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**Birds at risk in warming southern African deserts –  
inferences from behavioural and physiological  
thermoregulation**



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## Abstract

Although many studies have investigated adaptations to heat stress, this study explored using observational data to determine how and when birds use a combination of both behavioural and physiological thermoregulation. The study focused on avian species' responses to high ambient temperature. Ambient temperature is a variable to which birds are particularly sensitive and which climate-change models predict will increase disproportionately rapidly in southern Africa's hot deserts, especially the Kalahari. The effect of ambient temperature on microsite use and foraging were analysed in order to investigate whether and under what conditions these forms of behavioural thermoregulation were used and by which species. The majority of ground-foragers made increasing use of shaded microsites as temperatures rose. This pattern was not apparent among strictly arboreal foragers because, even at high ambient temperatures, these birds are able to continue to forage in shaded and relatively cool microclimates. Species belonging to the guilds which forage at the ground surface are thus more vulnerable to having to make a trade-off between active foraging and seeking shade. The incidence of heat-dissipation behaviour was studied using three different combinations of observation times and resolutions. Under current conditions, the majority of species use evaporative cooling as a means of physiological thermoregulation, implying that the frequency and/or duration with which they will have to do this in the future may increase, elevating their vulnerability to climate change. Not all species responded to rising ambient temperatures in similar manners. Apart from ambient temperature, the variables explaining the response of heat dissipation are body mass, foraging guild and the interaction between ambient temperature and guild. The traits that predisposed species to being particularly vulnerable to high ambient temperatures were large body size and obligate ground-foraging. By contrast, the species that are most resilient to high ambient temperatures are arboreal insectivores – species whose diets are water-rich and whose foraging micro-habitats are largely shaded. It is these species which will be among the best adapted to the rising ambient temperatures predicted for the future. The study also aimed to determine the best practice for the observational study of heat dissipation. Based on the importance of detecting heat stress at low temperatures, a 30-second observation period (and whether or not heat-dissipation behaviour occurs at any time during this period) is recommended over instantaneous scans. The most labour-intensive method (of recording the time spent in heat-dissipation) adds little understanding to the binary response data.

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## CHAPTER 1: Literature Review

### Climate change

#### Global trends

The profound influence of climate on species and ecosystems has been well documented in the literature (Andrewartha & Birch 1954; Janzen 1994; Parmesan *et al.* 2000; Stenseth *et al.* 2002; Lovegrove 2003; Crick 2004). It is this established relationship which makes the global temperature rise of between 0.3 and 0.8°C (as documented over the last century - IPCC 1996; Houghton *et al.* 2001) concerning in terms of its longer term consequences. The plausible link between recent changes in climate and observed changes in species and communities is now largely accepted (Brown *et al.* 1999; Parmesan *et al.* 1999; Pounds *et al.* 1999; IPCC 2001a; Peñuelas & Filella 2001; Walther *et al.* 2002; Parmesan & Yohe 2003; Root *et al.* 2003; Walther *et al.* 2005). Some birds are adversely affected by average ambient temperature increases as small as 1°C (Shoo *et al.* 2005), so it is unsurprising that many taxa have undergone recent changes in their ranges (Parmesan *et al.* 1999; Thomas & Lennon 1999; Hughes 2000; Parmesan & Yohe 2003; Root *et al.* 2003; Thomas *et al.* 2004; Wilson *et al.* 2005), phenologies (Parmesan 1996; Crick *et al.* 1997; Bradley *et al.* 1999; Brown *et al.* 1999; Dunn & Winkler 1999; Roy & Sparks 2000; Walther *et al.* 2002; Parmesan & Yohe 2003; Root *et al.* 2003; Marra *et al.* 2005; Root *et al.* 2005), and morphologies (Kingsolver 1995; Chamaillé-Jammes *et al.* 2006). In some cases, these changes represent a serious threat to biodiversity (Thomas *et al.* 2004; Jiguet *et al.* 2006; IPCC 2007). Current rates of extinction are estimated to be 100–1000 times greater than pre-human rates (Lawton & May 1995; Pimm *et al.* 1995), with global climate change being one of the primary drivers (Karl & Trenberth 2003): as many as one million species may become extinct in the next 40 years (Parmesan & Yohe 2003; Thomas *et al.* 2004).

#### Global predictions

Although emissions have been curbed in some parts of the world, the 2050 climate projections (WorldClim database: Hijmans *et al.* 2005) are unlikely to be avoided (Sinervo *et al.* 2010). Indeed, the greenhouse gases emitted over the next 100 years are likely to cause the most rapid and accelerated climate change (IPCC 2007) that the Earth has experienced since at least the end of the last glaciation (i.e. 18 000 years ago) (Chapin *et al.* 2000). Climate change involves much more than merely a change in ambient temperature ( $T_a$ ). This

“change” is likely to produce novel environmental scenarios (Kearney *et al.* 2010), with changes in rainfall regimes (IPCC 1996; Hannah *et al.* 2002); declining water balances (Hannah *et al.* 2002), a generally more variable climate (IPCC 1996; Easterling *et al.* 2000; IPCC 2002; Wormsworth & Mallon 2006); and an increased frequency of extreme weather events (IPCC 1996; Easterling *et al.* 2000; Hannah *et al.* 2002).

### Local trends and predictions

Africa has been identified as the most vulnerable of all continents (IPCC 2001b). The greatest increase in daily maximum temperature over the past 20 years has occurred in Africa (IPCC 2001b), which is also predicted to become increasingly warm and arid and to experience an increased frequency of weather anomalies (Zwiers & Kharin 1998; IPCC 2001b). Despite these ominous forebodings for Africa’s climate, the impacts on African birds have been little explored (Erasmus *et al.* 2002; Wichmann *et al.* 2003; Simmons *et al.* 2004). In keeping with the rest of the continent, southern Africa is equally expected to experience a more dynamic and variable climate in the future (IPCC 2001b), as well as an increase in the duration and frequency of extreme temperatures (Kruger & Shongwe 2004; Wormsworth & Mallon 2006). These changes would include a 2-3°C rise in mean annual temperature within the next 50 years (IPCC 2001b), as well as lower rainfall in most areas (IPCC 2001b). Although global trends are well established in comparison to changes occurring on a regional scale (IPCC 1995), the Kalahari Desert is the area predicted to undergo the fastest warming within southern Africa (Moise & Hudson 2008). Along with future predictions for other deserts, the summer  $T_a$  maxima of the Kalahari is expected to rise by 3–5°C (IPCC 2007) and rainfall variability is likely to increase (Moise & Hudson 2008).

### Climate models

Many predictions about the consequences of climate change are based on models (e.g. Peterson *et al.* 2002; Thuiller 2003; Thomas *et al.* 2004; Thuiller *et al.* 2005). The strength of inferences and the predictive power of such models depends upon the identification of key limiting processes (Hannah *et al.* 2002; Kearney *et al.* 2010) which, according to Angilletta (2009) can be attained through the quantification of thermo-tolerances and investigating the potential to adapt to environmental change. Most studies that have investigated the response of species to change have focussed on climate itself (the long-term change) as the predictor variable (Peterson *et al.* 2002; Thomas *et al.* 2004; McKechnie & Wolf 2010). However, species respond to extreme weather events – and thus respond to changes occurring within



extremely short-time frames. These include documented reproductive responses to daily temperature variation (Pendlebury *et al.* 2004) and drought (e.g. Herremans 2004; Bolger *et al.* 2005). There has also been incidences of mortality as a result of severe winter storms and temperatures (e.g. Altwegg *et al.* 2006; Newton 2007; Frederiksen *et al.* 2008). Extreme heat waves have also led to catastrophic avian mortality with birds reaching lethal body temperatures (Finlayson 1932; Keast 1960). In these situations, species are not responding to a change in climate, but rather a change in weather (Easterling *et al.* 2000; Parmesan *et al.* 2000). Indeed, the impact of weather on the population biology of birds has become a major field of study by ornithologists over the past half century (Crick 2004). Analyses across ecologically relevant time scales are critical if we are to link changes in species' behaviour and distribution with a changing environment (Root & Schneider 1995).

