a provisioning experiment (provisioned, not provisioned) and all 2-way variable interactions.

To determine the effects of temperature on pre-fledging size I ran an LMM on chick mass and tarsus length of 12 day-old chicks (morning measures for 26 near-fledge nestlings). Explanatory terms in three separate models were (i) the average temperature over the entire nestling period (first 12 days), (ii) the number of days over 35^{0}C and (iii) number of days over 40^{0}C during the nestling period.

Results:

During the study period, between October 5th and December 5th 2016, a total of 27 adults took part in 115 control and 113 feeding focals as part of experiment one; 17 adults took part in 67 trials as part of experiment two, and body mass and tarsus length data were collected from 49 chicks from 23 broods. All stages of breeding were observed, from nest building to adults provisioning fledglings, and over 100 nests were recorded. Daily maximum temperatures ranged from 22.2 to 42.4^{0}C (Figure 1) and temperatures trended upward overall during the study period consistent with progression towards the summer solstice. A total of 11 mm of rain fell over four separate days, two of which were consecutive (October 22nd & 23rd). Additionally, wingdrooping and or panting were not recorded below 27^{0}C during any control or feeding focal.

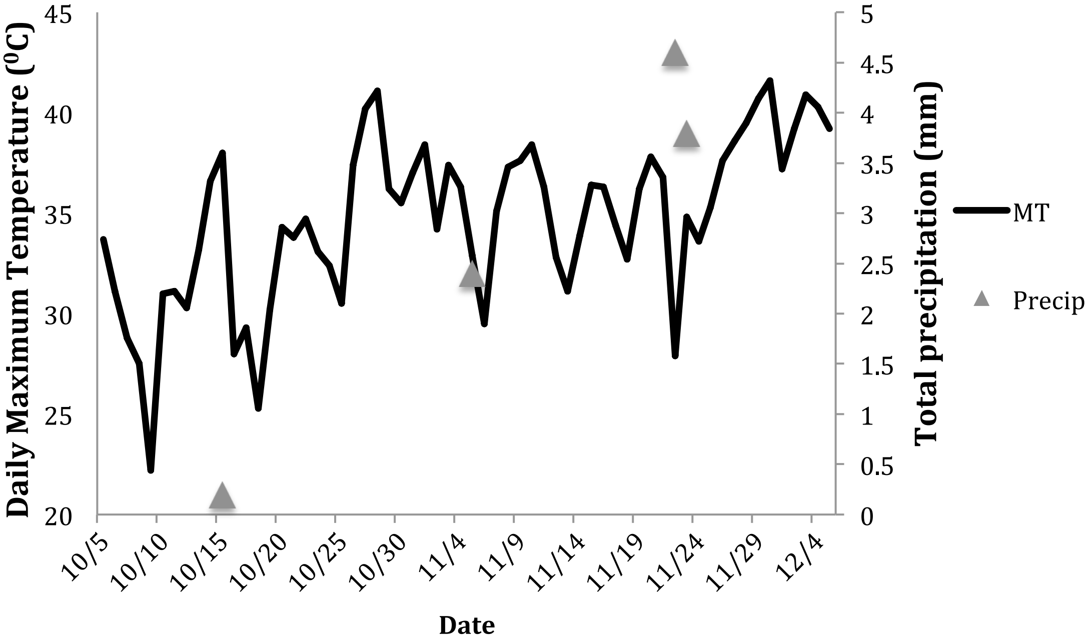

Figure 1: Daily maximum temperature (^{0}C, solid black line, MT) and daily rainfall totals (mm, solid triangles, Precip) for the Kuruman River Reserve from October 5th – December 5th, 2016.

Experiment one: temperature and its effects on heat dissipation behaviour.

Two competing models strongly suggest that panting increases with temperature (averaged model estimate = 0.94 ± 0.12, 95% confidence interval [0.70, 1.18], z-value = 7.65); (Table 1 and Table 2). Additionally, the second model, which included the interaction between temperature and focal period, showed a non-significant trend of higher rates of panting during feeding focals compared to control focals at higher temperatures (Table 2, Figure 2a).

Similarly analyses of wingdrooping (single top model) showed that average temperature had a significant effect on wingdrooping (averaged model estimate = 1.30 ± 0.11, 95% confidence interval [1.09, 1.52], z-value = 11.96); (Table 2). Specifically, as average temperature during control and feeding focals increased, the proportion of time spent wingdrooping increased. Additionally, individuals spent more time wingdrooping in feeding focals than controls (averaged model estimate = 14.66 ± 4.60, 95% confidence interval [5.49, 23.73], z-value = 3.19); (Table 2). In addition, there was a significant interaction between type of focal (control or feeding) and temperature, such that, compared to control focals, individuals spent a greater proportion of time wingdrooping during feeding focals at lower temperatures, yet wingdrooping increased more rapidly during control focals at higher temperatures (averaged model estimate = -0.44 ± 0.13, 95% confidence interval [-0.71, -0.17], z-value = -3.29); (Table 2); (Figure 2b).

