The influence of temperature on parental investment in Common Fiscal and consequences for nestling growth

PHENIAS SADONDO

DST-NRF Centre of Excellence
Percy FitzPatrick Institute
University of Cape Town
Rondebosch 7701
South Africa

Supervisors:

Dr Susan Cunningham

Dr Rowan Martin

Professor Peter Ryan

Submitted in partial fulfilment of Master of Science in Conservation Biology
by coursework and dissertation

Submitted: 17 February 2014

ABSTRACT

Global climate models project a 1.5-4°C increase in the Earth's temperature by 2100. Africa, especially southern Africa, is expected to experience not only an increase in average temperatures but also an increase in the frequency and duration of extreme temperature events. Increasing temperatures will result in increased vulnerability to heat and drought stress to biodiversity. A recent paper by Cunningham et al. (2013) showed that temperature has a negative effect on daily mass gain in the nestlings of Common Fiscal (*Lanius collaris*) breeding in the southern Kalahari. This effect may be driven by parents modifying their provisioning rates at high temperature, but the mechanisms underpinning the relationship are not known. I investigate the influence of temperature on parental investment in Common Fiscal and the consequences of high temperatures for nestling growth using data from videos that were filmed in the Kalahari, Northern Cape, South Africa. Daily mass gain by nestlings increased with increasing provisioning rate and decreased in relation to the proportion of time chicks spent panting. Prey provisioning decreased with temperature in larger broods, however, there was no evidence to suggest that parents trade off provisioning and nest attendance. This might mean that prey availability is reduced at high temperatures, or that parents prioritise their own thermoregulation over provisioning. However, sex-specific analysis of provisioning showed that adult female provisioning decreased with temperature for younger nestlings (six-day) and increased slightly for older nestlings (14-days old). On the other hand, male provisioning decreased with temperature for both young and old nestlings. Both male and female parents altered their parental care behaviour in response to temperature, and appeared to respond to one another's decisions when so doing. The influence of temperature on parental behaviours such as provisioning rate, and nestling physiological processes such as panting, had negative consequences for nestling growth. Panting is an energetic process which expends a lot of energy for thermoregulation at high temperature. Prey provisioning, which was supposed to cater for the additional energy requirements during panting, however decreased with temperature posing serious constraints on nestlings' daily mass gain and growth. Understanding the effect of temperature on species behaviour and physiological mechanisms will help us to understand the effects of climate on species' fitness and survival.

ACKNOWLEDGEMENTS

I am very grateful to the DST/NRF Centre of Excellence at Percy FitzPatrick Institute at the University of Cape Town for allowing me an opportunity to do this research under the Hot Birds Project. Many thanks to the Hot Birds Project Team, particularly Dr Susan Cunningham, for all the data used in this research.

Firstly, I would like to thank my supervisors; Dr Susan Cunningham, Dr Rowan Martin and Professor Peter Ryan for being there always (even on Skype) and being patient with me throughout the course of the project. To Dr Cunningham, thank you once again for bailing me out when my initial project failed to work, and for the backup data when my laptop and hard drive were stolen during the project period. Secondly, I would like to thank my parents and the Sadondo family for believing in me. I would also like to thank Dr Rob Little and Mrs Hilary Buchanan for all the encouraging and uplifting words, even a simple chat in the corridors was calming. To my girlfriend, Cleopatra Mupanda, thank you for being there. To CB 2013 class, thank you all for being an amazing family. Finally, I would like to thank God who is my source of strength.

Plagiarism declaration

1. I know that plagiarism is wrong. Plagiarism is to use another's work and pretend that it is one's own.

2. I have used the *Conservation Biology* Journal style for citation and referencing. Each contribution to, and quotation in, this assignment from the work(s) of other people has been attributed, and has been cited and referenced.

3. I acknowledge that copying someone else’s assignment or essay, or part of it, is wrong and that this assignment is my own work.

4. I have not allowed, and will not allow, anyone to copy my work with the intention of passing it off as his or her own work.

Signature…………………………………………………………..

Date…………………………………………………………………

Table of contents

INTRODUCTION

Climate Change and birds

Warming of the Earth's climate is now undisputed (Alexander 2006; Kruger and Sekele2012; IPCC 2006). The 20th century experienced about 0.6ºC increase in temperature (Christensen et al. 2007), the first decade of the 21st century was the warmest in recorded history (Hansen and Soto 2012), and an increase of about 0.2ºC per decade is projected by the IPCC for the next two decades (IPCC 2006). Global climate models project a 1.5-4ºC increase in the Earth's average temperature by 2100 (Solomon 2007; World Bank 2012).

Africa, and especially southern Africa, is expected to experience not only an increase in average temperatures but also in the frequency and duration of extreme temperature events (Christensen et al. 2007). In this region, the Kalahari is expected to experience the largest temperature increase (Moise and Hudson 2008). In South Africa it is predicted that biodiversity will be affected due to heat stress and habitat loss, especially in semi-arid regions of the Northern Cape and parts of the Western Cape (Christensen et al. 2007; Kruger and Sekele 2012; Kruger and Shongwe 2004). For this reason climate change poses an imminent risk to the birds of South Africa's semi-arid and arid zones.

Increasing temperatures will result in increased vulnerability to heat and drought stress which will likely lead to increased mortality and species extinction (Parmesan and Yohe 2003; World Bank 2012). Birds and other endotherms respond to increasing temperatures through behavioural, physiological and structural adjustments for thermoregulation (Calder and King 1974; Wolf 2000), with potential impacts on their fitness (Miller and Stillman 2012). For example, more water and energy expended on thermoregulation means that there is less to invest in raising offspring or maintaining a constant body condition (Dawson 1982). This trade off might also affect survivorship if thermoregulation is prioritised over flying away from approaching predators (Martin 1988; Valeix et al. 2008).

Effects of temperature on endotherms

Endothermic animals have the ability to self-regulate their internal temperature within a narrow range which is usually higher than the external environment (Scholander et al. 1954). In very hot conditions, however, when ambient temperatures approach or exceed body temperature, there is a threat of hyperthermia or overheating, which may induce mass mortalities (Finlayson 1932; Welbergen et al. 2008; Towie 2009; Towie 2010). Under these conditions, endotherms must make physiological and/or behavioural adjustments to increase heat loss and maintain a fairly constant internal temperature. Although facultative hyperthermia, allowing body temperature to increase, is another strategy that endotherms such as mammals can use, this scope is limited in birds which tend to have higher body temperature than mammals (McKechnie and Wolf 2010). Therefore heat loss is mainly achieved through evaporative cooling, e.g. panting, or by vasodilation which facilitates heat loss from the skin by convection and radiation, although this is only viable when ambient temperatures are less than body temperature (Terblanch et al. 2009; Calder and King 1974). Complementing the physiological adjustments are behavioural thermoregulatory mechanisms which include moving into the shade in order to reduce direct exposure from the sun, or postural changes to increase convective heat loss as long as ambient temperatures remain below body temperature (Wolf 2000).

Endotherms depend on an optimal threshold, or ‘critical tolerance limit’, and can survive only for a very short time if this critical tolerance limit is exceeded (Miller and Stillman 2012). In order to understand how different organisms respond differently to environmental changes like temperature, fitness or the lifetime reproductive success of the organism must ideally be measured (ditto). However, since it is difficult to measure fitness (Pianka 1976), performance indices such as growth rate, and respiration rates are therefore used to proxy fitness (Huey and Kingsolver 1989; Spicer and Gaston 1999; Pörtner et al. 2006; Angilletta 2009). Performance typically is maximised under a range of optimal temperatures (the "thermoneutral zone" or TNZ) and declines at temperatures outside of the TNZ (Miller and Stillman 2012). In endotherms, basal metabolism is minimal within the TNZ, increasing at temperatures above and below the TNZ as endotherms increase their metabolic rate to maintain a constant body temperature through physiological responses (e.g. shivering to warm, or sweating/panting to cool) (Hey 1975; Miller and Stillman 2012). Laboratory-based estimates of TNZ are not always observed in the field because free ranging animals can respond to increasing temperature through behavioural mechanisms like changing posture and moving away from direct heat exposure into shade with no increase in metabolic cost (Cossins and Bowler 1987; Crawshaw 1980). These behavioural thermoregulation mechanisms may, however, come with a cost to foraging and other behaviours. Hence energetic benefits are not always realised when regulating temperature behaviourally (Fernandez et al. 2002).

As global temperatures rise, organisms can either adapt or die (Williams et al. 2008; Hughes 2000). Hughes (2000) highlighted that climate change is already affecting many organisms' physiology, distribution and phenology. High temperatures can impact directly on survival and fitness of organisms as a result of physiological effects (Hoffman 2010). For example, the survival of desert dwelling banner-tailed kangaroo rats (*Dipodomys spectabilis*) is jeopardised by exposure to high temperatures (Moses et al. 2012).

In Australia, extreme heat waves are increasing in frequency, causing mass die-offs with recent occurrences in 2009, 2010 and 2012 being responsible for the death of thousands of birds (Towie 2009; Towie 2010; McKechnie et al. 2012). Such events are not confined to Australia only, with cases recorded in the American south-west, India and South Africa, albeit not on the same large scale (Miller 1963; McKechnie et al. 2012).

Implications of increasing temperature for birds' prey

Many terrestrial bird species are largely insectivorous (Stratford and Stouffer 1999), and most insects are ectothermic (Deutsch et al. 2008). Hence, they are likely to be affected differently by temperature because they cannot use the same physiological mechanisms for thermoregulation as endotherms (Liu et al. 1995). Ectotherms are organisms whose body temperature is determined by the environment, and thus there is a link between ambient temperature and their metabolic rate (Hertz et al. 1988). For this reason, extreme fluctuations in environmental temperatures can cause major stress or upset their internal regulatory systems (Deutsch et al. 2008). Ectotherms constitute the majority of terrestrial biodiversity (Wilson 1992), and are most likely to be adversely affected by climate change because their basic physiological functions such as locomotion, growth and reproduction strongly depend on the environmental temperature (Deutsch et al. 2008). For example, local population declines and extinctions of *Sclereporus* lizard in Mexico have been attributed to rising temperatures which result in the lizards spending much time in the shade rather than foraging during the breeding season, when female energy demands peak (Sinervo et al. 2010). Although insects can make behavioural alterations, similar to endotherms, to reduce direct heat exposure, reduction in prey availability for insectivorous birds means reduction in water intake, since they get most water from their prey (Willmer 1982).

Effects of temperature on offspring growth: the role of parental care

Extremely hot conditions have led to breeding failures in some birds (Bolger et al. 2005; Crick 2004). Although some studies have attributed these failures to phenological changes in the onset of breeding, (e.g. in great tits, *Parus major*, Visser et al. 2009), in other circumstances the mechanisms remain poorly understood (Dunn and Winkler 2010; Sutherland et al. 2004). Temperature affects birds not only by altering their metabolic rates but also through indirect effects on the birds' behaviour and that of their prey. This affects their ability to forage and the ability to carry out other essential behaviours, such as courtship (Crick 2004). Temperature can also affect breeding success through starvation of the offspring (Newton 1998). Therefore prolonged extreme weather can result in catastrophic effects on bird populations (Stenseth et al. 2002). Climate change is already causing changes in the phenology of some birds, especially in timing of migration and nesting (Robinson et al. 2009). As a result of these phenological miscues, some migratory birds respond inappropriately to changing conditions, while in others there is no response at all to climate change (Crick 2004). A study by Altewegg et al. (2012) found that, as a result of climate change, swallows are now leaving northern parts of South Africa eight days earlier than they did twenty years ago, and are shortening their stay in areas where they previously stayed longer.