### **Conditions and challenges of hot arid environments**

Thermal environments in nature can be remarkably complex (Walsberg & Wolf 1996), and have even been described as “impossible to define” for the terrestrial environment (Bakken 1976). However, the following four variables contribute to environmental temperature (the effective temperature an organism experiences): ambient temperature, solar radiation, wind and humidity (e.g. Porter & Gates 1969; Bakken *et al.* 1981). Of these, temperature is the variable to which birds are particularly susceptible (Wolf 2000; Williams & Tieleman 2002, 2005).

Common features characterising deserts are great seasonal and daily extremes of ambient temperature, unpredictable and scarce water, low relative humidity, and a shortage of food and shade (Austin 1976; Lovegrove 1993; McCarty 2001; Williams & Tieleman 2005; White *et al.* 2007; Bicudo *et al.* 2010). Of these, the two main challenges faced by desert-dwellers are extreme heat and limited water (Ricklefs & Hainsworth 1968). Deserts receive more radiation than any other part of the planet (Williams & Tieleman 2005) with the resulting high potential evapotranspiration further reducing the already scarce free water sources (White *et al.* 2007). The combination of extreme heat and limited options to replenish body fluids presents critical conditions for effective temperature regulation and water balance in resident animals (Ricklefs & Hainsworth 1968) and contributes to making deserts some of the harshest terrestrial environments (Williams & Tieleman 2005), even for those organisms adapted to hyper-aridity (Dean *et al.* 2009).

Heat-load problems are expected to occur most frequently in places where heat gain is high and heat-loss potential is low (Battley *et al.* 2003). Environmental variables that will affect any organism will be those that influence the acquisition of food required for growth and reproduction (Porter *et al.* 1973). Environmental temperature affects body temperature, in turn controlling decisions about when to switch from one behaviour to another (Houston & McNamara 1999). Several studies have demonstrated that animals reduce activity at high temperatures as the need for thermoregulation becomes increasingly pressing (e.g. Goldstein 1984; Carmi-Winkler *et al.* 1987; Williams 2001). Metabolic heat production (and thus body temperature) can also increase more than ten-fold with activity (Bicudo *et al.* 2010).

The direct effect of temperature on the physiology of organisms has been investigated in some detail (e.g. Woodward 1987; Schmidt-Nielson 1997; Wood & McDonald 1997). Body temperature is unaffected by fluctuating thermal conditions at moderate ambient temperatures (Kendeigh 1969), but as temperature rises above a certain point, metabolic rate increases exponentially (Gillooly *et al.* 2001). This is usually accompanied by an increase, often linear, in body temperature (Weathers 1981). When the temperature of the physical environment approximates or exceeds body temperature, the thermal gradient for passive heat transfer (radiation, conduction and convection) is compromised (Lasiewski & Seymour 1972; Wolf 2000). It is at this point that birds use evaporative water loss to regulate the gain of body heat (Wolf 2000): in desert and semi-desert environments, the potential to use such a cooling mechanism is limited by the scarcity of water (Lovegrove 1993; Tieleman & Williams 2002, White *et al.* 2007) and attendant risk of dehydration (Weathers 1981; Lovegrove 1993). Problems of water loss are intensified in endotherms because of the increased evaporative and excretory water loss associated with their high rate of metabolism (Williams & Tieleman 2002): water loss from the skin of desert mammals and birds is approximately ten times higher than that of desert reptiles (Lovegrove 1993).

## **Adaptations to desert living**

### Background

Under conditions of increasing thermal stress, given enough time or adequate dispersal ability, species may shift to more favourable thermal environments, or adjust to new environments through behavioural plasticity, physiological plasticity, or adaptation (Sinervo *et al.* 2010). Such adaptation has been described as “a phenotypic trait that results in the highest fitness among a specified set of variants in a given environment” (Reeve & Sherman

1993); or “any trait that lessens heat stress and reduces water loss, and thus aids in meeting opposing requirements of water balance and temperature regulation” (Austin 1976). Despite evidence of climate change affecting species’ ranges and phenologies, evidence of climate-change-driven extinctions is lacking (Hare & Meinshausen 2006), implying a certain level of adaptation among species (Hughes 2000; Walther *et al.* 2002).

### Ectotherms vs endotherms

Ectotherms are often regarded as thermal specialists (Deutsch *et al.* 2008). Reptiles maintain remarkably constant body temperatures over a wide range of ambient temperatures by adjusting activity and exposure (Cowles & Bogert 1944). Respiratory water is also conserved in desert-dwelling arthropods by the modified waxy cuticle (Williams & Tieleman 2005), while arid-zone amphibians minimise cutaneous water loss through lipid secretions onto their skin (Jorgensen 1997). In contrast to ectotherms, which can tolerate relatively wide temperature fluctuations due to their deriving most of their body heat from outside sources (Lovegrove 1993), endotherms (mammals and birds) are, at face value, poor candidates for successful occupation of deserts (Williams & Tieleman 2002). For birds in particular, high rates of evaporative water loss and mass-specific metabolism (Williams & Tieleman 2005), along with their relatively small body size (McKechnie & Wolf 2010), do not seem to favour a desert lifestyle (Williams & Tieleman 2001). Unlike many desert mammals that are nocturnal and fossorial (Ricklefs & Hainsworth 1968; Bicudo *et al.* 2010), desert birds are active during the day and make limited use of cool microsites (Wolf 2000; Williams & Tieleman 2005, McKechnie & Wolf 2010); and therefore confront the hottest parts of the desert day directly (Wolf 2000). In fact, unlike mammals, the similarity in physiology between desert and non-desert birds led to early conclusions that birds have no special adaptations to desert living (Bartholomew & Cade 1963). Subsequently, however, birds have been found to possess subtle adaptations and preadaptations (Austin 1976), allowing for their residency in the hottest and driest deserts in the world (Williams & Tieleman 2001). These include higher evaporative cooling efficiencies, lower metabolic rates and greater tolerances for high ambient temperatures, relative to closely-related mesic forms (e.g. Salt 1952, Hudson & Kimzey 1966).

Thirty years ago, thermoregulatory responses of desert birds had been studied for very few species (Lasiewski & Seymour 1972), making generalisations difficult. Since then, both physiological responses (Bartholomew & Cade 1963; McNab & Morrison 1963; Schmidt-

Nielsen *et al.* 1970; Lustick *et al.* 1979; Wolf & Walsberg 1996; Tieleman & Williams 2000; Tieleman *et al.* 2002; Williams & Tieleman 2005) and behavioural responses (Vorhies 1928; Bartholomew 1966; Ricklefs & Hainsworth 1968; Dawson & Bennett 1981; Walsberg 1993) of desert birds have been studied in some detail. However, few studies (e.g. Dawson & Bennett 1981; Wolf 2000) have looked at both types of thermoregulation and the interaction between them.