Finally, investigation of wingdrooping combined with panting (single top model) showed that average temperature had a significant effect on wingdrooping combined with panting (averaged model estimate = 1.16 ± 0.17, 95% confidence interval [0.86, 1.53], z-value = 6.75); (Table 2). As temperatures increased the proportion of time spent wingdrooping combined with panting also increased (Figure 2c). Additionally there was a non-significant trend suggesting wingdrooping combined with panting was higher during feeding focals compared to control focals.

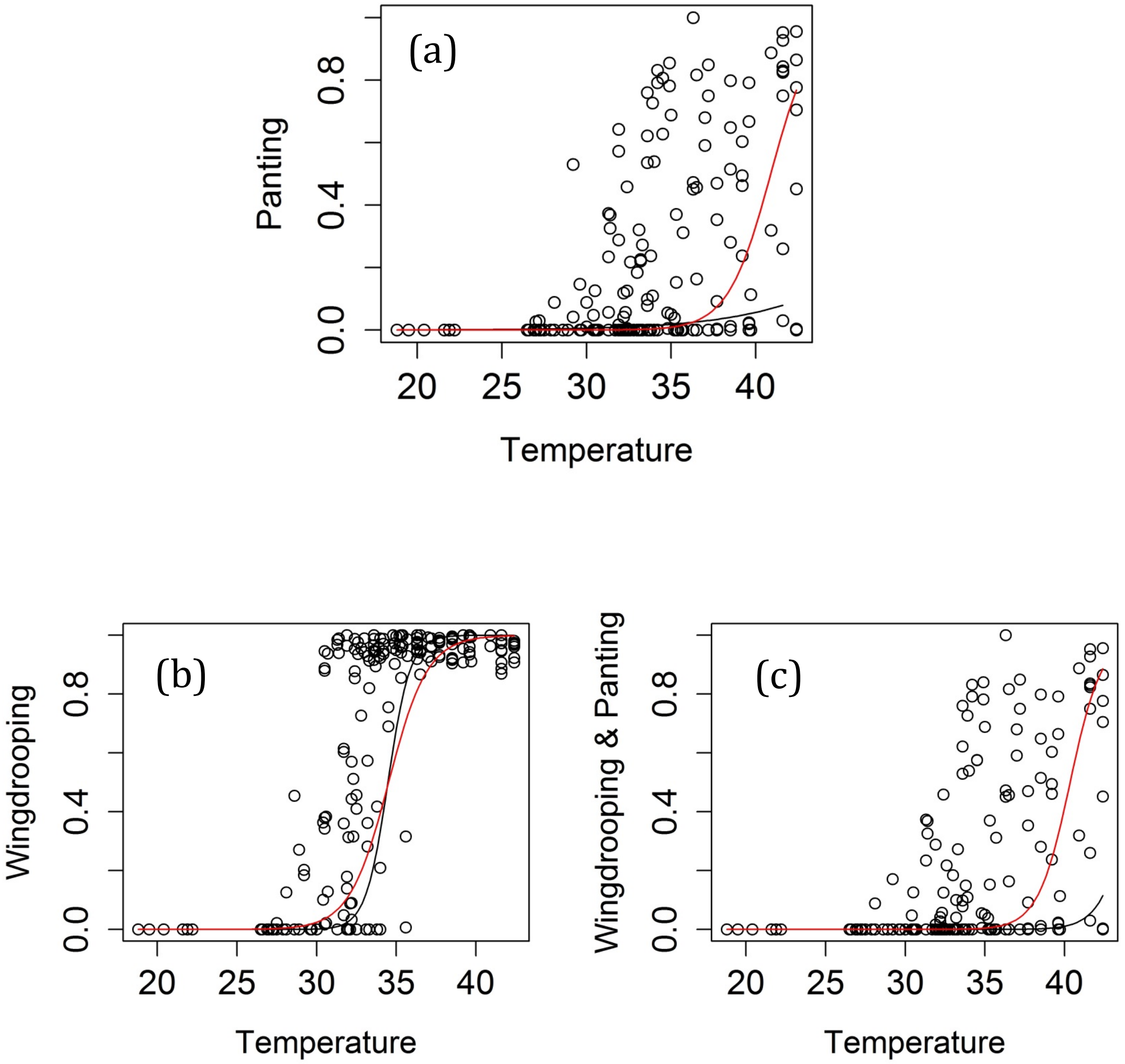

Figure 2. The proportion of time Fork-tailed Drongos spent displaying heat dissipation (HD) behaviour (panting, wingdrooping, or wingdrooping combined with panting) during control and feeding focals as a function of the average temperature (^{0}C) during the observation. Open circles represents individuals displaying HD behaviour during feeding (solid red line) or control focals (solid black line). Lines of best fit show predictions from a binomial GLMM. The proportion of time individuals spent (a) panting and (b) Wingdrooping combined with panting were positively affected by temperature. (c) During feeding focals , (when they foraged for provisioned food) individuals spent a greater proportion of time wingdrooping at lower temperatures than in control focals, but the rate of increase in wingdrooping was greater during control focals at higher temperatures.

Table 1: Competing global models for the proportion of time individuals spent panting.