In altricial birds, parents must expend considerable effort and energy on thermoregulation and prey provisioning for the chicks (Luck 2001). This might become increasingly difficult if a warming climate increases their own thermoregulatory costs while potentially also decreasing prey availability. The provision of parental care must be viewed in the context of life history trade-offs and sexual conflict over parental care (Székely and Cuthill 1999). In extremely hot and resource-poor environments, biparental provisioning and caring of the chicks might be required in order to meet thermoregulatory requirements and increase the chances of offspring survival (Rankin 2007; Luck 2001). Biparenting is not only for the benefit of the offspring but it also help the parents to cope with heat stress themselves whilst relieving each other (Al Rashidi et al. 2010). As such, biparental care might then be triggered by the local ambient temperature as in Kentish plovers (*Charadrius alexandrines*), with extreme heat accounting for an increase in incubation time for both parents (Vinzce et al. 2013).

Although in monogamous species parents cooperate to rear their offspring, there is also an element of conflict because the benefit of care is shared between the biological parents, but the cost of care is born by each individual parent (Rankin 2007). For example, in Kentish Plovers the female commonly deserts the brood after incubation, leaving the male to raise the offspring alone (Warriner et al. 1986; Székely and Williams 1995). This means some broods are raised by both parents whereas others are raised by the male parent alone, which has implications on parental ability to meet the nestlings' thermoregulatory demands (Szekely and Cuthill 1999). In nestlings which are burdened by reduced parental care and increased thermoregulatory costs at high temperatures, growth rate may be reduced (Michaud and Leonard 2000; May and Lott 2001). However, as temperatures rise, parental cooperation in raising the nestlings may be increased with parents balancing between provisioning and thermoregulation in order to improve nestlings' fitness and survival (Luck 2001). In some arid zone passerine species, rising temperatures have been noted to cause reduced provisioning rates to chicks (Goodbred and Holmes 1996; Cunningham et al. 2013; Ricklefs and Wikelski 2002; Monaghan 2008). On the other hand, nest attendance behaviour by parents can reduce the direct effects of temperature by shading and brooding the nestlings. But if they have to trade off provisioning with nest attendance, this may result in an increase in indirect effects on energy/water intake (Ford et al. 2001).

The frequency and intensity of heat waves are predicted to increase as a result of climate change (IPCC 2007). The effects of heat waves on biodiversity are therefore likely to increase too (Parmesan and Yohe 2003).While studying the effects of temperature on Common Fiscal (*Lanius collaris*) in the Kalahari, Cunningham et al. (2013) found that daily mass gain of nestlings decreases with temperature and there is evidence to suggest that this results, at least in part, from a reduction in provisioning rates by adults (Cunningham et al. 2013; Emms and Verbeek 1991; Hamer and Thompson 1997; James and Hamer 2000). What is striking is that once affected, nestlings do not recover from the negative impacts of hot weather during the rapid stages of growth, in fact hot days during the nestling period result in smaller and lighter fledglings (Cunningham et al. 2013). Reductions in provisioning during hot weather were greatest for larger broods of nestlings, but reductions in daily mass gain applied to all nestlings regardless of brood size (Cunningham et al. 2013). Therefore, it is unclear whether reductions in daily mass gain by Common Fiscal nestlings are due entirely to the effects of reduced provisioning rate or whether there are other contributing factors. In addition to provisioning, the other non-mutually exclusive hypothesis may be that the direct physiological effects of temperature on the nestlings resulted in changes in water and energy balance, thus impacting on daily mass gain. While parents adjusted their provisioning rates with temperature (Cunningham et al. 2013), it is unknown if they traded this off with shading and brooding the nestlings for thermoregulation.

Against this background, I investigated the influence of temperature on parental investment in Common Fiscal and how this affected nestling growth. My first aim was to determine whether there was a trade off between total nest attendance (brooding and shading) by the parents, and total daily provisioning rate as temperatures increase. In this case I predicted that total provisioning will be traded against nest attendance time, suggesting that if the parents are not hunting for food then they might be attending the nest at high temperature. With a possibility that males and females may be affected differently by temperature, I also determined the effect of temperature on sex-specific provisioning rates. I wanted to find how the trends shown by each of the parents related to total (combined) provisioning rates at high temperature. In addition to this, I also wanted to discover if each parent's provisioning behaviour was influenced by the behaviour of the other parent. Furthermore, I wanted to determine if the size of prey brought to the nest was influenced by temperature, in order to establish whether the birds were able to compensate for decrease in provisioning to some extent by increasing prey size or whether the impact is exacerbated because prey size also decreases.

As parents play an important role in the thermoregulation of the nestlings, I also determined the effect of temperature on total nest attendance (shading and brooding). In addition, I tested whether there were sex-linked differences in parental responses to increasing thermoregulatory demands of nestlings. Finally, I investigated how temperature affects levels of physiological heat stress (as indicated by panting behaviour) experienced by Common Fiscal nestlings. Both parental behavioural and nestlings' physiological responses have implications on nestlings' growth, therefore I investigated the effects of provisioning rate and nestlings' panting on nestlings' daily mass gain.

By answering these questions, I hoped to elucidate the mechanisms by which increasing daily maximum temperature affects nestling growth. Understanding the mechanisms that link temperature to fitness should be valuable in predicting the impacts of rising temperatures on populations, by providing a direct link between climate change and demography.

MATERIALS AND METHODS

Ethics statement

The methods used in this study conform to the standards and expectations set by the University of Cape Town Animals Ethics Committee (clearance #2011/V21/PH). Permission to conduct the research on private land in Tswalu Kalahari Reserve was granted by the landowners and the Northern Cape Conservancy (permit #Fauna 1088/2011). Bird ringing and handling was done by experienced individuals licenced by the South African Bird Ringing Unit (SAFRING).

Study site

This study was carried out in a 10 km^2 study area in the 100 000 ha Tswalu Kalahari Reserve, Northern Cape, South Africa (27°13'S, 22°22'E). Tswalu lies in a transition zone between the Nama-Karoo and Savannah biomes and combines sand dunes, sandy plains and Kalahari savannahs. The vegetation of Tswalu consists of shrubby Kalahari dune bushveld on the plains, Kalahari mountain bushveld on the mountains and hills and Kalahari plains thorn bushveld in the north and north-east (van Rooyen 1999). The Kalahari savannahs comprise sparse grasses (mainly *Eragrostis* spp., *Panicum* spp., and *Aristida* spp.) and trees and shrubs such as *Acacia erioloba, A. haematoxylin, A. mollifera, Boscia albitrunca, Terminalia sericea,* and *Rhigozum trichotomum* (Jeltsch et al. 1996). Rainfall averages about 500 mm per year, falling mainly in summer (October-March) when maximum daily temperatures can reach 45°C (Mares 1999; Silberbauer 1981). The Kalahari can also experience frost in winter between June and August (Silberbauer 1981).

This study was carried out in two breeding seasons of the Common Fiscal during the austral summer: November 2010 – March 2011 (air temperatures range 8.7-38.7°C) and November 2011 – February 2012, (air temperature range 9.3-39.1°C). Average daily rainfall was 4 mm in

2010/11 and 3 mm in 2011/12. However, rainfall was erratic with most falling heavily during thunderstorms interspersed with long dry periods. Meteorological data were collected using an onsite weather station (VantagePro 2, Davis Instruments, Hayward, California).

Study species and population

The Common Fiscal is a black and white shrike (*Laniidae*), 21–23 cm long and weighing 25–50 g, that is widespread across sub-Saharan Africa (Sinclair and Ryan 2009). It has a characteristic black bill, eyes and legs, 'V' shaped white scapular feathers and a relatively long tail with white outer feathers and white tips on the other feathers. Desert races have a white supercilium, and partially due to this feature the Kalahari population is often regarded as a subspecies (*L. c. subcoronatus*), but genetic analyses do not support this (Fuchs et al. 2011). The Common Fiscal forages from exposed perches, taking a diversity of prey including insects, small birds, lizards, frogs, rodents and fruit (Soobramoney et al. 2004). It inhabits a wide range of open habitats from grasslands to Acacia thornvelds and woodlands where there are perches for hunting, but it avoids dense habitats (Harris 2000). Its broad habitat tolerance and diverse diet contribute to its success; the population is thought to be increasing (ditto), and is listed as least concern by the IUCN (BirdLife International 2013).

Pairs are socially monogamous and defend a territory which may be as small as 1 ha (Sinclair and Ryan 2009), but at the study site, territories ranged from 3–10 ha. Established pairs are resident in their territory and the species is not known to make large scale movements (Hockey et al. 2005). During the breeding season, which usually starts in August and ends in March, the female commonly lays an average of 3–4 eggs in a bulky, open cup nest built in a dense shrub or tree. Incubation, which lasts 12–16 days, is done entirely by the female (Harris 2000).

For this study, 54 individuals (28 males and 26 females) were captured using springtraps baited with giant mealworms (*Zophobas morio*). Birds were sexed on flank colour, which is rufous only in the female. Individual birds were fitted with a unique combination of three plastic colour bands (JC Hughes, UK) and a uniquely numbered aluminium or Incoloy band for individual bird identification. Monitoring was then focused on 21 breeding pairs of colour banded individuals. However, two pairs contained unbanded females which were difficult to catch. Of the 21 pairs, 15 produced broods which survived for at least six days after hatching, therefore these contributed to the analyses in this study. The total number of broods for the analyses was 19, because four pairs contributed two broods. Only six-, ten- and 14-day old nestlings were used for the analyses because they had enough datasets to carry out statistical analyses.

Data recording

Parental care and nestling behaviour was quantified from video recordings which were made using Sony HDR-XR 160E and Panasonic SDR-S50 video cameras. The cameras were mounted on tripods 2-5 m from the nest at 06h00 on an observation day (defined as time between when the cameras were mounted in the morning and dismounted in the evening of that particular day). Ideally an observation day lasted for 12 hours (from 06h00–18h00), however, on some days this was impossible due to weather disturbances like heavy rains and thunderstorms which necessitated early recovery of the equipment. The aspects of parental care behaviour I quantified were the number of prey items delivered to each nest per observation day, standardised to a 12 hr day in order to correct for unequal lengths, the size of prey items relative to parent bill size, and nest attendance (which included brooding and shading). In the nestlings I quantified the percentage of time the nestlings spent panting per observation day. All nestlings were weighed to the nearest 0.01g on a top pan balance just prior to turning on the cameras in the morning, and immediately after switching them off in the evening. Each weighing session took approximately less than ninety seconds to complete. These data were used to calculate percentage increase in body mass per nestling over 12 hrs.

Prey size and provisioning rate

From the videos, I estimated the prey size by classifying each prey item as either small (≤ bill size) or large (> bill size) using the parent's beak as the reference for size. I extracted the total number of prey items fed to the chicks by both parents on an observation day. A provisioning event was defined as when either parent brought food to the nest and fed it to at least one nestling. I standardised the number of provisions to a 12 hr day by dividing the total number of provisions per observation day by the number of video recording hours and then multiplying it by 12 (this was to account for discrepancies in video recording length). Provisioning rates were also calculated separately for each parent.