### Physiological thermoregulation

#### *High metabolic rates and body temperatures*

The full range of physiological mechanisms that may have evolved to reduce evaporative water loss in desert birds remains uncertain (Williams & Tieleman 2002). However, there are a number of physiological mechanisms that have been proposed as being likely. These include the excretion of uric acid rather than an aqueous solution as in mammals (Bartholomew & Cade 1963; Bicudo *et al.* 2010); a counter-current heat exchange system in the nasal passages that lowers respiratory water loss (Schmidt-Nielsen *et al.* 1970); a lipid modification of the stratum corneum of the skin of desert birds reducing total evaporative water loss (Williams & Tieleman 2005); and a reduced basal metabolic rate in comparison to non-arid taxa (Bartholomew & Cade 1963; McNab & Morrison 1963; Hudson & Kimzey 1966; Tieleman & Williams 2000, 2002; Williams & Tieleman 2005). Advantages attributed to reduced basal metabolism include lower overall energy demand and lower respiratory water loss (Williams & Tieleman 2005), as well as reduced rates of heat production (McNab & Morrison 1963, Williams & Tieleman 2005), both of which may be strongly selected for in the extreme environments that characterise deserts (Williams & Tieleman 2002, 2005; White *et al.* 2007).

High core body temperature is another avian feature that may facilitate desert residency and may thus be selected for in such environments (Williams & Tieleman 2002). Indeed, desert birds have the highest body temperatures of all vertebrates, 3–4°C higher than those of mammals (Wolf 2000) and averaging a relatively constant temperature of between 39–42 °C in moderate  $T_a$  (Bartholomew & Cade 1963). However, most birds have the ability to become hyperthermic when heat-stressed (Lasiewski & Seymour 1972), whereby body temperature increases by an additional 2–4°C (Wolf 2000). This allows for the bird to tolerate sublethal, reversible increases in body temperature (McKechnie & Wolf 2010). Hyperthermia has been demonstrated in many birds exposed to ambient temperatures of 45°C, thereby reducing total

evaporative water loss by about 50% (Williams & Tieleman 2005). For this reason, it has been proposed as another physiological mechanism that has evolved to reduce total evaporative water loss in desert birds (Weathers 1981; Dawson 1984).

### *Heat-dissipation behaviour*

When  $T_a$  exceeds body temperature, the only avenue available to maintain body temperature below lethal limits (known to be around 46–47°C) is through evaporative cooling, either from respiratory passages or from the skin (James 1970; Dawson 1982; Williams & Tieleman 2005; Bicudo *et al.* 2010). An example of this enhanced dependence on evaporative cooling in rising temperature is the four-fold increase in evaporative water loss of Abert's and Brown Towhees (*Pipilo aberti* and *P. fuscus*) observed between 30 and 40°C (Bartholomew & Cade 1963), as well as the exponential loss of water in Verdins (*Auriparus flaviceps*) (Wolf & Walsberg 1996) and Hoopoe and Dunn's Larks (*Alaemon alaudipes* and *Eremalauda dunnii*) at temperatures exceeding approximately 37°C (Tieleman *et al.* 2002). An increased reliance on evaporative cooling is achieved through heat-dissipation mechanisms of panting, gular fluttering, wing spreading, head drooping and ptilo-erection. Panting increases the rate and amplitude of breathing movements (Lasiewski & Bartholomew 1966), a well-known behaviour that increases evaporative heat loss (Battley *et al.* 2003) by facilitating buccal evaporation (Weathers 1981). Most birds pant when subjected to heat stress, but some supplement evaporation from the respiratory tract by fluttering the gular area (Bartholomew *et al.* 1968). Gular fluttering involves a rapid oscillation of the floor of the mouth, causing more quick and shallow breathing which moves more air over the moist respiratory surfaces than normal, and effectively cools the blood in that region (Lovegrove 1993). Wing spreading is hypothesised to serve three functions, one of which is thermoregulation (Clark 1969) as observed in a number of species in severe heat conditions (Heath 1962; Bartholomew *et al.* 1968; Curry-Lindahl 1970). Ptilo-erection (i.e. the raising of the back feathers) helps to avoid heat load (Battley *et al.* 2003) by increasing the distance between the 'heating surface' and the body while increasing airflow through the feather layer (Bartholomew 1966).

### Behavioural thermoregulation

Several authors are in agreement that pre-adaptive and adaptive physiological features alone appear insufficient to allow many species to adapt completely to desert living (e.g. Austin 1976, Huey 1991, Anava *et al.* 2001, Huey & Tewksbury 2009), and that additional activity modifications are necessary to allow for the dissipation of more heat and the reduction of

heat production (Bucher 1981). Although basal metabolic rate is reduced by about 20% in desert compared to non-desert larks, the overall energy expenditure (i.e. field metabolic rate) is almost almost 50% lower, highlighting the importance of behavioural thermoregulation (Tieleman & Williams 2000). Behavioural mechanisms of thermoregulation are those defined as relying on the avoidance or reduction of heat stress, rather than on conserving water (Ricklefs & Hainsworth 1968). The same authors also note that desert birds had received little attention with regard to the importance of behaviour for reducing heat stress. This form of thermoregulation involves the use of cooler microsites and a shift towards inactivity, behaviours which have long been recorded (e.g. Vorhies 1928; Walsberg 1993; Ricklefs & Hainsworth 1968; Dawson and Bennett 1981).

#### *The use of cooler microsites to reduce heat stress*

The study of how and why organisms select particular habitats has long been central to ecology (Huey 1991). Unlike most aquatic environments, terrestrial environments often offer diverse heat sources and sinks, and 'retreats' that organisms can take advantage of to avoid thermal stress (Feder & Hofmann 1999). Organisms do not experience the climatic conditions measured by weather stations (i.e. macroclimate), but seek out micro-climates/sites that buffer ambient conditions (Kearney & Porter 2009). This is particularly true for birds living in desert environments, whose survival times would be reduced at most temperatures if under continuous exposure to the sun (Wolf 2000). There appears to be active selection of specific microsites or thermal refuges, which serve to minimise rates of both heat gain and evaporative water loss (Wolf 2000). The amount of thermoregulation required is extremely sensitive to variation in the local physical environment (Walsberg 1986). For this reason, the selection of microsites is critical, effectively impacting the fraction of an animal's energy budget available for vital activities such as foraging.

#### *Trade-offs between foraging and heat management*

The optimal pattern of time allocated to various behaviours, and the time at which to switch from one behaviour to another (e.g. from foraging to resting), may shift when a variable such as body temperature changes (Houston & McNamara 1999). An important correlate of desert residency is the suppression of activity during the hottest periods of the day, reflecting the need to minimise evaporative water loss (Wolf 2000). Food intake of endotherms is often inversely related to environmental temperatures (Huey 1991); with a greater proportion of time allocated to inactivity at high temperatures (Vorhies 1928; Ricklefs & Hainsworth 1968;

Lasiewski & Seymour 1972; Austin 1976). Activity is associated with heat gains (McKechnie & Wolf 2010) because metabolic rates are elevated above resting levels (Brown *et al.* 1978; Nagy 1987). Activity in hot weather may thus result in body temperatures exceeding the critical thermal maximum, leading to death (Sinervo *et al.* 2010).