Model	df	logLik	AICc	ΔAIC	Weight
Panting					
C.or.E + Exp.Temp.	5	-767.83	1545.9	0.00	0.71
C.or.E + Temp + C.or.E*Exp.Temp.	6	-767.68	1547.7	1.82	0.29

*C.or.E represents whether the individual was panting during a control focal (C) or experiment (E), Exp.Temp. = Average temperature during the experiment.

Table 2: Full model averages of the generalized linear mixed models identifying the significance of each variable against the proportion of time individuals spent displaying heat dissipation behaviour.

Variable	Estimate	95% Confidence Interval	Standard Error	z-value
Panting (Averaged estimates from two competing models)				
C.or.F	3.19	-4.33, 10.71	3.82	0.83
Temperature	0.94	-0.70, -1.18**	0.12	7.65
C.or.F*Temperature	-0.03	-0.47, 0.26	0.11	0.26
Wingdrooping (Only one top model)				
C.or.F	14.66	5.49, 23.73**	4.60	3.19
Temperature	1.30	1.09, 1.52**	0.11	11.96
C.or.F*Temperature	-0.44	-0.71, -0.17**	0.13	-3.29
Wingdrooping and Panting (Only one top model)				
C.or.F	4.29	-9.79, 18.73	7.28	0.59
Temperature	1.16	0.86, 1.53**	0.17	6.75
C.or.F*Temperature	-0.06	-0.47, 0.34	0.21	0.76

* C.or.F represents whether the individual was panting during a control focal (C) or feeding focal (F), Temperature =Average temperature during the observational period.

Experiment one: effects of high temperatures on willingness to forage

The average temperature during control and feeding focals (single top model) had a significant effect on the number of natural foraging attempts (averaged model estimate = -0.13 ± 0.01, 95% confidence interval [-0.15, -0.11], z-value = -11.82); (Table 3). Additionally, the number of natural foraging attempts was significantly different between control and feeding focals attempts (averaged model estimate = -1.11 ± 0.12, 95% confidence interval [-1.35, -0.87], z-value = -9.03); (Table 3). Compared to control focals, individuals were less likely to make natural foraging attempts during feeding focals (Figure 3a).

There was only one top model for the analysis of willingness to forage for offered mealworms during feeding trials. This model showed that average temperature had a significant effect on the proportion of worms refused (not flown for) during feeding trials (averaged model estimate = 0.48 ± 0.05, 95% confidence interval [0.38, 0.58], z-value = 9.28); (Table 3). As temperature increased so did the proportion of worms refused (Figure 3b).

Table 3: Full model averages of the generalized linear mixed models identifying the significance of each variable against the number of natural foraging attempts made during control and feeding focals, and the proportion of worms refused during feeding focals.

Variable	Estimate	95% Confidence Interval	Standard Error	z-value
Natural foraging attempts (Only one top model)				
C.or.F	-1.11	-1.35, -0.87**	0.12	-9.03
Temperature	-0.13	-0.15, -0.11**	0.01	-11.82
Worms refused (Only one top model)				
Temperature	0.48	0.38, 0.58**	0.05	9.28

*C.or.F represents whether the individual was foraging during a control focal (C) or feeding focal (F), Temperature =Average temperature during the observational or trial period.

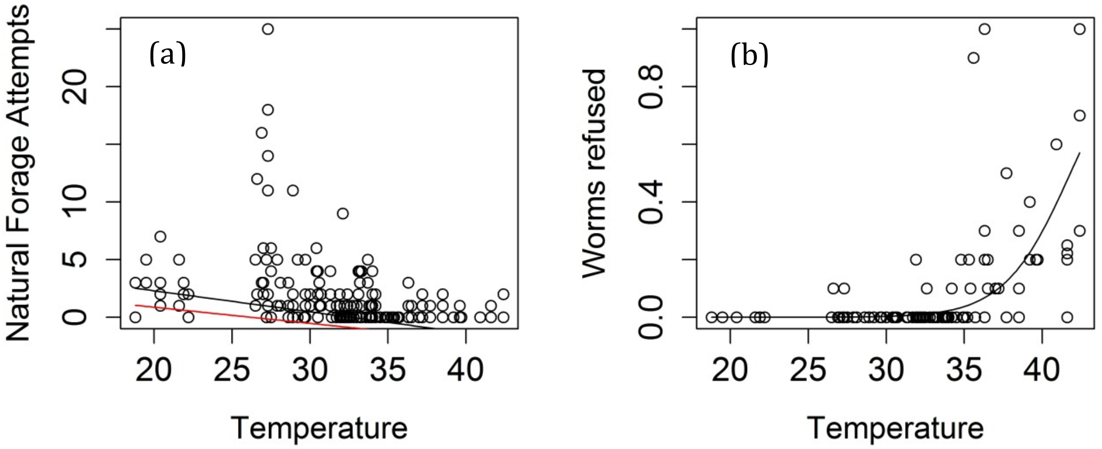

Figure 3. The number of natural forage attempts during control and feeding focals and proportion of worms refused (not flown for) during feeding focals by Fork-tailed Drongos as a function of the average temperature (^{0}C) during the observation. (a) At higher temperatures drongos decrease the number of natural foraging attempts during focals, and overall made fewer attempts in feeding focals (when they also foraged for provisioned food) than controls. Open circles represent individuals foraging during feeding (solid red line) or control focals (solid black line). Lines of best fit show predictions from a binomial GLMM. (b) The proportion of provisioned worms refused by Fork-tailed Drongos during feeding focals increased as the average temperature (^{0}C) during the focal increased. Open circles represents proportion of provisioned worms individuals refusing to fly for during experiments (solid black line). The line of best fit shows predictions from a binomial GLMM.