Nest attendance

I defined nest attendance as the total time spent by either parent brooding or shading the nestlings. Brooding is when the bird sits over and covers the nestlings and shading is when the bird stands in the nest or on the rim with wings open (ranges from just a little bit open to forming an umbrella over the whole nest), to provide shade from the sun. Both brooding and shading are mechanisms used by parents for aiding thermoregulation of the nestlings (Stark and Ricklefs 1998). I obtained the total time each parent spent either shading or brooding per day by recording the time at which the activity (either brooding or shading) started (t_s) and ended (t_e). The difference between t_s and t_e (seconds) was equivalent to the time spent undertaking the activity. I summed these times per day to determine the total time spent either shading or brooding per day, and used this to estimate the daily nest attendance time as a proportion of the total observation period.

Panting rates (heat dissipation)

I defined panting as when the nestlings open their beaks and increase in the rate and amplitude of breathing to help dissipate heat (Salt 1964). I also recorded other signs of heat stress like wing spreading in the older nestlings as an indication of panting and heat dissipation. I used JWatcher 1.0 (Blumstein and Daniel 2007), which is a tool for quantitative analysis of a continuously observed behaviour, to extract panting data from the videos. JWatcher is an event recorder which logs time when computer keys are pressed that is used to estimate the duration of behaviours and intervals between them (Blumstein and Daniel 2007). I recorded when at least one nestling started to panting until all the nestlings stopped panting. This was summed for each day of observation and expressed as a percentage of the total observation period. Panting was only recorded during the time when the parents were not shading or brooding the nestlings because only then was it possible to see what was happening.

Statistical analyses

All analyses were conducted in the R statistical environment using packages lme4 version 0.999375-35 for mixed effects modelling (Bates and Maechler 2010) and MuMln version 0.13.14 for model comparisons (Barton and Barton 2013) using the dredge function which gives the Akaike Information Criterion (AIC) values and model weights. I also tested for over-dispersion by comparing the residual deviance to the residual degrees of freedom in all the models (Zeileis et al. 2007). Using the mcp.fnc function of the LMERConvenience package (Tremblay and Ransijn 2013), I checked the residuals of the fitted models to graph criticism plots for mixed models. For all analyses, I modelled the response variables using fixed-effects parameters after incorporating the random-effects of brood identity nested within the male identity (used as a proxy for pair identity) in the model, and the default parameter estimation criterion was the restricted (residual) maximum likelihood (REML).

In cases where competing models had ΔAIC<2 units, I chose the simpler model regardless of the weight because there was no evidence to suggest that the additional parameters improved model fit (Arnold 2010). However, this does not necessarily suggest that the additional parameters have no effect at all on the response variable, rather that there was simply not enough evidence to confirm this. In my discussion I refer to these competing models where appropriate, for example where they provide potentially important alternative interpretations of the data.

Effect of temperature on provisioning rate

To determine whether there was a trade off between total nest attendance (brooding and shading) by the parents, and total daily provisioning rate as temperatures increased, I fitted a glmer model with Poisson error structure. Provisioning rate per nestling standardised to a 12 hr day was the response variable and I included the following fixed factors: brood size, T_{max} (daily maximum temperature), nestling age, percentage of time spent attending the nest and all the two way interactions.

Similarly, I fitted a glmer model with Poisson error structure to test for prey provisions by the female per 12 hr day. I included the following fixed factors in the global model: brood size, T_{max}, nestling age, prey provisions by the male per 12 hr day (mprv), percentage of time the female spent attending the nest in a 12 hr day (fns), and all the two way interactions between other parameters except fns because including these destabilised the model. Testing only for the main effect of fns still allowed me to assess whether there was a trade off between nest attendance and provisioning rate in the female.

For male provisioning, I fitted the same glmer model with Poisson error structure and the total prey provisions by the male per 12 hr day as the response variable. In the model, I included the following fixed factors; brood size, T_{max}, nestling age, prey provisions by the female (fprv), percentage of time the male spent attending the nest (mns), and all the two way interactions between other factors excluding mns which was inserted in the model to see if there was any trade off between nest attendance and provisioning rate by the male.

Effect of temperature on prey size and nest attendance

A glmer model with a binomial family was fitted to prey size as only two size categories were recognised. Brood size, T_{max}, nestling age and all interactions were included in the global model.

The same model structure was applied to assess factors influencing total nest attendance (percentage of time the nest was attended by at least one parent), with fixed factors brood size, T_{max}, nestling age and all the two way interactions. In addition, I included an observation level random effect in the model in order to fix for over-dispersion.

I used a similar glmer model with a binomial error structure to assess factors influencing the percentage of time the female parent spent attending the nest. The fixed factors I fitted in the model were brood size, nestling age, T_{max}, the percentage of time the male spent attending the nest (mns) and all the two way interactions.

Finally to test for male nest attendance I fitted a glmer model with a binomial error structure and the percentage of time the male spent attending the nest as the response variable. Methodical addition of factors showed that brood size, nestling age, T_{max}, the percentage of time the male spent attending the nest (fns) and only interactions between brood size and fns, brood size and T_{max}, T_{max} and fns and nestling age and fns were the parameters that could be fitted without destabilising the model.

Effects of provisioning and panting rate on daily mass gain

I fitted lmer models with Gaussian error structure to test for the effect of both provisioning and panting rate on daily mass gain. I included the following fixed factors in the model to assess the effect of provisioning on nestling mass gain: nestling age, T_{max} and prey provisioning per nestling per 12 hr day (ppn) and all the two way interactions.

In order to assess the effect of panting rate on daily mass gain I included the fixed factors nestling age, the percentage of time the nestlings spent panting (ppnt) and all the two way interactions. I did not include T_{max} in the latter model because it is correlated to ppnt hence, this would have destabilised the model.

RESULTS

Overall contributions of male and female to parental care

Male parents provisioned nestlings significantly more often than females (male 49.2±29.2 feeds per day±1 sd, female 23.3±14.5; z = 16.14, p < 0.0001; Fig. 1). However, females spent more time attending the nest (either brooding or shading the nestlings: male 2.5±7.2 %, female 33.9±23.3 %; z = -9.80, p < 0.0001; Fig. 2).

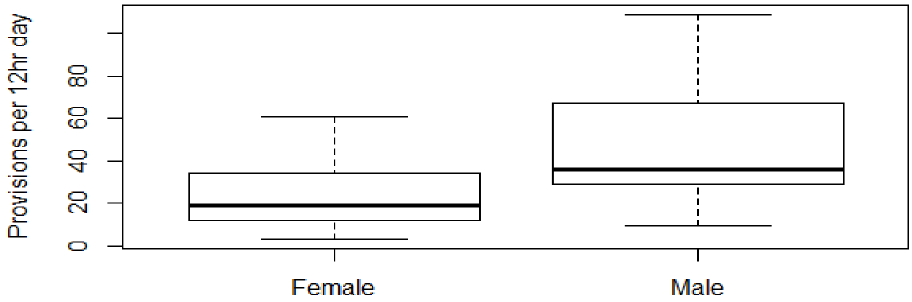

Figure 1: The number of prey delivered to the nest per day by female and male Common Fiscal (*Lanius collaris*) in Tswalu Kalahari Reserve during 2010/2011 and 2011/2012 summer seasons.

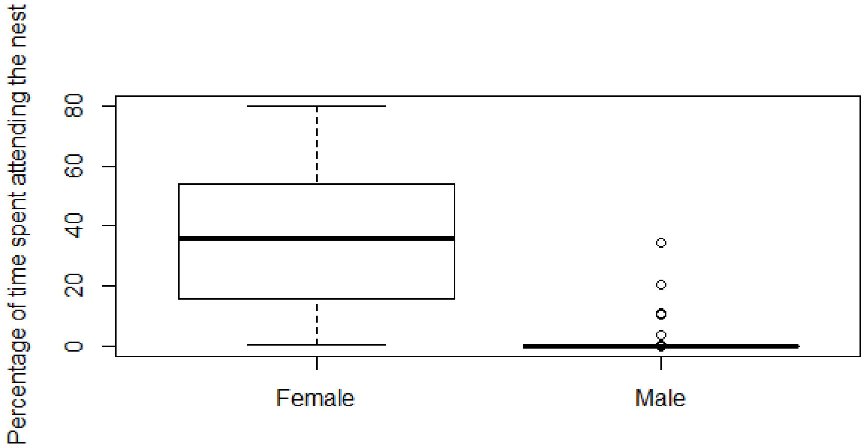

Figure 2: The percentage of time spent attending the nest by the female and the male parents (*Lanius collaris*) in Tswalu Kalahari Reserve during 2010/2011 and 2011/2012 summer seasons.

Effect of temperature on provisioning rate and prey size

Provisioning rate: The model by Cunningham et al. 2013, reproduced below with permission, showed that T_{max} had an effect on provisioning, and that this effect is modified by brood size (Table 1 and Table 2). Larger broods experienced a larger decrease in provisions than smaller broods. This was corroborated by the visual observation of the data which showed that when it was cooler (low T_{max}), larger broods were provisioned at higher rates than smaller broods but when it was hotter (high T_{max}), brood size no longer influenced total provision rate (Cunningham et al. 2013). Provisioning rate increased with brood size (Fig. 3). The outlier in the brood size 2 (Fig. 3) might be because of emergence of some abundant prey such as termites at that time.

I added the percentage of time spent attending the nest (pna) and its interactions with other variables into this model to assess whether there was any trade off between total provisioning rate and total nest attendance. However, this model had an AICc value >2 point higher than the model fitted without pna, and showed that nest attendance had no effect on total provisioning i.e. there is no trading off between provisioning and nest attendance. The best model to explain this dataset is therefore the same as the one published by Cunningham et.al (2013).

Table 1: Top five models explaining variation in prey provisioning rate by Common Fiscal from 28 full day observations of 12 broods and 12 pairs.

Model	**K**	**AIC**	**ΔAIC**	**Weight**
[1]Size + [2]age + T_{max} + brood size*T_{max}	8	300.5	0.00	0.88
Size + age + T_{max} + age*T_{max}	10	307.5	7.01	0.03
Size + age + T_{max} + size*T_{max}	10	307.9	7.42	0.02
Size + T_{max} + size*T_{max}	6	308.6	8.06	0.02
Age + T_{max} + age*T_{max}	8	308.7	8.17	0.02

[1]Size: brood size. Age: [2]Nestling age.

Global model: brood size + T_{max}+ nestling age + brood size*T_{max} + brood size*nestling age + T_{max}*nestling age. Family: Poisson.

Table 2: Factors affecting total prey provisioning, estimates of effect sizes, standard errors (SE), Z-values and estimated p-values.