### **Vulnerability to high temperature**

The question of what makes some species more vulnerable than others has evoked considerable interest (Krebs *et al.* 1999; Warren *et al.* 2001). Different species within communities are responding in a non-uniform manner to climate change (La Sorte *et al.* 2009), with evidence for this from butterflies in Britain (Warren *et al.* 2001; Mene'ndez *et al.* 2006) and plants on Marion Island (Le Roux & McGeoch 2008). In line with this, is the fact that some species are expected to benefit, and others to suffer from a changed climate (Erasmus *et al.* 2002). The magnitudes of geographic and phenological shifts during recent climate change have also varied greatly among species (Parmesan 2006, 2007), potentially reflecting different thermo-tolerances. Failure to understand the mechanism behind these differences tolerance levels appears to be a major shortfall of large-scale predictions (Helmuth *et al.* 2005) such as envelope models (Buckley 2008) and species distribution models (Kearney & Porter 2009). According to Jiguet *et al.* (2006), thermal range could be used as one critical measure of the potential risk of species to climate change. Other possible factors that could determine whether species are vulnerable or resilient to high ambient temperatures are body size and guild (i.e. foraging location and diet).

### Body size

It is widely accepted that body size is the characteristic of an organism that influences the most aspects of its biology (including energy expenditure and acquisition - Brown *et al.* 1978; Bozinovic & Medel 1988). Organisms under the same temperature conditions may withstand very different combinations of environmental conditions and heat stress, depending on morphological characteristics, such as size (Weathers 1981; Huey 1991; Kearney & Porter 2009). This is as a result of birds exchanging heat with their surroundings at rates proportional to their surface areas, while heat storage is proportional to body mass (Weathers 1981). The rate at which body temperature increases with ambient temperature should vary inversely with size (Weathers 1981), with larger birds having the 'upper hand' (James 1970) due the more gradual change in body temperature because of stored heat (Kearney & Porter 2009). If balancing the water budget is paramount (e.g. Bartholomew & Cade 1963;

McKechnie & Wolf 2010), then the high mass-specific metabolism (Stevenson & Bryant 2000) and large surface-area-to-volume-ratios of small birds (Austin 1976) require that they must respond rapidly to changes in the thermal environment if they are to maintain homeostasis (Wolf 2000).

Two unpublished studies on heat-dissipation behaviour in birds of southern Africa's Kalahari Desert have been conducted in two study sites, over two successive summers. From data collected in Kgalagadi Transfrontier Park (KTFP), size emerged as a robust indicator for predicting species' vulnerability to rising temperatures; with larger birds showing heat stress at lower temperatures than smaller birds (Cordingley 2008, unpubl. data). The bird community at Tswalu Kalahari Reserve (Tswalu), on the south-eastern fringes of the Kalahari showed the same response with regards to size. However, size was not the only variable explaining these differences. Under increasing temperature, the proportion of heat-stressed individuals increased at a more gradual rate in large birds as oppose to smaller birds. Large-bodied birds may have to spend more time dissipating heat, but their large size may allow them to do this for sustained periods of time (A. McKechnie, *pers. comm.*). At this point it is important to note that although correlates of body-size variation are well documented, their biological causes and consequences are often complex and poorly understood (Brown *et al.* 1978).

#### Foraging guild and diet

Ground-dwelling and ground-nesting birds are expected to be less resilient than arboreal species to high-temperature anomalies, based on their narrow thermal range – defined as the difference between the thermal maximum (i.e. mean of local spring/summer average monthly temperatures for the hottest 50 breeding grid cells in Europe) and the thermal minimum (i.e. mean spring/summer temperature of coldest 50 breeding cells in Europe) (Jiguet *et al.* 2006, Oparin 2008). Because birds living in deserts often do not have access to drinking water, they must rely on their diet to supply their water needs (Williams & Tieleman 2001). There are strong indications that water might be a major consideration in the selection of food items (Tieleman & Williams 2002). With seeds containing only about 10% or less water, it is difficult for granivores to achieve independence from free water (Bartholomew & Cade 1963). Insectivorous and carnivorous desert birds are generally assumed to be less dependent on free water because of the preformed water in their food (Bartholomew & Cade 1963; Lovegrove 1993; Bicudo *et al.* 2010).



### Community impacts from variation in vulnerability

Most studies that have attempted to model impacts of a changing climate on species have been single-species in nature (La Sorte *et al.* 2009). This may mask broader scale community-level effects (Helmuth *et al.* 2005), with most ecosystem processes coming about through the interactions among species (Chapin *et al.* 2000). Differing responses to climate change across taxa means that species composition, and thus functioning of the community, is also likely to be altered (Loreau *et al.* 2001). Within communities, many interspecific interactions are closely tied or mutualistic, increasing the probability that the loss of any one species will have cascading effects on the rest of the system (Chapin *et al.* 2000). The impacts of climate change on biodiversity therefore manifest at higher levels of organization such as populations, communities, and ecosystems (McCarty 2001; Kearney & Porter 2009). Although there is no disputing the effect of climate on individual species, the mechanism by which these effects arise and the consequences that they have for long-term population persistence remain poorly understood (La Sorte *et al.* 2009; Charmantier *et al.* 2010). Because of this, McCarty (2001) concludes that although investigation into the response of individual species may contribute to understanding the effects of recent climate change, more powerful tests would be achieved through the analyses of groups of organisms or entire community.

## CHAPTER 2

### Introduction

In concert with climate change predictions made for much of the world, southern Africa is predicted to experience a more dynamic and variable climate in the future (IPCC 2001b). Within southern Africa, the Kalahari Desert is the area predicted to undergo the fastest rate of change (Moise & Hudson 2008). This change in climate is expected to involve an increase in summer temperature maxima (IPCC 2007), an increase in the duration and frequency of extreme high temperatures (Kruger & Shongwe 2004), as well as greater variability in rainfall patterns (Moise & Hudson 2008). With extreme heat and water limitation being two of the major challenges to organisms living in hot, arid environments (Ricklefs & Hainsworth 1968), should these predictions come to pass they will make desert-dwelling an even more formidable task for its inhabitants than it is at present. Although the accurate prediction of how ecosystems are likely to respond to climate change is very much needed in a world undergoing accelerated warming, it is also perhaps the biggest challenge in our conservation efforts (Angilletta 2009).

Birds have certain adaptations that allow them to cope with the harsh temperatures that characterise deserts (Austin 1976; Williams & Tieleman 2005; White *et al.* 2007). These include behavioural and physiological adaptations; both of which have been studied independently in great detail. Behavioural adaptations are based on the premise that temperature affects vital activities through constraining activity patterns (Houston & McNamara 1999). Responses would thus include a retreat to microsites that minimise heat gain and water loss (Feder & Hofmann 1999; Wolf 2000), as well as reduced foraging effort (Huey 1991; McKechnie & Wolf 2010). The quantification of a direct link between stress behaviours and what they indicate in terms of physiology validates the use of behavioural observations as indicators of stress (Withers & Williams 1990). For this reason, the visible expression of heat stress in the form heat-dissipation behaviour (shown by all species (Lasiewski & Seymour 1972; Weathers 1981) formed the basis of this study. Heat dissipation behaviours provide effective means of evaporative cooling, achieved through actively increasing the rate of water loss (Williams & Tieleman 2005). Therefore, although increasing the risk of dehydration (Weathers 1981; Lovegrove 1993), it represents an important mechanism to avoid overheating (James 1970; Dawson 1982; Williams & Tieleman 2005).