Experiment two: effects of high temperatures on provisioning

Three competing models showed that the average temperature during experimental trials had a significant negative effect on the proportion of worms parent drongos provisioned to nestlings (averaged model estimate = -0.11 ± 0.03, 95% confidence interval [-0.16, -0.15], z-value = 3.89); (Table 4 and Table 5). As temperatures increased, the proportion of worms provisioned to nestlings decreased (Figure 4a). Additionally, the age of chicks in the nest had a significant positive effect on the proportion of worms provisioned (Estimate = 0.09 ± 0.03, 95% Confidence Interval [0.01, 0.95], z-value = 3.38; Table 4 and Table 5). Furthermore, the two top models indicated that greater brood size increased the proportion of worms that were provisioned to the nest.

There were three competing models for the proportion of worms ignored during experiment two (i.e., worms which were offered to the drongo, but not flown for at all). All three competing models showed that the average temperature during experiments (Estimate = 0.26 ± 0.10, 95% Confidence Interval [0.04, 0.46], z-value = 2.41) and the age of chicks in the nest (Estimate = -0.50 ± Standard Error = 0.15, 95% Confidence Interval [-0.78, -0.21], z-value = 3.42) had a significant negative effect on the proportion of worms ignored (Table 4 and Table 5). As temperatures increased the proportion of worms ignored increased (Figure 4b).

Five competing models showed that the average temperature during experiments (Estimate = 0.09 ± 0.03, 95% Confidence Interval [0.04, 0.14], z-value = 3.44) had a significant positive effect on the proportion of worms consumed by the adult drongo (as opposed to provisioned to the nest or ignored, Table 4 and Table 5). As temperatures increased the proportion of worms consumed increased (Figure 4c). Although chick age was included in the top four models it did not have a significant effect on the proportion of worms consumed.