Variable	**Estimate**	**SE**	**Z-value**	**p-values**
T_{max}	0.07	0.03	2.31	0.02*
Size	1.51	0.37	4.12	<0.01***
Age:				
6-d	1.57	1.01	1.54	0.12
10-d	1.78	1.00	1.79	0.07
14-d	1.63	1.00	1.62	0.11
Size*T_{max}	-0.04	0.01	-3.85	<0.01***

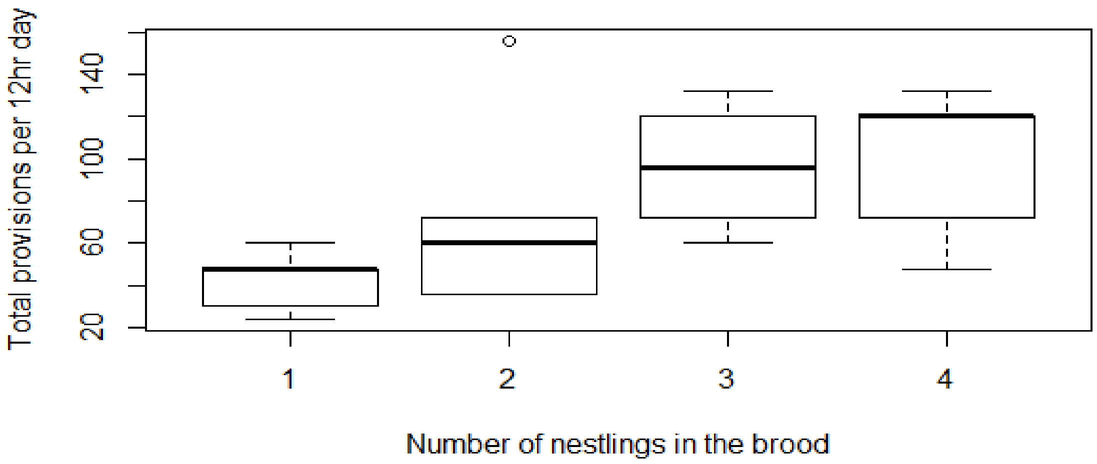

Figure 3: Effect of brood size on the number of prey provisions per day by Common Fiscal (*Lanius collaris*) in Tswalu Kalahari Reserve during 2010/2011 and 2011/2012 summer seasons.

Prey size: None of the variables I studied, including T_{max}, had any influence on prey size. The simplest model for size of prey delivered to the nest was the null model containing only the random effects of brood identity nested within male identity. However, two competing models suggested that nestling age and brood size may have an effect on prey size (Table 3).

Table 3: Top five models for effect of temperature on prey size by Common Fiscal from 35 observations of 20 broods and 14 pairs.

Model	**K**	**AIC**	**ΔAIC**	**Weight**
Age	5	216.2	0.00	0.38
Size + age	6	218.1	1.92	0.15
Null	3	218.1	1.93	0.15
Size	4	218.9	2.68	0.10
Age + T_{max}	6	219.2	3.00	0.08

Global model: brood size + nestling age + T_{max} + T_{max}*nestling age + nestling age*brood size + T_{max}*brood size.

Family: binomial.

Prey provisioning by the female and the male

Female provisioning: T_{max} had a negative effect on prey provisioning by the female in six-day nestlings, on the other hand, it had a positive effect on provisioning rate for 14-day nestlings. T_{max} had no effect on prey provisioned to ten-day old nestlings. Increasing female nest attendance decreased the proportion of prey provisioning by the female (Table 5). Nestling age, T_{max}, percentage of time the female attended the nest per day (fns), and an interaction between nestling age and T_{max} all influenced the number of prey delivered to the chicks by the female per day (Table 4). The effect of temperature was modified by nestling age.

Table 4: Top five models for explaining variation in prey provisioning rates by female Common Fiscal from 33 full day observations of 18 broods and 14 pairs.

Model	**k**	**AIC**	**ΔAIC**	**Weight**
Age + T_{max} + fns + age*T_{max}	9	289.2	0.00	0.63
Age + T_{max} + fns + [1]mprv + age*T_{max}	10	292.8	3.62	0.10
Size + age + T_{max} + fns + age*T_{max}	10	293.2	4.06	0.08
Age + T_{max} + age*T_{max}	8	296.0	6.86	0.02
Age + mprv + age*mprv	8	296.3	7.15	0.02

[1] mprv = male provisions in 12hrs. Global model: brood size + T_{max} + nestling age + mprv + mprv*brood size + mprv*T_{max} + mprv*nestling age + brood size*T_{max} + brood size*nestling age + T_{max}*nestling age. Family: Poisson.

Table 5: Factors affecting provisioning rate by the female, estimates of effect sizes, standard errors (SE), Z-values and estimated p-values.

Variable	**Estimate**	**SE**	**Z-values**	**p-values**
Age:				
6-d	8.46	1.06	7.97	<0.01***
10-d	2.21	1.27	1.74	0.08
14-d	0.15	1.51	0.10	0.92
Age*T_{max}:				
6-d	-0.13	0.03	-4.60	<0.01***
10-d	0.06	0.04	1.58	0.11
14-d	0.10	0.04	2.28	0.02*
[1]Fns	-0.02	0.00	-4.20	<0.01***

[1]Fns = female nest attendance

Male provisioning: On the other hand, prey provisioning by the male was influenced by brood size, nestling age, prey provisions by the female (fprv), T_{max}, an interaction between brood size and fprv, and an interaction between nestling age and fprv (Table 6). T_{max} had a negative effect on male provision rate. Female provisioning rate had a negative effect on male provisioning rate, and this effect was modified by nestling age and brood size. I did not investigate independently the three-way interaction between these variables because this would have destabilised the model, but the effect was slightly more pronounced for ten-day and 14-day old nestlings than six-day old nestlings. Furthermore, fprv had a negative effect on male provisioning rate but this effect was reduced by brood size (Table 7).

Table 6: Top five models for effect of temperature on prey provisioning by the male Common Fiscal from 33 full day observations of 18 broods from 14 pairs.

Model	**k**	**AIC**	**ΔAIC**	**Weight**
Size + age + T_{max} + fprv + brood size*fprv + age*fprv	11	307.5	0.00	0.47
Size + age + T_{max} + fprv + mns + size*fprv + nestling age*fprv	12	310.7	3.16	0.10
Size + age + fprv + mns + size*fprv + age*fprv	11	311.9	4.31	0.05
Size + age + T_{max} + fprv + size*fprv + age*fprv + T_{max}*fprv	12	312.6	5.01	0.04
Size + age + fprv + mns + size*T_{max} + brood size*fprv + age*fprv	12	312.6	5.01	0.04

Global model: brood size + T_{max} + nestling age + fprv + mns + fprv*brood size + fprv*T_{max} + fprv*nestling age + brood size*T_{max} + brood size*nestling age + T_{max}*nestling age. Model family: Poisson.

Table 7: Factors affecting prey provisioning by the male, estimates of effect sizes, standard errors (SE), Z-values and estimated p-values.

Variable	**Estimate**	**SE**	**Z-value**	**p-values**
Age:				
6-d	6.91	0.86	8.07	<0.01***
10-d	7.55	0.89	8.52	<0.01***
14-d	7.51	0.89	8.47	<0.01***
Age*[1]fprv:				
6-d	-0.05	0.01	-3.78	<0.001***
10-d	-0.09	0.02	-4.98	<0.01***
14-d	-0.09	0.02	-5.32	<0.01***
Size	-0.45	0.15	-3.06	<0.001**
Fprv	-0.05	0.01	-3.78	<0.001***
T_{max}	-0.06	0.02	-3.36	<0.001**
Size*fprv	0.02	0.01	4.44	<0.01***

[1] Fprv = female provisioning

Effect of temperature on nest attendance

The simplest model contained only nestling age, further suggesting that T_{max} had no influence on nest attendance (although a more complex competing model contained both nestling age and T_{max}; Table 8). There were two competing models to describe total percent of time the nest was attended per day by either adults (male and female contributions combined). The simplest model showed unsurprisingly that total nest attendance decreased with nestling age (Table 9, Fig. 4).

Table 8: Top five models for effect of temperature on daily nest attendance by Common Fiscal from 35 full day observations of 20 broods and 14 pairs.

Model	**k**	**AIC**	**ΔAIC**	**Weight**
Age	6	686.5	0.00	0.47
Age + T_{max}	7	687.8	1.30	0.24
Size + nestling age	7	689.6	3.07	0.10
Size + age + size* age	9	690.5	4.01	0.06
Size + age + T_{max}	8	690.9	4.39	0.05

Global model: brood size + nestling age + T_{max} + T_{max}*nestling age + nestling age*brood size + T_{max}*brood size.

Model family: binomial.

Table 9: Factors affecting total daily nest attendance by Common Fiscal, estimates of effect sizes, standard errors (SE), Z-values and estimated p-values.

Variable	**Estimate**	**SE**	**Z value**	**p-values**
Age:				
6-d	0.46	0.35	1.32	0.19
10-d	-0.84	0.38	-2.18	0.03*
14-d	-2.98	0.39	-7.76	<0.01***

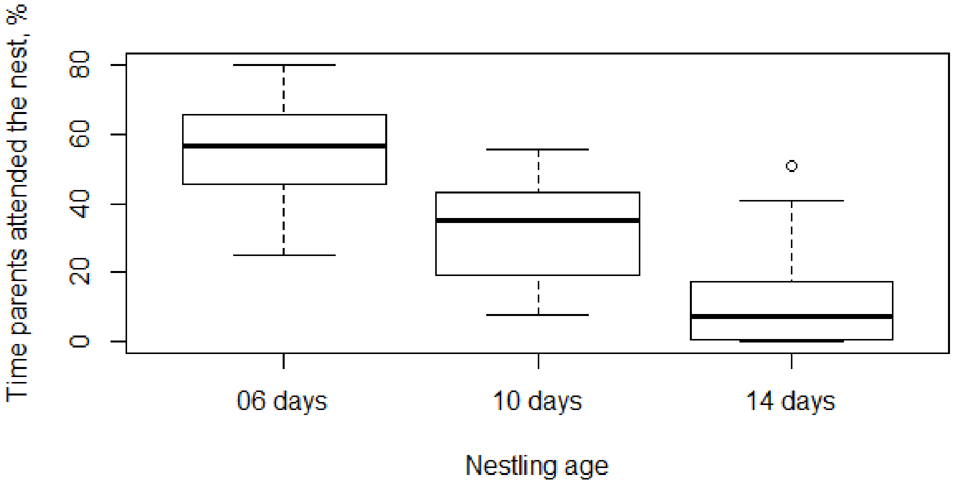

Figure 4: The effect of nestling age on percentage of time Common Fiscal parents attended the nest (*Lanius collaris*) in Tswalu Kalahari Reserve during 2010/2011 and 2011/2012 summer seasons.

Female nest attendance: With respect to sex-specific nest attendance, the simplest model on the effect of temperature on female nest attendance showed that T_{max} had no effect. Furthermore, no competing model contained T_{max} either (Table 10). However, female nest attendance decreased with nestling age, with the least attendance at 14-day old nestlings (Table 11).

Table 10: Top five models for effect of temperature on nest attendance by Common Fiscal females from 18 full day observations of 18 broods from 14 pairs.

Model	**k**	**AIC**	**ΔAIC**	**Weight**
Age + [1]mns	7	675.6	0.00	0.25
Size + age + size* age	9	676.4	0.80	0.17
Age	6	676.5	0.93	0.16
Size + age + mns + size* age	10	677.1	1.45	0.12
Age + T_{max} + T_{max}	8	678.9	3.26	0.05

[1]mns = male nest attendance time. Global model: brood size + nestling age + mns + T_{max} + brood size*nestling age + brood size*T_{max} + nestling age*T_{max} + mns*T_{max} + mns*brood size + mns*nestling age. Model family: binomial.

Table 11: Factors affecting total nest attendance by Common Fiscal females, estimates of effect sizes, standard errors (SE), Z-values and estimated p-values.

Variable	**Estimate**	**SE**	**Z-value**	**p-values**
Age:				
6-d	0.38	0.33	1.16	0.24
10-d	-0.89	0.36	-2.46	0.01*
14-d	-3.42	0.36	-9.42	<0.01***

Male nest attendance: In contrast to female nest attendance, the simplest model for the effect of temperature on male nest attendance (Table 12) showed that T_{max} had a positive influence on male nest attendance. Increasing T_{max} increased the proportion of time the male parent spent attending the nest (Table 13, Fig. 5).