As discussed in Chapter 1, similar patterns of heat-dissipation behaviour emerged from Kgalagadi Trans-Frontier Park (KTFP) and Tswalu Kalahari Reserve (Tswalu). One noteworthy difference however, was the variation in the minimum ambient temperature ( $T_a$ ) at which heat-dissipation behaviour occurred, with birds at Tswalu showing heat stress at consistently lower ambient temperatures than those at KTFP. This could be a result of the differing methodologies used in the documentation of heat dissipation. Heat-dissipation behaviour was established from instantaneous scans at KTFP (Type 1), and from 30-second observations at Tswalu (Type 2) (both measured as binary responses). The methodology used to measure temperature also differed between the two studies, where a thermocouple from a running vehicle was used to record temperature at KTFP, while temperature records at Tswalu were based solely on weather station measurements. The consequences of using different methodologies are important if we are to draw accurate conclusions from documented heat-stress behaviour.

There has been some scepticism regarding the importance of climate change on wild systems (Lomborg 2001). According to Parmesan & Yohe (2003), this is largely due to ignoring small, systematic trends that become important in the longer term. This is where the studying of responses of species to weather becomes highly relevant, because, from an individual organism's perspective climate is simply a cumulative sequence of weather events (e.g. McKechnie & Wolf 2010). Although many climatic variables are predicted to change (Easterling *et al.* 2000; Walther *et al.* 2002; Hannah *et al.* 2002; IPCC 2002; Wormsworth & Mallon 2006), extreme heat is the variable that ranks among the most threatening aspects of anthropogenic climate change (Angilletta 2009). Birds are also particularly susceptible to high  $T_a$  because they are (mostly) diurnal, and have high metabolic rates and body temperatures (Wolf 2000; Williams & Tieleman 2002, 2005).

The significant influence of climate on species is well-established in the literature (e.g. Root 1988, Parmesan 1996, McCarty 2001, Pearson & Dawson 2003), where the climatic influence is strongly mediated through species-specific physiological thresholds of temperature tolerance. In support of this, species do respond differently to extreme heat and thus differ in their vulnerability to increases in ambient temperature (McNeely 1995; La Sorte *et al.* 2009). The fact that different species respond differently to high ambient temperatures also implies that the composition and functioning of most communities and ecosystems is likely to change (Erasmus *et al.* 2002). Tolerance levels for individual species are not well established, and

without these the predicting of consequences of current and predicted climate change for biodiversity will be a major challenge (McNeely 1995).

Based on previous work and preliminary evidence, large birds are likely to experience heat stress at lower ambient temperatures than small birds: however, the rate that stress accelerates as temperature rises is more gradual than for smaller birds (Bartholomew & Cade 1963; Austin 1976; Stevenson & Bryant 2000; McKechnie & Wolf 2010). Foraging behaviour and the availability of shaded microsites are likely to be important correlates of vulnerability to rising temperatures. Obligate ground-dwellers are likely to be most vulnerable by virtue of their inability to exploit the cooler ambient temperatures away from the ground surface (e.g. Kotzen 2003). The limited areas of shade provided by trees at ground level (especially in desert and semi-desert environments) also means that there are limited opportunities for birds to continue foraging under conditions of high  $T_a$ . Birds that are ground foragers, but are able to seek shade in microsites away from the ground surface (in trees and shrubs) will have more shaded sites available, even if they don't have better options for extended foraging periods. The least vulnerable to high  $T_a$  however, are predicted to be those birds that forage off-ground, where not only is it cooler, but where microsites are three-dimensional and thus largely shaded. Species with an animal-based diet (mostly insectivores and carnivores) are also expected to be less vulnerable to dehydration by virtue of a high proportion of preformed water in their diet relative to species with a plant-based diet (mostly granivores - Bartholomew & Cade 1963).

### **Objectives and Rationale**

This study aims to investigate how thermoregulation (both behavioural and physiological) is used by different species to cope with the challenge of extreme heat. A second objective is to establish the combination of traits that determine vulnerability or resilience to heat, providing insight into how desert bird communities are likely to change in the face of changing climate. Lastly, best practice for studying heat-dissipation behaviour will be investigated.

The rate at which climate change is taking place is drastic (IPCC 1992, 1995, 2002, 2007), and is only set to worsen (e.g. IPCC 2007; Sinervo *et al.* 2010). With the composition of desert bird communities predicted to change (Wolf 2000), and the climate of the Kalahari Desert predicted to change the fastest within southern Africa (Moise & Hudson 2008), understanding how this bird assemblage is responding to current weather will be important in

predicting its future trajectory. With growing evidence that some species may find it difficult to adapt to climate change (Harrington *et al.* 1999), exploring the characteristics of what makes species vulnerable or resilient (Jiguet *et al.* 2006) through field-based observations of temperature thresholds (Geiser *et al.* 2007; White *et al.* 2007; Angilletta 2009) will allow the identification of those most at risk. This in turn may inform future conservation priorities (McCarty 2001; Julliard *et al.* 2004a; Hulme 2005; Jiguet *et al.* 2006; Kearney *et al.* 2010).

### **Questions, Hypotheses and Predictions**

*Behavioural thermoregulation - Question 1a: Is microsite use affected by  $T_a$ ?*

$H_0$  = Microsite use is independent of ambient temperature. The same microsites are used, regardless of ambient temperature.

$H_1$  = Microsite used will change as ambient temperatures rise, with shaded (and, where possible, off-ground) microsites favoured over sun-exposed, on-ground microsites. As temperature rises, shaded microsites will become increasingly favoured. The retreat to shade is predicted to be most pronounced among ground-foraging species dependent upon projected shade from trees and bushes.

*Behavioural thermoregulation - Question 1b: Is foraging activity reduced when  $T_a$  rises?*

$H_0$  = Foraging is independent of temperature. There is no significant reduction in foraging as temperature rises.

$H_1$  = Foraging will be reduced at higher temperatures because of the need to seek shade for thermoregulation. There will be a significant negative relationship between foraging activity and temperature, most pronounced for obligate ground-foragers and least pronounced in species that forage off-ground.

*Physiological thermoregulation - Question 2a: How do patterns of heat dissipation differ between species?*

$H_0$  = Heat-stress, and therefore the use of heat-dissipation in thermoregulation, is uniform among all species, starting at approximately the same temperature and increasing in severity at the same rate as temperature increases.

$H_1$  = Species differ in their physiological response to heat. Not all species will show a significant increase in heat dissipation with increasing temperature; and of those species that do, the severity of heat-stress with temperature will differ among them.

*Physiological thermoregulation - Question 2b: What is the best observational methodology to use when documenting heat dissipation?*

$H_0$  = Conclusions about the onset and severity of heat stress will be the same whether behaviour is recorded using instantaneous scans (binary response), a 30-second observation period (binary response), or the proportion of time spent heat-stressed in 30 seconds (continuous response).

$H_1$  = Conclusions about heat stress (for the same species) will differ depending on the method used to observe birds. Relative to other types of data, data based on instantaneous scans are likely to underestimate both the onset and severity of heat stress.

*Behavioural and Physiological thermoregulation - Question 3: What is the trait or combination of traits that predispose some species to being more particularly vulnerable to high  $T_a$ ?*

$H_0$  = All species are equally vulnerable to high ambient temperature. Thermoregulation is used in the same way across all species, ergo temperature will be the only variable explaining the thermoregulatory responses for all species.

$H_1$  = Some species will be more vulnerable to high temperatures than others, depending on their size, foraging guild or a combination of the two. Large, ground-foraging, granivorous species are predicted to be most vulnerable in high temperature conditions.