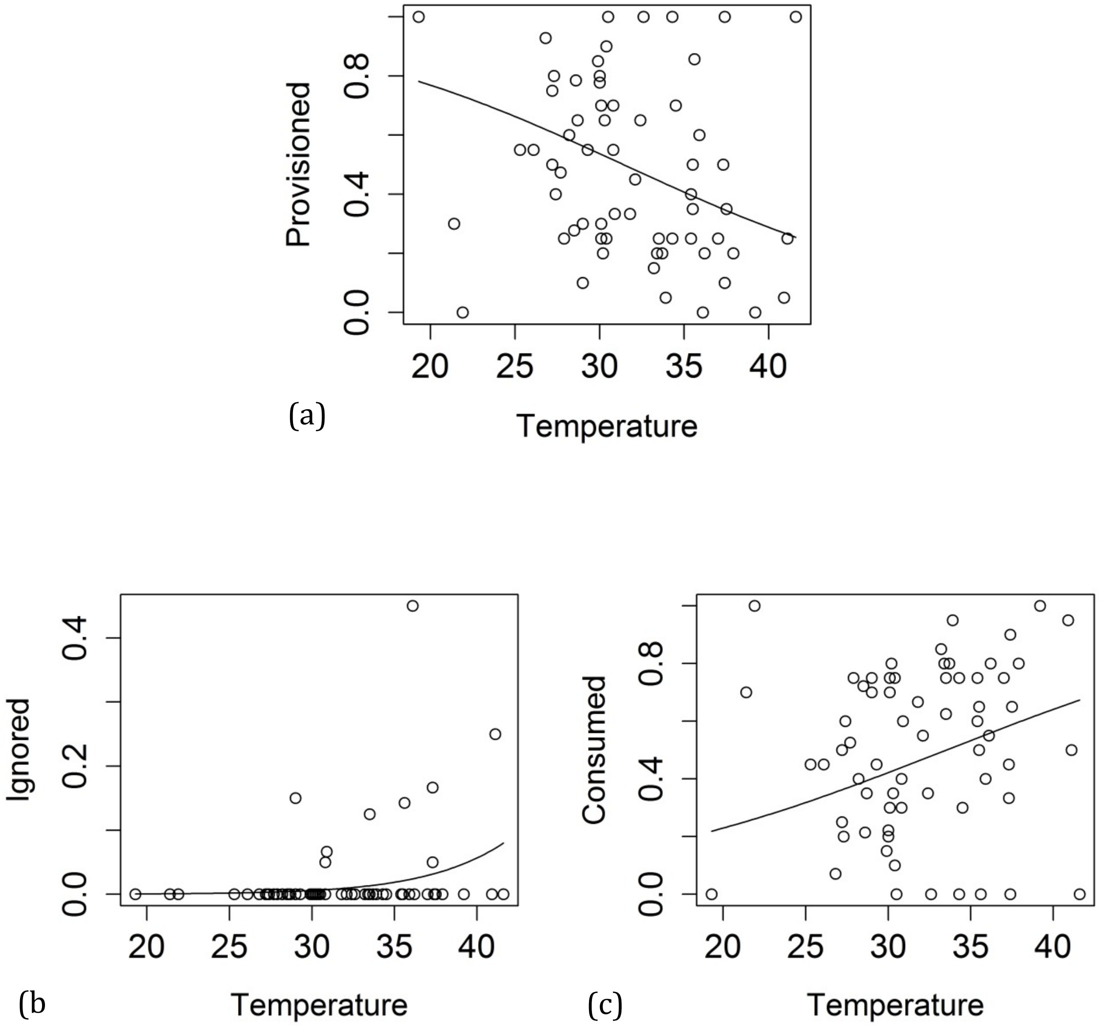

Figure 4: The proportion of worms (a) provisioned to the nest, (b) ignored, or (c) consumed by adult provisioning drongos during experimental trials as a function of the average temperature (^{0}C) during the trial. (a) At higher average temperatures drongos provisioned a lower proportion of the worms provided. As temperatures increased the proportion of worms ignored increased (b), yet so did the total number consumed by the adult (c). Open circles represents proportion of provisioned, ignored, or consumed worms during experiments. Lines of best fit show predictions from a binomial GLMM (solid black line).

Table 4: Competing global models for the proportion of mealworms (i.) provisioned to nestlings, (ii.) ignored, or (iii.) consumed by Fork-tailed Drongos. Note that average temperature during the time of the experiment was significant in all models.

Model	df	logLik	AICc	ΔAIC	Weight
(i.) Provisioned					
Temp + Chick age + Brood size	5	-211.23	433.5	0.00	0.34
Temp + Chick age + Brood size + S	6	-210.12	433.6	0.19	0.31
Temp + Chick age	4	-212.89	434.4	0.96	0.21
(ii.) Ignored					
Temp + Chick age	4	-42.63	95.9	0.00	0.38
Temp + Chick age + S	5	-42.90	96.8	0.88	0.25
Temp + Chick age + Brood size	5	-43.22	97.4	1.52	0.18
(iii.) Consumed					
Temp + Chick age	4	-212.83	434.3	0.00	0.26
Temp + Chick age + S	5	-211.99	435.0	0.66	0.19
Temp + Chick age + Brood size + S	6	-211.12	435.6	1.32	0.14
Temp + Chick age + Brood size	5	-212.34	435.7	1.35	0.13
Temp	3	-214.79	436.0	1.66	0.11

*Chick age = the age of chicks in the nest, determined by number of days since they hatched, Temp = Average temperature during experiment. S = Sex of the individual

Table 5: Full model averages of the generalized linear mixed models identifying the proportion of mealworms (i.) provisioned to nestlings, (ii.) ignored, or (iii.) consumed by Fork-tailed Drongos. Note that average temperature during the time of the experiment was significant in all models.

Variable	Estimate	95% Confidence Interval	Standard Error	z-value
(i.) Provisioned (Three competing models)				
Chick age	0.09	0.04, 0.14**	0.03	3.38
Temperature	-0.11	-0.16, -0.05**	0.03	3.89
Brood size	0.36	0.01, 0.95	0.29	1.23
Sex	-0.28	-1.82, 0.25	0.49	0.57
(ii.) Ignored (Three competing models)				
Chick age	-0.50	-0.78, -0.21**	0.15	3.42
Temperature	0.26	0.04, 0.46**	0.10	2.41
Brood size	-0.17	-3.06, 1.50	0.70	0.48
Sex	-0.34	-2.83, 0.63	0.62	0.27
(iii.) Consumed (Five competing models)				
Chick age	-0.04	-0.10, -0.00	0.03	1.50
Temperature	0.09	0.04, 0.14**	0.03	3.44
Brood size	-0.09	-0.79, 0.20	0.19	0.48
Sex	-0.32	-0.34, 2.01	0.55	0.59

*Chick age = the age of chicks in the nest, determined by number of days since they hatched, Temp = Average temperature during experiment.

How does temperature affect chick mass and tarsus growth:

There were three competing models (Table 6) for daily nestling mass change. Although not supported in the top model, maximum daily temperature was supported in the second two models, indicating a non-significant trend for mass gain to decrease with increasing temperature (Table 7). In addition, the interaction between temperature and whether a provisioning experiment was run, indicates a non-significant trend for mass gain to decrease with higher temperatures when chicks are not part of a provisioning experiment. Chick age was the only significant variable determining chick daily mass gain and was supported in all three models (Table 7). As chick age increased daily mass gain decreased (Figure 5).

Only one top model was selected for daily tarsus growth rate and included chick age, brood size, whether the chick's parent was a part of a provisioning experiment, and the interaction between provisioning experiment and brood size (Table 6). However, tarsus growth rates were not significantly affected by daily maximum temperature (Table 7).

Table 6: Competing global models for (i.) daily mass change and (ii.) daily tarsus growth by Fork-tailed Drongo nestlings.