Table 12: Top five models for effect of temperature on nest attendance by Common Fiscal males from 33 full day observations of 18 broods from 14 pairs.

Model	**k**	**AIC**	**ΔAIC**	**Weight**
[1]Fns + T_{max}	6	187.2	0.00	0.24
Size + fns + T_{max} + size*fns	8	188.2	1.02	0.14
T_{max}	5	188.7	1.52	0.11
Size + fns + T_{max}	7	189.2	1.98	0.09
Fns + T_{max} + fns*T_{max}	7	189.9	2.67	0.06

[1]Fns = female nest attendance time. Global model: brood size + nestling age + fns + T_{max} + brood size*fns + brood size*T_{max} + nestling age*fns + fns + T_{max}. Family: binomial.

Table 13: Factors affecting nest attendance by Common Fiscal males, estimates of effect sizes, standard errors (SE), Z values and estimated p-values.

Variable	**Estimate**	**SE**	**Z-value**	**p-values**
Intercept	-71.82	2.10	-34.12	<0.01***
T_{max}	1.78	0.05	36.13	<0.01***

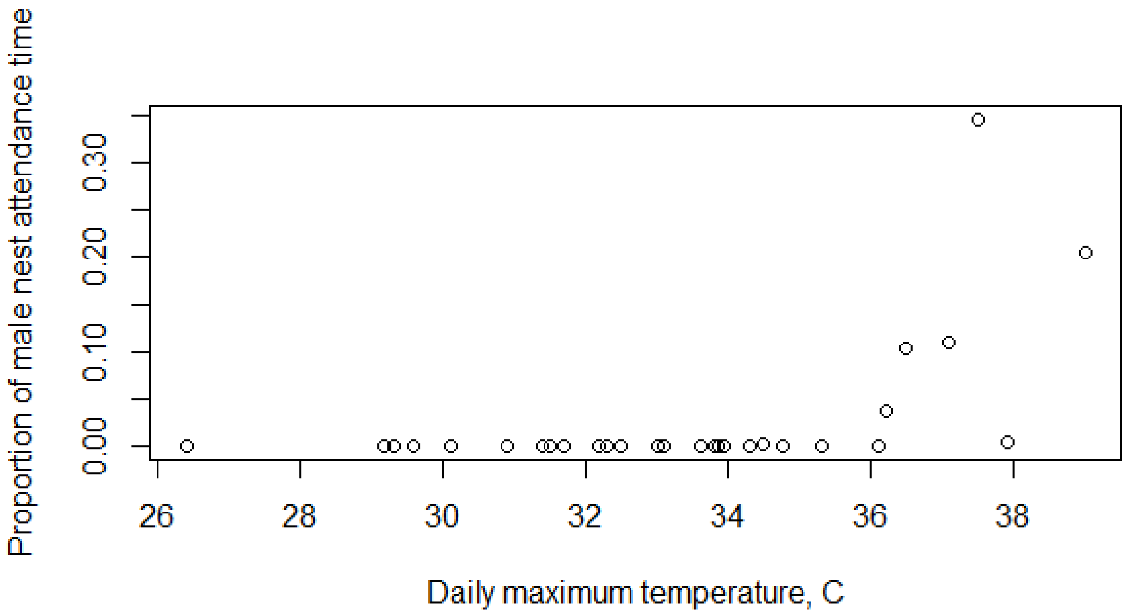

Figure 5: Effect of daily maximum temperature on the proportion of time the male Common Fiscal (*Lanius collaris*) attended the nest relative to total nest attendance time in Tswalu Kalahari Reserve during 2010/2011 and 2011/2012 summer seasons.

Effect of temperature on panting

Six-day and ten-day nestlings never spent >1% of the time of the day panting, but 14-day nestlings spent up to 6% of the day panting (Fig. 6). The effect of temperature on the proportion of time spent panting by the nestlings was modified by nestling age (Table 15). Time spent panting by six- and fourteen-day nestlings, but not by ten-day nestlings, was positively influenced by T_{max} (Fig. 6a-c). There was weak evidence to suggest that time spent panting by six-day old nestlings was also negatively influenced.

Table 14. Top five models for effect of temperature on proportion of daily time spent panting by Common Fiscal nestlings from 35 full day observations of 20 broods and 14 pairs.

Model	**k**	**AIC**	**ΔAIC**	**weight**
Size + age + T_{max} + size* age + age*T_{max}	11	385.6	0.00	0.87
Size + age + T_{max} + size* age + size*T_{max} + age*T_{max}	12	389.5	3.84	0.13
Age + T_{max} + age*T_{max}	8	402.5	16.85	0.00
Size + age + T_{max} + age*T_{max}	9	405.6	19.96	0.00
Size + age + T_{max} + size*T_{max} + age*T_{max}	10	409.3	23.68	0.00

Global model: nestling age+ T_{max} + T_{max}*nestling age + brood size + brood size*nestling age + brood size*T_{max}.

Model family: binomial

Table 15: Factors affecting proportion of daily time spent panting by Common Fiscal nestlings, estimates of effect sizes, standard errors (SE), Z-values and estimated p-values.

Variable	**Estimate**	**SE**	**Z-value**	**p-values**
Age:				
6-d	-6.70	0.31	-21.78	<0.01***
10-d	-5.54	0.47	-11.81	<0.01***
14-d	-7.55	0.35	-21.58	<0.01***
Age* size:				
6-d	-0.08	0.04	-2.03	0.04*
10-d	-0.01	0.04	-0.32	0.75
14-d	0.06	0.03	1.90	0.06
Age*T_{max}:				
6-d	0.04	0.01	5.32	<0.01***
10-d	-0.00	0.01	0.08	0.94
14-d	0.12	0.01	12.02	<0.01***

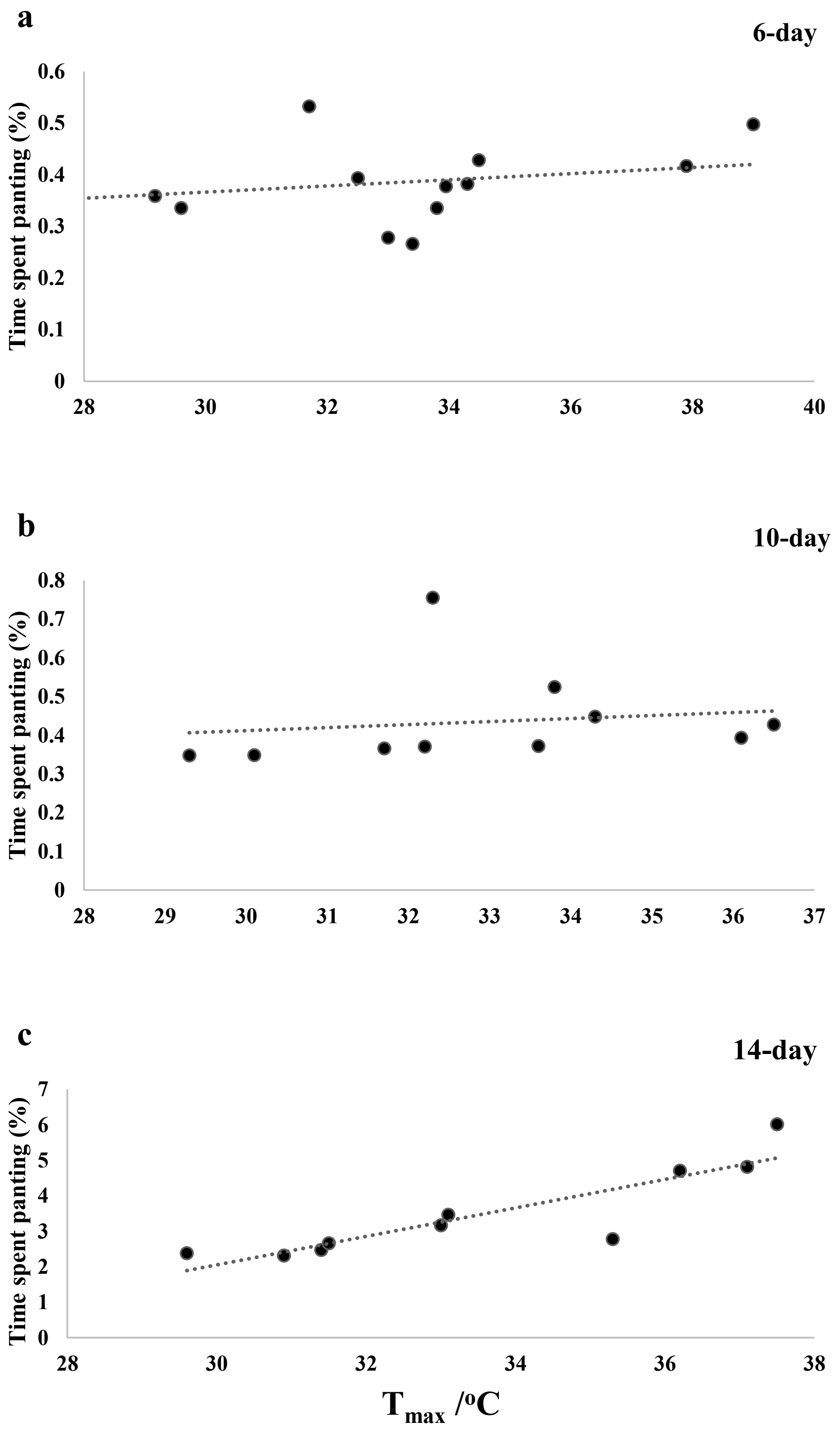

Figure 6: Effect of temperature on Common Fiscal (*Lanius collaris*) panting rate modified by nestling age in Tswalu Kalahari Reserve during 2010/2011 and 2011/2012 summer seasons.

Effect of provisioning and panting rate on daily mass gain

Effects of provisioning and T_{max} on nestling mass gain: Prey provisioning rates per nestling per day (ppn) had a positive effect on nestlings' daily mass gain (Table 16, 17). The best model showed that in addition to ppn, T_{max} also had an influence on nestlings' daily mass gain. T_{max} had a negative effect on daily mass gain by six-day old nestlings (Fig. 7a), although, there was not sufficient evidence to suggest the same effect on ten- and 14-day old nestlings (Fig. 7b-c).

Table 16. Top five models for effect provisioning on Common Fiscal nestling daily mass gain in 32 full day observations of 18 broods and 14 pairs.

Model	**k**	**AIC**	**ΔAIC**	**Weight**
Age + T_{max} + ppn + age*T_{max}	10	216.3	0.00	0.69
Age + T_{max} + age*T_{max}	9	219.4	3.09	0.15
Age + T_{max} + ppn	8	220.6	4.35	0.08
Age + T_{max}	7	221.5	5.28	0.05
Age + ppn	7	224.9	8.62	0.01

Global Model: Nestling age + T_{max} + ppn + nestling age*T_{max} + nestling age*ppn + T_{max} + ppn. Model family: Gaussian.