## Study sites

The main study site was Dreghorn Kalahari Game Ranch (Dreghorn), with supplementary data collected at Kgalagadi Transfrontier Park (KTFP) and Tswalu Kalahari Reserve (Tswalu). Dreghorn extends across 4748 ha of the south-western Kalahari Desert. It is situated on the border of South Africa and Botswana (26.85851 S, 20.78527 E), with the KTFP to the north-west and Tswalu Kalahari Reserve to the south-east (Fig. 1). The region is both hot and arid, experiencing extreme fluctuations in temperature. It has a winter minimum of -10.3°C and summer maximum of 45.5°C (Steenkamp *et al.* 2008) and an annual rainfall of 235-500 mm (mostly in the summer months) (Lovegrove 1993). Rain often associated with thunderstorms (Lovegrove 1993), is unpredictable, infrequent and short-lived, and occurs mostly between January and April (Steenkamp *et al.* 2008). Dreghorn falls within a semi-arid desert, and within an arid savanna (Lovegrove 1993). It is comprised of long, high, parallel ridges of vegetated sand dunes, separated by flat, inter-dune plains. There is also a dry river bed running parallel to the Botswana border. The vegetation is mostly Kalahari thornveld (Leistner 1996), with grasses (e.g. *Stipagrostis*), shrubs (e.g. *Acacia melifera*, *Lycium* spp., and *Rhigozum trichotomum*) and trees (e.g. *Acacia erioloba*, *A. haematoxylon*, and *Boscia albitrunca*) covering the dunes and inter-dune valleys. The vegetation along the dry river bed is comprised almost entirely of large trees, predominantly *Acacia erioloba*. Dreghorn is home to a wide diversity of birds, representing a range of both sizes and guilds. Apart from the avian diversity, the site contains a wide variety of other fauna in the form of mammals, reptiles and insects. There are also free-range domesticated ostriches, goats and cattle.

The KTFP has a similar climate to that at Dreghorn; with large dry river beds as another commonality. Average temperatures at Tswalu are also historically cooler than at Dreghorn (Wunderground.com). Tswalu also supports more grasses and smaller trees, but has similar dune and inter-dune habitats to that of Dreghorn.

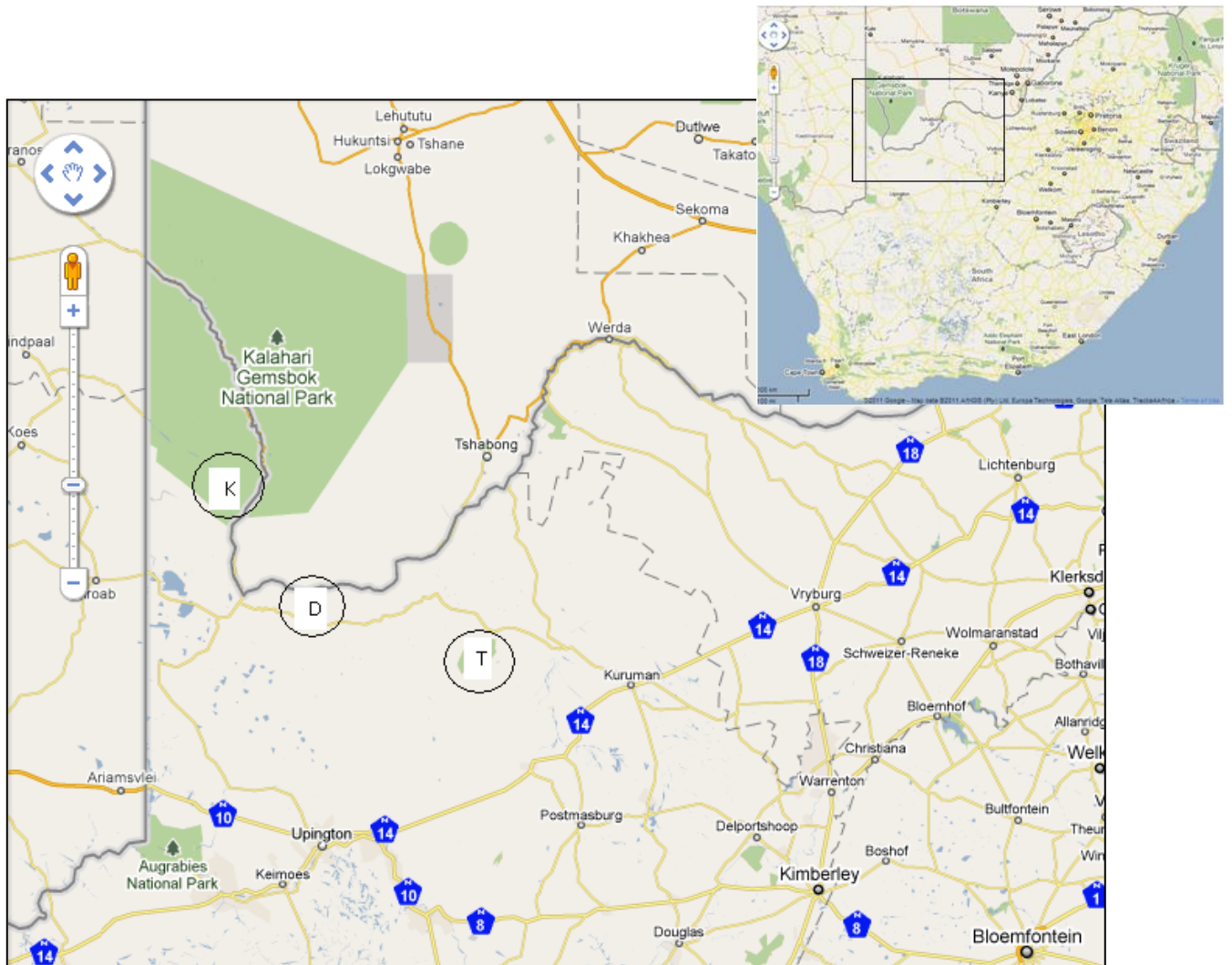


Figure 1: The location of Dreghorn Kalahari Game Ranch (D) in relation to the Kgalagadi Transfrontier Park (K) and Tswalu Kalahari Reserve (T).

## Method

### Data collection

#### Bird data

Data were collected over a period of five weeks during November/December 2010. Sampling mostly took place between 10h00 and 18h00, with the aim of observing birds across a wide range of temperatures (i.e. between 20°C and 40°C). Data were not collected during rain. Birds were observed from walking and driving transects. All habitat types were sampled and each transect was sited at random. Consecutive transects were at least 1 km apart, so as to prevent the re-sampling of same individuals. With the exception of birds in flight and those that appeared to have been affected by observer presence, the behaviour of all birds seen was recorded.



When a bird was located, an instantaneous observation was made (Type 1 data). This record included the individual's location (i.e. tree/shrub, grass or open ground), exposure (i.e. sun, dappled light or shade) and any form(s) of heat dissipation (i.e. panting, gular fluttering, wing-spreading, head-drooping, ptilo-erection). The bird was then observed for an additional 30-second period, during which any change in location, exposure or heat-dissipation behaviour was recorded using a dictaphone (Type 2 data). Details of the individual were then noted using a PDA (CyberTracker 3.206). This information included species identification, previous activity level, current activity level (i.e. mobile or stationary), locality specifics (i.e. tree species, dimensions, distance from the edge of canopy, and height from the ground), behaviour (e.g. foraging, resting, scanning, preening), as well as group size. Play-back of the recordings allowed for the duration of time spent to be calculated with regards to location, exposure level, as well as heat-dissipation behaviour (Type 3 data). Data collected at KTFP and Tswalu were combined with that collected at Dreghorn in order to increase sample size.