Model	df	logLik	AICc	ΔAIC	Weight
(i.) Daily mass change					
BS + CA + BS*Prov	8	-376.62	770.7	0.00	0.46
BS + CA + Temp + BS*Prov	9	-375.88	771.6	0.89	0.29
BS + CA + Temp + BS*Prov + Temp*Prov	10	-374.81	771.9	1.18	0.25
(ii.) Daily tarsus growth					
BS + CA + Prov + BS*Prov	8	-356.992	731.4	0.00	0.44

*BS = brood size, CA = Chick age as the number of days since hatching, Temp = the daily maximum temperature, Prov = individuals who had parents that participated in the provisioning experiment and may have been provided supplementary food.

Table 7: Full model averages of linear mixed models identifying the significance of each variable against Fork-tailed Drongo chicks' daily mass change and tarsus growth rate. Note the only variable to have a significant effect on daily mass change and tarsus growth rate was chick age.

Variable	Estimate	95% Confidence Interval	Standard Error	z-value
Daily chick mass change (Three competing models)				
Brood size	3.47	-0.67, 7.61	2.09	1.64
Chick age**	-2.15	-2.66, -1.65**	0.25	8.43
Provision	21.24	-11.40, 53.88	16.54	1.28
Max temp.	-0.26	-0.72, 0.21	0.23	1.09
Brood size*Prov	-5.38	-13.99, 3.23	4.34	1.23
Max temp*Prov	-0.56	-1.29, 0.17	0.37	1.50
Daily tarsus growth rate (Only one top model)				
Brood size	1.63	-1.02, 4.28	1.43	1.15
Chick age**	-0.60	-0.98, -0.19**	0.20	-2.92
Prov	0.22	-3.68, 20.44	6.42	1.28
Brood size*Prov	3.28	-8.34, 1.73	2.71	-1.21

* Max temp=daily maximum temperature, Prov = individuals who had parents that participated in the provisioning experiment and may have been provided supplementary food

How does temperature affect pre-fledging mass and tarsus length:

Mass: Pre-fledging (near fledge) mass was not significantly affected by: (i) the average temperature during the nesting period, although this term was included in two of four competing models for this analysis, (ii) the number of days over 35 degrees during the nestling period, nor (iii) number days over 40 degrees during the nestling period, though the number of days over 40 degrees was included in three of five competing models for this analysis. Additionally, brood size and whether or not the parents of the fledgling were part of a provisioning experiment had no significant effect on fledgling mass although both variables were included in top model sets for all analyses (Table 8 and 9).

Table 8: Competing models for pre-fledgling mass of Fork-tailed Drongo nestlings as a function of: (i) average temperature, (ii) number of days with maximum temperatures over 35^{0}C and (iii) number of days over 40^{0}C during the nestling period (first 12 days from hatching).

Model	df	logLik	AICc	ΔAIC	Weight
(i.) Pre-fledgling mass~Average Temp.					
Provision	4	-74.91	159.7	0.00	0.27
Provision + Brood Size	5	-73.37	159.7	0.02	0.27
Provision + Brood Size + Average Temp.	6	-72.55	161.5	1.80	0.11
Provision + Average Temp.	5	-74.35	161.7	1.97	0.10
(ii.) *Pre-fledgling mass*~≥35^{0}C					
Provision	4	-74.91	159.7	0.00	0.28
Provision + Brood Size	5	-73.37	159.7	0.02	0.27
(iii.) Pre-fledgling mass~≥40^{0}C					
Provision + ≥40^{0}C	5	-73.27	159.5	0.00	0.20
Provision + ≥40^{0}C + Brood Size	6	-71.61	159.6	0.11	0.19
Provision	4	-74.91	159.7	0.19	0.18
Provision + Brood Size	5	-73.37	159.7	0.21	0.18
Brood Size + ≥40^{0}C	5	-74.25	161.5	1.97	0.07

*Average Temp. = The average temperature during the entire nesting state; ≥35^{0}C and ≥40^{0}C = the number of days with daily maximums over each temperature. Note that average temperature and number of days over 35^{0}C were not included in both top models. A total of 26 pre-fledglings were measured during the entire season.

Table 9: Full model average of the linear mixed model identifying the significance of each variable against Fork-tailed Drongo fledgling mass as a function of the average temperature, number of days ≥35^{0}C , and number of days ≥35^{0}C during the entire nesting state (12 days from hatching).

Variable	Estimate	95% Confidence Interval	Standard Error	z-value
Average (Four competing models)				
Average Temperature	-0.01	-1.77, 1.69	0.44	0.02
Brood size	-0.08	-4.46, 4.14	1.47	0.05
Provision	-3.19	-10.17, 3.80	3.36	0.90
Days ≥35^{0}C (Two competing models)				
Brood size	-0.07	-4.46, 4.14	1.33	0.05
Provision	-3.18	-10.17, 3.80	3.27	0.92
Days ≥40^{0}C (Five competing models)				
Brood Size	-0.29	-4.67, 3.61	1.48	0.18
Provision	-3.08	-10.36, 3.59	3.34	0.87
≥40^{0}C	-0.70	-4.70, 2.21	1.39	0.48

* Average Temperature = the average temperature during the entire nesting state.

Tarsus length: There was only one top model selected for fledgling tarsus length and this model included none of the fixed factors in the global modle (i.e. the top model was the null model). There were no significant effects on fledgling tarsus length from any of the measured variables (Table 10).