Table 17: Effect of prey provisioning per nestling (ppn) on Common Fiscal nestlings' daily mass gain, estimates of effect sizes, standard errors (SE), and the t-values**.**

Variable	**Estimate**	**SE**	**t-value**
Age:			
6-d	90.43	15.64	5.78
10-d	-7.88	25.73	-0.31
14-d	-5.31	27.91	-0.19
Age*T_{max}:			
6-d	-2.20	0.47	-4.67
10-d	0.35	0.78	0.45
14-d	-0.04	0.79	-0.05
[1]Ppn	0.29	0.08	3.55

[1]Ppn = prey provisioning per nestling

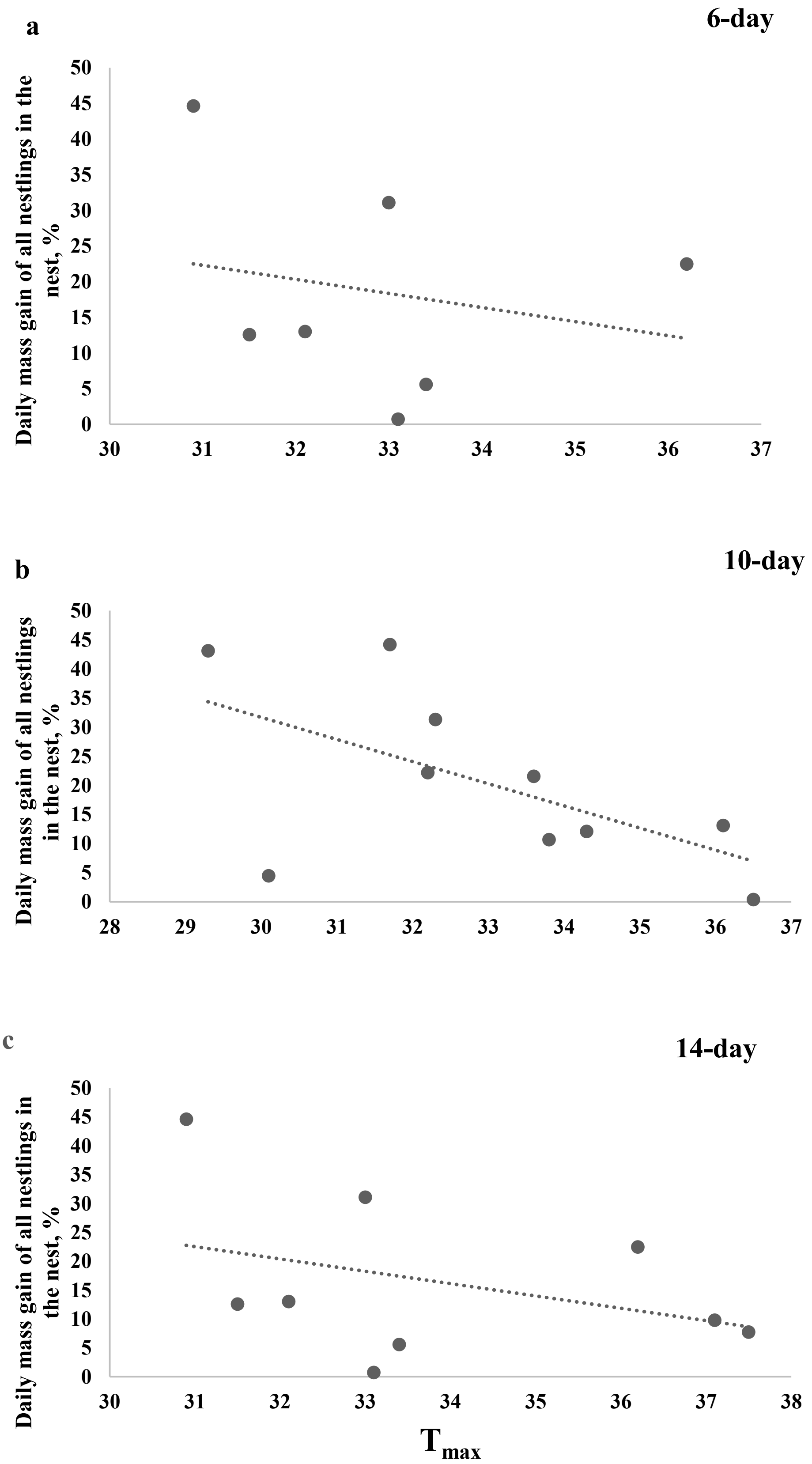

Figure 7: The effect of T_{max} on daily mass gain by Common Fiscals (*Lanius collaris*) nestlings as modified by nestling age.

Effects of panting on nestling mass gain: Percentage of daily time spent panting (ppnt) by nestlings had a negative effect on daily mass gain on six-day old nestlings (Fig. 8a, Table 18). However, there was not sufficient evidence to suggest that ppnt had any effect on daily mass gain among ten-day or 14-day old nestlings (Fig. 8b-c, Table 19).

Table 18: Top five models for the effect of panting rate on Common Fiscal nestlings' daily mass gain from 30 full day observations of 18 broods and 14 pairs.

Model	**K**	**AIC**	**ΔAIC**	**Weight**
Size + age + [1]ppnt + age*ppnt	10	208.4	0.00	0.33
Age + ppnt + age*ppnt	9	208.7	0.29	0.29
Size + age + ppnt + size*age + age*ppnt	12	209.0	0.62	0.25
Size + age + ppnt + size*age + size*ppnt + age*ppnt	13	211.3	2.90	0.08
Size + age + ppnt + size*ppnt + age*ppnt	11	212.1	3.68	0.05

[1] ppnt = panting rate. Global model: Brood size + nestling age + ppnt + brood size*nestling age + brood size*ppnt + nestling age*ppnt. Model family: Gaussian

Table 19: Effect of panting rate on Common Fiscal nestlings' daily mass gain, estimates of effect sizes, standard errors (SE), and the t-values.

Variable	Estimate	SE	t value
Age:			
6-d	55.19	10.64	5.19
10-d	13.30	8.18	1.63
14-d	10.09	7.49	1.35
Age*[1]ppnt:			
6-d	-74.18	27.15	-2.73
10-d	0.51	18.12	0.03
14-d	-1.78	1.97	-0.90

[1] ppnt = proportion of time the nestlings spent panting

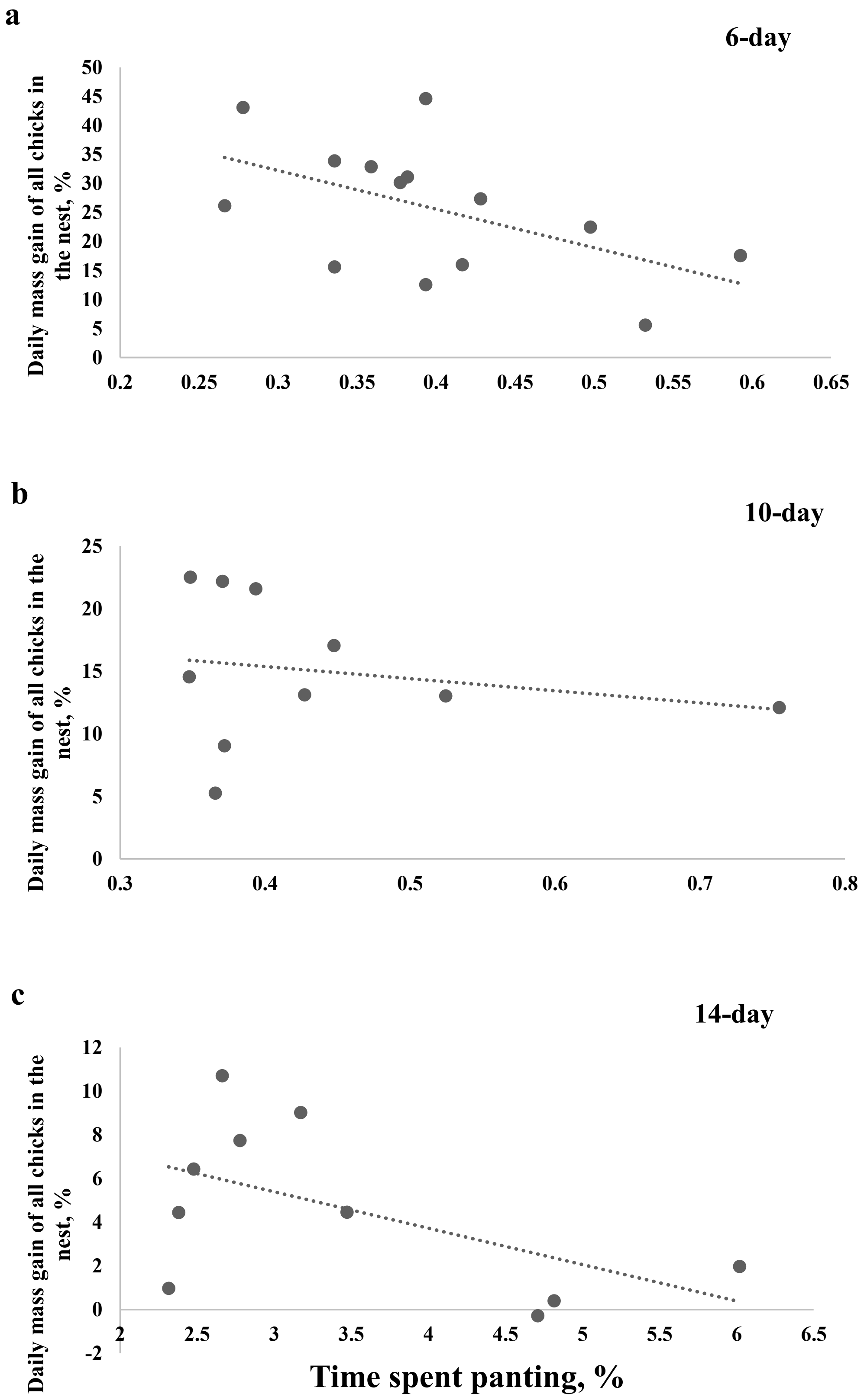

Figure 8: Effect of panting rate on Common Fiscal (*Lanius collaris*) nestlings' daily mass gain as modified by nestling age.

DISCUSSION

Cunningham et al. (2013) showed that temperature has a negative effect on daily mass gain in six-day old Common Fiscal nestlings, but that this effect is not statistically significant in older nestlings. They also reported that nestlings do not recover from the negative impacts of hot weather during the rapid stages of growth, evidenced by smaller and lighter nestlings as a result of hot days during the nestling period. I explore the mechanisms underpinning these results.

Effect of temperature on prey provisioning

Males dominate provisioning, especially when the chicks are small and the female undertakes almost all brooding. Reduction in provisioning in hot conditions might have been influenced by reduced prey availability, when prey organisms hide away from direct sun and heat. Birds might compensate for this by shifting to bigger prey (Ashmole 1968), but in this case none of the measured variables had any effect on the size of prey delivered to the nest. Although prey provisioning decreased with temperature, there was no evidence to suggest that it is traded off with nest attendance. This might suggest that parents still hunt at high temperature, however, at a limited success rate (Martin 1987, S. J. Cunningham unpublished data). Parents may also consume the largest proportion of the captured prey themselves in order to meet their own energy and water requirements which will be high during periods of high temperature as a result of the need for thermoregulation (Farmer 2000).