#### Climate data

Macroclimatic variables were recorded using a weather station (Davis 6152, Hayward, CA). The temperature sensor was calibrated in a temperature-controlled chamber before assembling it at the study site no more than 5.5 km from sites where transects were conducted and situating it to avoid influence from surrounding structures. The ambient temperature at the time of each bird observation (i.e. microclimatic variable) was also recorded using an Omega hh21A k-type thermocouple, where the temperature probe was placed inside a polystyrene cup and held over a radiation shield. Both the cup and the underside of the shield were covered in tin foil and held approximately 1 m from the ground, under the shade of a tree where possible.

In order to calibrate the thermocouple against the weather station, temperature was measured using both pieces of equipment simultaneously and in close proximity. This was done under varying temperatures and weather conditions. Temperature was measured differently at KTFP in that thermocouples were not calibrated against a weather station and in some cases were measured from a running vehicle, in which case thermocouple were held from a 400 mm-long stick. Therefore, these same Thermo-Hygro thermocouples were also calibrated in the same way as the one used at Dreghorn. In order to correct temperature measurements taken from the vehicle, this methodology was replicated, followed by temperature measurements taken with the same thermocouples at least 10 m away from the vehicle.

## Data analyses

Of all the species observed (Appendix A - Table A1), only those with 20 or more observations, or those sampled under a broad range of temperatures, were used for analyses. In order for the microclimatic data to be used (i.e. temperatures measured at each observation with a thermocouple), the thermocouple measurements were calibrated against those taken by the weather station, and corrected based on the following equation, where  $T_w$  is the temperature measured by the weather station and  $T_d$  is the temperature measured by the thermocouple (Appendix B - Fig. B1).

$$(1) T_w = 1.1182 T_d - 4.4498$$

## Behavioural thermoregulation

### *Microsite use*

The relationship between microsite use and temperature was determined by comparing patterns of use (i.e. location with regards to ground surface, and exposure to the sun) under conditions of low and high temperatures. To make this comparison, the lowest 25% and the highest 25% of recorded temperatures were selected. Each temperature record was allocated a rank based on the associated microsite that was most used during that 30-second observation. The ranking system was as follows: On-ground in sun = 1, On-ground out of sun = 2, Off-ground in sun = 3, Off-ground out of sun = 4. Open-ground and grass habitats were classified as “on-ground”, while “off-ground” included trees, shrubs and man-made-structures. The two independent groups of low and high temperatures were then compared for each species using a Mann-Whitney U-test (Statistica 2009).

### *Foraging*

The relationship between foraging and ambient temperature was analysed using Generalised Linear Models (GLMs) (R 2.11.1 2010). Foraging behaviour recorded during instantaneous scans was used as the response variable (i.e. 0 = Not foraging, 1 = Foraging), and temperature as the predictor variable. For perch-and-pounce and perch-and-sally species such as flycatchers and bee-eaters, scanning for prey was also classified as foraging behaviour. The presence or absence of foraging was then plotted against ambient temperature for each species, after which a Binomial GLM was fitted to each species-specific relationship and added to the plot in the form of a logistic regression. The significance of the effect of

temperature on foraging was then determined by comparing the response in the absence of this predictor variable.

### Physiological thermoregulation

#### *Correcting for effects of methodological differences between Dreghorn and Kgalagadi*

For the most part, sample sizes for heat-dissipation behaviour were insufficient to generate significant logistic regressions. For this reason, the Dreghorn data were combined with those collected at KTFP and at Tswalu. Although KTFP and Dreghorn are sufficiently close to one another to assume a similar climate; the methodology with regards to measuring temperature differed between the two. Several measurements were taken in a similar way, but using different thermocouples and with a different type of radiation shield. Although it would have been preferential to link actual data to the precise thermocouple that was used - this was not known, and thus called for the pooling of thermocouple measurements. Through the calibration of the thermocouples used at KTFP ( $T_k$ ) against the weather station at Dreghorn ( $T_w$ ), the temperature records collected in this way were corrected based on the following equation (Appendix C - Fig. C2).

$$(2) T_w = 1.128 T_k - 6.037$$

In order to correct for the possible effect of the vehicle on temperature measurements taken at KTFP, these measurements ( $T_{kv}$ ) were calibrated against those taken away from the vehicle ( $T_k$ ), with temperatures adjusted based on the following equation (Appendix C - Fig. C3).

$$(3) T_k = 0.844 T_{kv} + 5.799$$

With vehicle effects accounted for, measurements were corrected according to Equation 2.

#### *Type 1 data: instantaneous scans made at Dreghorn and KTFP*

As with foraging, heat-dissipation is a binary response (i.e. 0 = No heat-dissipation, 1 = Heat-dissipation). This response variable was then plotted against ambient temperature for all species with a sufficient sample size (R 2.11.1 2010). Binomial GLMs were again fitted to each species-specific relationship. In the case of a significant relationship, the temperature at which 50% of the birds of any one species are predicted to display heat-dissipation ( $HD_{50}$ ) was determined for each species.

### *Correcting for site differences between Dreghorn and Tswalu*

The Tswalu study relied solely on temperature measurements taken at a weather station. For this reason, thermocouple measurements taken at Dreghorn were ignored when analysing Type 2 data. Another important difference between the two sites is a thermal gradient that exists between the generally warmer Dreghorn, and cooler Tswalu climate (wunderground.com), with the potential for species to develop different acclimation and tolerance levels. As a result, lumping data from these two sites would mean that the predicted HD<sub>50</sub> values would potentially be overestimated if a greater sample size came from Dreghorn, and underestimated if Tswalu data contributed most observations to the sample. In order to deal with this discrepancy, a combined HD<sub>50</sub> was calculated using a correction factor. This factor was determined using only those species which had a large enough sample size and which showed a sufficient amount of heat-dissipation. The species which met these criteria were Cape Turtle Dove, Marico Flycatcher, Sociable Weaver and White-browed Sparrow-Weaver (see Appendix A – Table A1 for scientific names). A binomial GLM between heat-dissipation and temperature was fitted for each of these species at each site. The values of HD<sub>50</sub> were then compared (Appendix D - Table D2), with Dreghorn birds first showing stress at ambient temperatures 3.28°C higher than the temperatures at which Tswalu birds became stressed. These model species were then used to correct for the thermal gradient depending on which site contributed the greater sample size. Under the conditions of equal sample size, the true average HD<sub>50</sub> between the two sites would fall exactly midway between the average difference (i.e. 1.64°C below the HD<sub>50</sub> for Dreghorn and 1.64°C above the HD<sub>50</sub> for Tswalu). The weighted averages ( $W_{av}$ ) were derived from the following equation:

$$(4) \quad W_{av} = 3.28 - \left( \frac{\text{smaller } n}{\text{larger } n} * 3.28 \right)$$

### *Type 2: 30-second observations made at Dreghorn and Tswalu*

The same method as for Type 1 data was used to determine whether ambient temperature significantly affected heat-dissipation behaviour. This relationship was tested for significance in the same way, where if significant, the HD<sub>50</sub> value was determined. As there was evidence that birds at Dreghorn were more heat-acclimated than the same species at Tswalu, the correction factor was then added to the calculated HD<sub>50</sub> value if Tswalu contributed most to the total sample size, and *vice versa*.