Table 10: Summary of the linear mixed model identifying the significance of each variable against Fork-tailed Drongo fledgling tarsus length.

Variable	Estimate	95% Confidence Interval	Standard Error	z-value
Brood size	0.01	-0.09, 0.11	0.06	0.84
Provision	0.05	-0.08, 0.20	0.09	0.57
Average	0.01	-0.08, 0.10	0.06	0.84
Days ≥35^{0}C	0.01	-0.06, 0.08	0.05	0.83
Days ≥40^{0}C	-0.01	-0.09, 0.08	0.05	0.87

* Average Temperature = the average temperature during the entire nesting state; Days ≥35^{0}C/≥40^{0}C = number of days ≥ 35^{0}C/≥40^{0}C during entire chick stage.

Discussion

My experiments showed that high temperatures led to a decrease in Fork-tailed Drongos' willingness to forage independent of food availability, and an increase in heat dissipation behaviours. This suggests that foraging is constrained during hot periods by the physiological costs of activity over and above any changes in availability of prey. Furthermore, as temperatures increased, birds with nestlings consumed a larger proportion of prey and consequently provisioned fewer items to the nest, highlighting that temperature may have an effect on parental care. As temperatures increased from 30 to 35^{0}C, adults reduced the percentage of items they provisioned from 55% down to 35% of total prey foraged. In contrast to studies on other species (Cunningham et al., 2013; du Plessis et al., 2012; Sadondo, 2014; Wiley and Ridley, 2016) and despite these large, strong effects of temperature on willingness to forage and willingness to provision foraged prey to offspring, I found only very weak evidence that maximum daily temperatures or the frequency of hot days during the nesting period affected the growth rate of nestlings or the size they attained prior to fledging.

Effects and costs of high temperatures on foraging:

My prediction that the thermoregulatory costs associated with activity would constrain foraging at high temperatures was supported by the results of this study. Experiment One showed that when prey availability is constant and temperatures increased, drongos were less willing to forage compared to cooler temperatures. The likely cause of this decrease in willingness to forage is the thermoregulatory costs that foraging requires at high temperatures (Carmi-Winkler et al, 1987), rather than food availability. Cost associated with foraging and thermoregulation at higher temperatures comes in the form of water loss via increased rates of heat dissipation behaviour, such as panting and or wingdrooping (Wolf, 2000). Specifically, panting comes at the direct cost of evaporative water loss by increasing the rate of airflow throughout the respiratory tract, which extracts internal moisture (Maclean, 1996; Dawson, 1982). Wingdrooping may also help promote trans-cutaneous water loss by increasing airflow under the wings (Wolf and

Walsberg, 1996). Put simply, if a bird spends a greater proportion of time displaying HD behaviour, it is losing water, and will need to compensate for this loss, by drinking more or increasing food intake to extract water from food sources (Cade et al., 1965). I observed that during control and feeding focals while the number of natural foraging attempts did not increase with temperature, the proportion of time spent exhibiting HD behaviour did increase. This suggests that temperature alone is sufficient to induce HD behaviour, even where activity does not increase. This is consistent with research on several other desert-dwelling birds (Du Plessis et al., 2012; Cunningham et al., 2013; Smit et al., 2013; Smit et al., 2016). Results additionally showed that HD behaviour was higher during feeding focals than during controls at higher temperatures, suggesting that more frequent foraging at higher temperatures does increase HD behaviour. The reason this trend was non-significant is likely due to a lower sample size of hot days and the fact that drongos were less willing to forage for presented prey at higher temperatures. Together these results suggest that the costs of heat dissipation in terms of EWL constrain foraging at higher temperatures. Additional constraints on foraging at higher temperatures may be the risk of reaching high body temperatures. An action such as flying to hawk prey or probing into the ground requires additional metabolic heat production, which could raise the body temperature above a sustainable level.

Effects of high temperatures on provisioning:

A decrease in provisioning rates at high temperatures has been shown in several desert-dwelling bird species (Austin 1976; Cunningham et al. 2013; Luck 2001; Ricklefs and Hainsworth 1968). The results from Experiment two showed that as temperatures increased breeding drongos provisioned less and consumed more prey items. Compared to non-provisioning birds, breeding individuals typically increase foraging effort by three to five times when caring for offspring (Walsberg 1983). This substantial increase in foraging effort may be more difficult to maintain on hotter days as foraging comes with a cost of energy and water loss, which may or may not be balanced by foraging intake. Additionally, it may not be an increase in costs alone that leads to decreased provisioning rates but also a reduction in foraging efficiency. As shown by du Plessis et al. (2012), foraging efficiency of southern pied babblers decreased as temperatures increased. Therefore, if breeding adults were to continue foraging in order to provision at higher temperatures, the energy and water required to do so may not be compensated by the prey items caught, which possibly will cause them to suffer greater thermoregulatory stress. Thus, to make up for this reduction in foraging payoffs, in addition to maintaining thermoregulation at higher temperatures, they may consume a greater proportion of prey items, e.g. mealworms in Experiment Two, and reduce the number of flights that need to be taken to the nest in order to provision. In support of this, as temperatures exceeded ~32.5^{0}C, experimental individuals with nestlings shifted their parental care by consuming the majority (> 50%) of prey items instead of provisioning them to their offspring. Although adult mass data was not collected in this study, breeding southern pied babblers were found to be less capable of maintaining body mass under higher temperatures compared to non-provisioning babblers, and this was likely the result of additional cost in energy and metabolic heat production resulting from provisioning effort (Wiley and Ridley 2016). Future research should include adult drongo body mass to see if temperature has a greater effect on breeding individuals, which have increased energy demands, compared to non-provisioning individuals, as shown in Wiley and Ridley (2016). Furthermore, a decrease in provisioning rates at higher temperatures could function to increase future reproductive success, as long lived birds, such as drongos, are less likely to risk their own mortality in favour of their current brood of offspring (Canestrari and Baglione 2007; Ghalambor and Martin 2000).