Effect of temperature on nest attendance and chick panting

Caring for nestlings is one of the main reproductive stresses altricial birds have to cope with, balancing between providing food and maintaining nestlings' body temperature (Tomback and Murphy 1981). Female nest attendance is determined mainly by chick age. In contrast, males adjust their nest attendance behaviour in response to temperature. Total nest attendance (combined effort of both sexes) appears only to be affected by nestling age. This may be so because altricial birds develop the ability to thermoregulate endogenously through the nestling period (Stark and Ricklefs 1998). Younger nestlings require both brooding and shading for body temperature regulation, whereas older nestlings are better able to regulate their body temperature (ditto). Female nest attendance is not affected by temperature, but male nest attendance is, this may suggest that the male contributes to nestling thermoregulation through shading at high temperatures, supplementing the contribution of the female. However, is no evidence to suggest that this affects his daily provisioning rate.

Increasing temperature results in increased panting, and therefore respiratory evaporative water loss and energy consumption (Ivanov 2006; Akin 2011), by six-day and especially 14-day old nestlings. An increase in panting with temperature, despite increased shading effort by the male on hot days, might suggest that shading is only partly effective against high temperatures i.e. it is effective only in helping chicks avoid lethal hyperthermia, but cannot totally eliminate thermoregulatory costs.

Consequences for nestlings' daily mass gain

Re-running the model presented in Cunningham et al. (2013) shows that temperature negatively affects daily mass gain of six-day old nestlings, but not ten-day or 14-day old nestlings. Unsurprisingly, provisioning rate had a positive effect on daily mass gain, and this has a direct bearing on nestling size and survival (Dawson and Bortolotti 2000). Direct effects of high ambient temperatures on metabolism (Ricklefs 1983) and indirect effects of temperature on prey provisioning (Golet et al. 2000) respectively have consequences for nestling fitness, growth and survival.

The proportion of time spent panting had a negative effect on daily mass gain in six-day old nestlings. Cunningham et al. (2013) showed that temperature had a negative effect on growth rates of younger nestlings, and my results suggest that panting might be one of the mechanisms by which growth is impacted. The extra water lost during physiological thermoregulation might explain the decrease in the daily mass. The increased panting rate correlated with a reduction in daily mass gain for six- but not 14-day old chicks. The absence of evidence to suggest a decline in daily mass gain on 14-day nestlings, regardless of them panting more, might suggest that the increase in female provisions to these nestlings at high temperature is cushioning them against a decrease in daily mass.

In summary, overall provisioning is affected by temperature, but overall nest attendance is not. Panting rates increase with temperature, especially among older chicks. Therefore it appears likely that the mechanism underlying the negative effect of high temperature on growth of six-day nestlings may be both physiological, related to the energy and/or water costs of nestling thermoregulation, and behavioural related to reduced parental provisioning at high temperature. Both these mechanisms have a direct bearing on energy requirements. Panting expends more energy but a decrease in provisioning at high temperature means nestlings may be less able to cope with the energy requirements of panting. It is, however, worth stressing at this point that parameters like tarsus length and leg length may give a much better indication of growth as opposed to daily mass gain which is variable under different circumstances.

It is worrying that parents, even in this relatively mild temperature range (max 39°C) cannot increase provisioning to meet the increased energy/water demands of panting nestlings. Temperatures are expected to increase significantly in future (Moise and Hudson 2008) and parental behaviour currently seems unable to buffer the negative effects for nestlings. This appears to be especially the case for the youngest nestlings. These nestlings are the fastest growing of the three age classes examined, so any negative effects on growth might be magnified. They may also not be sufficiently physically developed to dissipate excess heat efficiently through panting. Cunningham et al. (2013) showed that hot weather during the nestling period results in smaller and lighter fledglings, suggesting these chicks are unable to catch up the ‘missed’ growth opportunities during the nestling period.

CONCLUSION

Temperature affects the parental investment on nestlings, causing a reduction in prey provisioning. This decrease in provisioning results in a decrease in daily mass gain of the youngest nestlings, during their period of fastest growth. Females increase their provisioning to older nestlings at high temperature. Although this has no effect on the total provisioning, it may be influential in cushioning against a decrease in daily mass gain. At high temperatures, parents are unable to adjust their nest attendance behaviour in order assist thermoregulation in nestlings. Although males respond to increasing temperature by increasing their nest attendance time, their efforts are not enough to influence overall nest attendance. High temperature therefore causes nestlings’ panting rate to increase. This increase in panting negatively affects daily mass gain in younger nestlings. With temperatures continuing to rise as a result of climate change, it is possible that survival and breeding success of Common Fiscal will be negatively affected. The results of this study suggest that other passerine birds in hot, dry climates may experience similar reductions in breeding performance.

REFERENCES

Akin, J. A. 2011. Homeostatic Processes for Thermoregulation. Nature Education Knowledge 3: 7.

Al Rashidi, M. A., Kosztolányi, C. Küpper, I. C. Cuthill, S. Javed, and T. Székely. 2010. The influence of a hot environment on parental cooperation of a ground-nesting shorebird, the Kentish plover *Charadrius alexandrinus*. Frontiers in Zoology 7: 1.

Alexander, L. V. 2006. Global observed changes in daily climate extremes of temperature and precipitation. Journal of Geophysical Research: Atmospheres 1984–2012.

Altwegg, R., K. Broms, B. Erni, P. Barnard, G. F. Midgley, and L. G. Underhill. 2012. Novel methods reveal shifts in migration phenology of barn swallows in South Africa. Proceedings of the Royal Society B: Biological Sciences 279:1485-1490.

Angilletta, M. J. 2009. Thermal Adaptation, a Theoretical and Empirical Synthesis. Oxford University Press, Oxford.

Arnold, T W. 2010. Uninformative parameters and model selection using Akaike's information criterion. The Journal of Wildlife Management 74: 1175-1178.

Ashmole, N. P. 1968. Body size, prey size, and ecological segregation in five sympatric tropical terns (Aves: *Laridae*). Systematic Biology 17: 292-304.

Barton, K., and M. K. Barton. 2013. Package ‘MuMIn’.

Bates, D., and M. Maechler. 2010. lme4: Linear mixed-effects models using S4 classe.URL http://CRAN.R-project.org/package=lme4. R package version 0.999375-37.

BirdLife International. 2014. Species factsheet: *Lanius collaris*. Downloaded from http://www.birdlife.org on 29/05/2014.

Blumstein, D. T., and J. C. Daniel. 2007. Quantifying Behavior the JWatcher Way. Sinauer Associates, Sunderland, MA.

Bolger, D. T., M. A. Patten, and D. C. Bostock. 2005. Avian reproductive failure in response to an extreme climatic event. Oecologia 142.3: 398-406.

Calder, W. A., and J. R. King. 1974. Thermal and caloric relations of birds. Avian biology 4: 259-413.

Christensen, J. H., et al. 2007. Regional climate projections. Climate Change, 2007: The Physical Science Basis. Contribution of Working group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change, University Press, Cambridge, Chapter 11: 847-940.

Cossins, A. R., and K. Bowler. 1987. Temperature Biology of Animals. Chapman and Hall, London.

Crawshaw, L. I. 1980. Temperature regulation in vertebrates. Annual review of physiology 42: 473-491.

Crick, H. Q. P. 2004. The impact of climate change on birds. Ibis 146: 48-56.

Cunningham, S. J., R.O. Martin, C. L. Hojem, and P. A. Hockey. 2013. Temperatures in excess of critical thresholds threaten nestling growth and survival in a rapidly-warming arid savannah: a study of common Fiscal. PLOS ONE 8:1-10.

Dawson, R. D., and G. R. Bortolotti. 2000. Reproductive success of American kestrels: the role of prey abundance and weather. Condor 102:814-822.

Dawson, W. R. 1982. Evaporative losses of water by birds. Comparative Biochemistry and Physiology Part A: Physiology 71: 495-509.

Deutsch, C. A., J. J. Tewksbury, R. B. Huey, K. S. Sheldon, C. K. Ghalambor, D. C. Haak, and P. R. Martin. 2008. Impacts of climate warming on terrestrial ectotherms across latitude. Proceedings of the National Academy of Sciences 105: 6668-6672.

Dunn, P. O., and D. W. Winkler, editors. 2010. Effects of climate change on timing of breeding and reproductive success in birds. Effects of climate change on birds: 113-128.

Emms, S. K., and N. A. M. Verbeek. 1991. Brood size, food provisioning and chick growth in the Pigeon Guillemot *Cepphus columba*. Condor: 943-951.

Farmer, C. G. 2000. Parental care: the key to understanding endothermy and other convergent features in birds and mammals. The American Naturalist 155: 326-334.

Fernández, M. J., M. López-Calleja, and F. Bozinovic. 2002. Interplay between the energetics of foraging and thermoregulatory costs in the green-backed fire crown hummingbird *Sephanoides sephaniodes*. Journal of Zoology 258: 319-326.

Finlayson, H. H. 1932. Heat in the interior of South Australia – holocaust of bird-life. South Australian Ornithologist 11: 158-160.

Ford, H. A., G. W Barrett, D. A. Saunders, and H. F. Recher. 2001. Why have birds in the woodlands of Southern Australia declined? Biological Conservation 97:71-88.

Fuchs, J., T. M. Crowe, and R.C. Bowie. 2011. Phytogeography of the fiscal shrike *Lanius collaris*: a novel pattern of genetic structure across the arid zones and savannas of Africa. Journal of Biogeography, 38:2210-2222.

Golet, G. H., K. J. Kuletz, D. D. Roby, and D. B. Irons. 2000. Adult prey choice affects chick growth and reproductive success in pigeon guillemots. The Auk 117: 82-91.

Goodbred, C. O. N., and R. T. Holmes. 1996. Factors affecting food provisioning of nestling Black-throated Blue Warblers. The Wilson Bulletin: 467-479.

Hamer, K. C., and D. R. Thompson. 1997. Provisioning and growth rates of nestling Fulmars *Fulmarus glacialis*: stochastic variation or regulation. Ibis 139: 31-39.

Hansen, E. and M. Sato, editors. 2012. Paleoclimate implications for human-made climate change. Climate Change. Springer, Vienna: 21-47.

Harris, T. 2000. Shrikes & Bush-shrikes: Including wood-shrikes, helmet-shrikes, flycatcher-shrikes, philentomas, batises and wattle-eyes. A&C Black, Edinburg.

Hertz, P. E., R. B. Huey, and J. R. Garland 1988. Time budgets, thermoregulation, and maximal performance: are ectotherms Olympians or boy scouts. American Zoologist 28: 927-938.

Hey, E. 1975. Thermal neutrality. British medical bulletin 31: 69-74.

Hockey, P. A. R., W. R. J. Dean, and P. Ryan. 2005. Roberts birds of southern Africa. Trustees of the John Voelcker Bird Book Fund.

Hoffmann, A. A. 2010. Physiological climatic limits in *Drosophila*: patterns and implications. Journal of Experimental Biology 213: 870-880.

Hoset, K. S., Y. N. G. V. E. Espmark, A. R. N. E. Moksnes, T. Haugan, M. Ingebrigtsen, and Lier, M. 2004. Effect of ambient temperature on food provisioning and reproductive success in snow buntings *Plectrophenax nivalis* in the high arctic. Ardea, 92:239-246.

Huey, B., and J. G. Kingsolver. 1989. Evolution of thermal sensitivity of ectotherm performance. Trends in Ecology & Evolution 4: 131-135.

Hughes, L. 2000. Biological consequences of global warming: is the signal already apparent? Trends in Ecology & Evolution 15: 56-61.

IPCC (Intergovernmental Panel on Climate Change). 2006. IPCC Fourth Assessment Report: The Physical Science Basis. Contribution of the Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change.