Effects of temperature on the growth rates and size of nestlings:

Despite the reduction in provisioning by adult drongos during hot periods, and the fact that temperatures reached 42.4^{0}C during the study period, surprisingly there appeared to be no significant effect of temperature on daily mass gain or tarsus growth in drongo chicks. These results contrast with the findings of Cunningham et al. (2013), which showed that temperature and adult provisioning rates affected common fiscal nestlings' body mass, with individuals raised during nestling periods within which maximum daily temperatures exceeded 35^{0}C weighing less than nestlings raised below 35^{0}C. In my study temperature was included in the competing models, but it had a non-significant negative effect on daily growth rates. Therefore, with a larger sample size of chicks and number of days above 35^{0}C, this negative trend may become significant. Additionally, neither the average temperature during the nestling period, nor the number of days >35^{0}C had any significant effect on pre-fledging size or tarsus length. This too is in contrast to other studies which have found that fledglings which experienced a greater frequency of days >33^{0}C during their nesting period had a reduced body mass (Cunningham et al., 2013; Rodríguez and Barba, 2016; Wada et al., 2015). Exactly how drongo nestlings continue to maintain a steady rate of mass gain and growth, during periods of high temperatures, is in need of further research.

There are several alternative hypotheses that may explain the apparent non-significant effect of temperature on nestling growth rates. Firstly, all competing models for pre-fledgling size and tarsus length included a variable describing whether the parents of the nest received supplemental food as part of the provisioning experiment (Experiment two). Although, this variable was non-significant it may be that the supplemental food available to parents of chicks taking part in Experiment two, may have buffered the impacts that temperature would normally have on nestling growth. Secondly, this study only measured the proportion of prey provisioned versus consumed by adults during the heat of the day. Therefore, it is possible that adults may be shifting their foraging patterns by increasing crepuscular or nocturnal foraging as a way to compensate for the loss of provisioning activity during periods of higher temperatures. Furthermore, unpublished data by T. Flower found that drongos may shade their nestlings at temperatures as low as 33^{0}C. As drongo nests tend to be on the outer branches of a tree where less shade is available, shading of nestlings at lower temperatures may mitigate the physiological impacts of direct sunlight on the chicks. Finally, due to high nest failure, a relatively small sample size of 26 individuals was collected for pre-fledgling mass and tarsus lengths, therefore a larger sample size could give a better representation of the link between temperature and growth.

Conclusion

The experimental results in this study identify that the physiological costs of foraging at higher temperatures are the likely cause of reductions in willingness to forage and offspring provisioning. When prey availability is held constant, at higher temperatures adults forage less and engage in more heat dissipation behavior, likely to reduce the risk of hyperthermia. Breeding drongos decrease provisioning rates to chicks, capture fewer available prey and increase their own consumption of captured prey under higher temperatures. Potentially, this too is to make up for a reduction in foraging payoffs or to increase future reproductive success, e.g. focusing on their own fitness, rather than on their chicks, so that they can reproduce again. However, there appeared to be no significant effect of temperature on offspring growth, suggesting that offspring do not suffer a cost from high temperatures, perhaps because parents compensate through behavioural shifts in foraging at cooler times of day.

Increases in maximum daily temperature may also raise a birds body temperature above a sustainable rate, increasing the probability of mortality.

By 2100, the mean annual temperature of the Kalahari Desert is predicted to increase by up to 4^0C (Moise and Hudson, 2008), while the frequency and intensity of heat waves is also expected to increase (IPCC 2012). This predicted increase in temperature is likely to have a significant impact on the thermoregulatory capabilities of its avian inhabitants. If higher temperatures cause a decrease in willingness to forage, then predicted increases in temperature may result in longer periods of time during which birds will not be actively foraging. These extended periods may come at a direct cost to adults, potentially being unable to maintain body mass, and chick provisioning, which could affect reproductive success and survival (Cunningham et al., 2013; du Plessis et al., 2012;Mumme et al., 2015; Ridley & Raihani, 2007; Ridley et al., 2008). This would likely have serious consequences at the population level, with decline likely in marginal environments and the proportion of a species range affected related to degree of climate change observed (Cunningham et al., 2013; du Plessis et al., 2012;Mumme et al., 2015; Ridley & Raihani, 2007; Ridley et al., 2008). A further understanding of the effects that temperature has on foraging, provisioning, and nestling growth rates is consequently essential to conservation as this will provide a realistic representation of how species may respond to a warmer world.

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