Ivanov, K. P. 2006. The development of the concepts of homeothermy and thermoregulation. Journal of Thermal Biology 31: 24–29.

James, A. R., and K. C. Hamer. 2000. Brood size and food provisioning in Common Terns *Sterna hirundo* and Arctic Terns *S. paradisaea*: consequences for chick growth. Ardea 88: 1.

Jeltsch, F., S. J. Milton, W. R. J. Dean, and N. van Rooyen. 1996. Tree spacing and coexistence in semiarid savannas. Journal of Ecology, 583-595

Kearney M., R. Shine., and W. P. Porter. 2009. The potential for behavioral thermoregulation to buffer "cold-blooded" animals against climate warming. Proceedings of the National Academy of Sciences of the United States of America 106:3835–3840.

Kendeigh, S. C. 1969. Energy responses of birds to their thermal environments. Wilson Bull 81: 441-449.

Kruger, A. C., and S. S. Sekele. 2012. Trends in extreme temperature indices in South Africa: 1962-2009. International Journal of Climatology 33: 661–676.

Kruger, A. C., and S. Shongwe. 2004. Temperature trends in South Africa: 1960–2003. International Journal of Climatology: 24: 1929-1945.

Liu, S. S., G. M. Zhang, and J. U. N. Zhu. 1995. Influence of temperature variations on rate of development in insects: analysis of case studies from entomological literature. Annals of the Entomological Society of America 88: 107-119.

Luck, G. W. 2001. Variability in provisioning rates to nestlings in the cooperatively breeding Rufous Treecreeper, *Climacteris rufa*. Emu 101: 221–224. DOI: 10.1046/j.1442-9993.2002.01173.x

Mares, M. A. ed. 1999. Encyclopaedia of deserts. University of Oklahoma Press, Oklahoma.

Martin, K. 1995. Patterns and mechanisms for age-dependent reproduction and survival in birds. American Zoologist 35:340-348.

Martin, T. E. 1987. Food as a limit on breeding birds: a life-history perspective. Annual Review of Ecology and Systematics: 453-487.

Martin, T. E. 1988 Processes organizing open-nesting bird assemblages: competition or nest predation? Evolutionary Ecology 2: 37-50.

May, J. D., and B. D. Lott. 2001. Relating weight gain and feed: gain of male and female broilers to rearing temperature. Poultry Science 80: 581–584 Available: http://www.ncbi.nlm.nih.gov/pubmed/11372706 (Accessed 20 Jan 14).

McKechnie, A. E., and B.O. Wolf. 2010. Climate change increases the likelihood of catastrophic avian mortality events during extreme heat waves. Biology Letters 6: 253-256.

McKechnie, A. E., P. A. R. Hockey, and B. O. Wolf. 2012. Feeling the heat: Australian landbirds and climate change. Emu 112: i-vii.

Michaud, T. and M. Leonard. 2000. The role of development, parental behavior, and nestmate competition in fledging of nestling Tree Swallows. Auk 117:996-1002.

Miller, A. H. 1963. Desert adaptations in birds. Proceedings of the XIII International Ornithological Congress, 666-674.

Miller, N. A., and J. H. Stillman. 2012. Physiological Optima and Critical Limits. Nature Education Knowledge 3: 1.

Moise, A. F., and D. A. Hudson. 2008. Probabilistic predictions of climate change for Australia and southern Africa using the reliability ensemble average of IPCC CMIP3 model simulations. Journal of Geophysical Research: Atmospheres 1984–2012.

Monaghan, P. 2008. Early growth conditions, phenotypic development and environmental change. Philosophical Transactions of the Royal Society B: Biological Sciences 363: 1635-1645.

Moses, M. R., J. K. Frey, and G. W. Roemer. 2012. Elevated surface temperature depresses survival of banner-tailed kangaroo rats: will climate change cook a desert icon? Oecologia 168: 257-268.

Newton, I. 1998. Population Limitation in Birds. Academic Press, London.

Parmesan, C., and G. Yohe. 2003. A globally coherent fingerprint of climate change impacts across natural systems. Nature 421: 37-42.

Pianka, E. R. 1976. Natural selection of optimal reproductive tactics. American Zoologist 16: 775-784.

Pörtner, H. O. et al. 2006. Trade-offs in thermal adaptation: The need for a molecular to ecological integration. Physiological and Biochemical Zoology 79: 295-313.

Rankin, D. J. 2007. Resolving the tragedy of the commons: the feedback between intraspecific conflict and population density. Journal of Evolutionary Biology 20: 173-180.

Rensel, M. A., T. E. Wilcoxen, and S. J. Schoech. 2010. The influence of nest attendance and provisioning on nestling stress physiology in the Florida scrub-jay. Hormones and behaviour 57:162-168.

Ricklefs, R. E. 1983. Some considerations on the reproductive energetics of pelagic seabirds. Studies in Avian Biology 8:84-94.

Ricklefs, R. E. 2000. Patterns of growth in birds. II. Growth rate and mode of development. Ibis 1

Ricklefs, R. E., and F. R. Hainsworth. 1968. Temperature dependent behavior of the cactus wren. Ecology 49: 227–233. DOI: 10.2307/1934451.

Ricklefs, R. E., and M. Wikelski. 2002. The physiology/life-history nexus. Trends in Ecology and Evolution, 17: 462-468.

Robinson, A. H. Q., Crick, J. A. Learmonth, I. M. Maclean, C. D. Thomas, F. Bairlein, and M. Visser, E. 2009. Travelling through a warming world: climate change and migratory species. Endangered Species Research 7.

Rose, A. P. 2009. Temporal and Individual Variation in Offspring Provisioning by Tree Swallows: A New Method of Automated Nest Attendance Monitoring." PLOS ONE 4: 4111.

Ruben, J. 1995. The evolution of endotherm in mammals and birds: from physiology to fossils. Annual Review of Physiology 57: 69-95.

Salt, G. W. 1964. Respiratory evaporation in birds. Biol. Rev.39:116-133.

Sanz, J. J., J. Potti, J. Moreno, S. Merino, and O. S. Frias. 2003. Climate change and fitness components of a migratory bird breeding in the Mediterranean region. Global Change Biology 9:461-472.

Scholander, P. F., R. Hock, V. Walters, and L. Irvine. 1950. Adaptation to cold in artic and tropical mammals and birds in relation to body temperature, insulation, and basal metabolic rate. Biol. Bull. 99: 259-271.

Schwagmeyer, P. L., and D. W. Mock. 2008. Parental provisioning and offspring fitness: size matters. Animal Behaviour 75: 291-298.

Silberbauer, G. B. 1981. Hunter and habitat in the central Kalahari Desert. CUP Archive.

Sinclair, I., and P. Ryan. 2009. Birds of Southern Africa: Complete Photographic Field Guide. Struik Nature. Cape Town.

Sinervo, B., F. Mendez-De-La-Cruz, D. B. Miles, B. Heulin, E. Bastiaans, Villagrán-Santa M. Cruz, and J. W. Sites. 2010. Erosion of lizard diversity by climate change and altered thermal niches. Science 328:894-899.

Solomon, S., editor. 2007. Climate change -the physical science basis: Working Group I contribution to the fourth assessment report of the IPCC. Vol. 4. Cambridge University Press, Cambridge.

Soobramoney, S., C. T. Downs, and N. J. Adams. 2004. Territorial behaviour and time budgets of the fiscal shrike *Lanius collaris* along an altitudinal gradient in South Africa. African Zoology 39: 137-143.

Spicer, G. S., and K. J. Gaston. 1999. Physiological Diversity and its Ecological Implications. Blackwell Science, Oxford.

Stark, J. M., and R. E. Ricklefs. 1998. Avian Growth and Development: Evolution within the Altricial-precocial Spectrum. Oxford University, Oxford

Stenseth, N. C., A. Mysterud, G. Ottersen, J. W. Hurrell, K. S. Chan, and M. Lima. 2002. Ecological effects of climate fluctuations. Science 297:1292-1296.

Stratford, J. A., and P. C. Stouffer. 1999. Local extinctions of terrestrial insectivorous birds in a fragmented landscape near Manaus, Brazil. Conservation Biology 13: 1416-1423.

Sutherland, W. J., I. Newton, and R. Green. 2004. Bird Ecology and Conservation: A Handbook of Techniques. No. 1, Oxford University Press, Oxford.

Székely, T., and I. C. Cuthill. 1999. Brood desertion in Kentish plover the value of parental care. Behavioral Ecology 10.2: 191-197.

Székely, T., and T. D. Williams. 1995. Costs and benefits of brood desertion in female Kentish plovers, *Charadrius alexandrinus*. Behavioral Ecology and Sociobiology 37: 155-161.

Terblanche, J. S., et al. 2009. Directional evolution of the slope of the metabolic rate–temperature relationship is correlated with climate. Physiological and Biochemical Zoology 82: 495-503.

Tomback, D. F., and J. R. Murphy. 1981. Food deprivation and temperature regulation in nestling ferruginous hawks. The Wilson Bulletin: 92-97.

Towie, N. 2009. Thousands of birds die in sweltering heat. PerthNow. Available: http://www.perthnow.com.au/news/thousands-of-birds-die-in-sweltering-heat/story-e6frg12c-1111118551504. (Accessed 2014 Feb 02).

Towie, N. 2010. More than a hundred White-tailed Black Cockatoos dead near Hopetown. In PerthNow.

Tremblay, A., and J. Ransijn. 2013. Package LMER Convenience Functions.

Valeix, M., H. Fritz, R. Matsika, F. Matsvimbo, and H. Madzikanda. 2008. The role of water abundance, thermoregulation, perceived predation risk and interference competition in water access by African herbivores. African Journal of Ecology 46: 402-410.

Van Rooyen, M. W. 1999. Functional aspects of short-lived plants. The Karoo: Ecological patterns and processes: 107-122.

Vincze, O., T. Székely, C. Küpper, M. AlRashidi, J. A. Amat, A. A. Ticó, and A. Kosztolányi. 2013. Local environment but not genetic differentiation influences biparental care in ten plover populations. PLOS ONE 8.

Visser, M. E., L. J. M. Holleman, and S. P. Caro. 2009 Temperature has a causal effect on avian timing of reproduction. Proceedings of the Royal Society B: Biological Sciences 276: 2323-2331.

Warriner, J. S., J. C. Warriner, G. W. Page, and L. E. Stenzel. 1986. Mating system and reproductive success of a small population of polygamous Snowy Plovers. The Wilson Bulletin: 15-37.

Welbergen, J. A., et al. 2008. Climate change and the effects of temperature extremes on Australian flying-foxes. Proceedings of the Royal Society B: Biological Sciences 275: 419-425.

Williams, S. E., L. P. Shoo, J. L. Isaac, A. A. Hoffmann, and G. Langham. 2008. Towards an integrated framework for assessing the vulnerability of species to climate change. PLOS biology 6:325.

Willmer, P. G. 1982. Microclimate and the environmental physiology of insects. Advances in insect physiology 16: 1-57.

Wilson, E. O. 1992. The Diversity of Life. Harvard University Press, Cambridge, MA.

Wolf, B. O. 2000 .Global warming and avian occupancy of hot deserts; a physiological and behavioral perspective. Revista Chilena de Historia Natural 73: 395-400.

World Bank Group, editors. 2012. World Development Indicators 2012. World Bank Publications, Washington DC.

Zeileis, A., C. Kleiber, and S. Jackman. 2007. Regression models for count data in R.