### *Comparison between methodologies*

The  $HD_{50}$  values determined from Type 1 and Type 2 data were compared using a Wilcoxon Matched-Pairs Test (Statistica 2009). Differences were also compared between cool and hot temperature conditions. Finally, the method yielding the highest resolution data (i.e. Type 3) was assessed in order to determine whether this level of complexity is in fact necessary to reach robust conclusions about inter-specific differences in heat stress. The duration of time spent in heat-dissipation was plotted against ambient temperature. Observations were divided according to the amount of time spent heat-stressed: 0%, 100%, and some of the time. Only the latter category was used to determine the relationship between ambient temperature and the time spent heat-stressed. These proportions were arcsine-transformed (Crawley 2007) due to non-normality (Kolmogorov-Smirnov test for normality,  $p < 0.01$ ) (Statistica 2009). These data were plotted after rounding each temperature to the nearest integer. A linear model was then fitted to the data, and the significance of the relationship determined.

### *Determining the explanatory variables behind heat-dissipation responses*

A total of three explanatory variables were selected as possibly influencing the need for heat-dissipation behaviour. These were ambient temperature, body mass, and guild (i.e. foraging location and diet). To avoid too many categories for the latter variable, all species were grouped into either on- or off-ground, and as having either a plant- or animal-based diet (based on the predominant food source). Because there were two continuous and one categorical explanatory variable, and a binary response, these data were analysed using multiple logistic regression with binomial errors and a logit link function (Crawley 2007). If the probability of an individual heat-dissipating is  $p$ , then the probability of obtaining  $y$  (where  $y$  is either heat-dissipating or not heat-dissipating) is given by the Bernoulli distribution:

$$(5) P(y) = p^y(1 - p)^{(1-y)},$$

where the variable  $y$  has a mean of  $p$  and a variance of  $p(1 - p)$ . The objective of this analysis is to determine how explanatory variables influence the value of  $p$  (Crawley 2007). Because Common Ostrich was an outlier with regards to body mass (orders of magnitude larger than any other species), and diet (generalist), it was removed from the analyses. The best possible combination of explanatory variables was selected using a stepwise selection procedure based on AIC (Akaike's Information Criterion) as the principal criterion. The AIC is a measure of

goodness-of-fit which takes the number of fitted parameters into account (Anderson *et al.* 2000). The AIC value is calculated by using the following equation:

$$(6) AIC = 2k - 2LL,$$

where  $k$  is the number of parameters and  $LL$  is the maximised log-likelihood function of the fitted model. Because the log-likelihood function decreases with every degree of freedom added, the lowest AIC value ensures that the most parsimonious set of explanatory variables for each model is selected (Burnham & Anderson 2004). The Akaike weights were also compared in order to determine the weight of evidence for one particular model over all other candidate models (Burnham & Anderson 2004), based on the equation:

$$(7) \frac{\exp\left(\frac{-\Delta_i}{2}\right)}{\sum_m^M \exp\left(\frac{-\Delta_i}{2}\right)}$$

where  $\Delta_i$  = difference in AIC values between that particular model and the best model (i.e. lowest AIC), and  $m$  = candidate models.

Deviance tables were also constructed for each model, which were again used in a stepwise manner to assess how much of the deviance could be explained by a new variable being added. This then allowed for the percentage of variance explained to be calculated. The significance of including a factor based on the degrees of freedom added to the model was evaluated by applying the  $\chi^2$ -statistic, as every added explanatory variable is approximately  $\chi^2$ -distributed (McCullagh & Nelder 1989).

The effects of each explanatory variable included in the best emerging model on heat-dissipation were investigated. Because the effects of temperature had already been determined, body mass and guild were analysed. Species were divided into two mass categories: 1) under 150 g, 2) above 150 g (Appendix A – Table A1). Species were further categorised into on-ground foragers, perch-hunting species that hunt from a perch, but capture their prey on the ground (e.g. Anteating Chat, Swallow-tailed Bee-eater), and those that foraged away from the ground (Appendix A - Table A1).

## Results

A total of 2225 observations were made of 67 bird species (Appendix A - Table A1). The species most frequently observed were Marico Flycatcher, Fork-tailed Drongo, Cape Turtle-Dove, and Sociable Weaver (see Appendix A - Table A1 for scientific names), with more than 150 observations of each. These species, along with the 24 others that were recorded on at least 20 occasions and another two for which data were collected over a wide range of temperatures (Northern Black Korhaan and Yellow Canary) were the species used in the analyses. The minimum temperature recorded during data collection at Dreghorn was 17.4 C and the maximum temperature was 39.9 C.

### Behavioural thermoregulation

#### *Microsite Use*

Nine species showed significant difference in microsite use as a function of temperature (Table 1 - Category A). The majority of these species were on-ground foragers (i.e. Kalahari Scrub-Robin, Scaly-feathered Finch, Sociable Weaver, Southern Yellow-billed Hornbill and White-browed Sparrow-Weaver), all of which showed an increase in the use of shaded (and sometimes off-ground) microsites in temperatures  $> 35$  C. The only obligate ground foragers that did not significantly change their use of microsite with increasing temperature were Crowned Lapwing, Cape Turtle-Dove and Common Ostrich. Category A also included three perch-hunting species (Fork-tailed Drongo, Marico Flycatcher and Lilac-breasted Roller). Based on the unadjusted p-value (i.e. the more conservative measure), the three species in Category B did not use significantly different microsites under differing temperature conditions, although differences in microsite use did approach significance (all  $p < 0.08$ ). Apart from Black-chested Prinia (Category A), all other off-ground foragers used microsites independently of surrounding temperatures (Mann-Whitney U-test:  $p > 0.05$ ) (i. e. Table 1 - Category B and C).

#### *Foraging*

Twenty of the 28 species showed a decrease in foraging activity with increasing temperature, but only four of these relationships were significant. The species which significantly reduced foraging activity when ambient temperatures were high were White-browed Sparrow-Weaver (Fig. 2), Fork-tailed Drongo, Marico Flycatcher, and Scaly-feathered Finch (GLM: all  $p < 0.05$ ). Northern Black Korhaan showed a near-significant reduction in foraging activity at

high temperatures ( $p=0.058$ ). This group therefore consisted of on-ground foragers and perch-hunters; with off-ground foragers being the only guild seemingly not having to use this form of thermoregulation. Chestnut-vented Tit-Babbler was the only species that increased its foraging activity at high temperatures ( $p < 0.05$  - Fig. 3).

Table 1: A summary of microsite use between cool and warm temperatures compared using a Mann-Whitney U-test. Species in Category A used significantly different microsities between temperatures, species in Category B approached significance (based on z-values unadjusted for ties), while species in Category C used similar microsities regardless of temperature (whether z was adjusted for ties or not).

	<b>Species</b>	<b>n</b>	<b>Cool ( C )</b>	<b>Hot ( C )</b>	<b>Microsites used</b>	<b>U</b>	<b>z</b>	<b>p</b>
A	Kalahari Scrub-Robin	56	24-30	36-40	All	868	-4.07	0.000
	Fork-tailed Drongo	20	19-31	36-40	3 + 4	86	-3.07	0.002
	Black-chested Prinia	16	21-30	36-40	3 + 4	48	-3.00	0.003
	Marico Flycatcher	62	21-31	35-39	All	1329	-2.96	0.003
	Scaly-feathered Finch	19	27-31	36-39	All	89	-2.66	0.008
	Lilac-breasted Roller	10	23-30	36-38	3 + 4	15	-2.61	0.009
	Sociable Weaver	42	18-31	36-39	All	616.5	-2.37	0.018
	Southern Yellow-billed Hornbill	24	22-30	35-38	All	174	-2.34	0.019
	White-browed Sparrow-Weaver	25	23-31	35-38	All	192.5	-2.32	0.020
B	Common Scimitarbill	10	23-30	35-39	3 + 4	25	-1.85	0.064
	Crowned Lapwing	10	19-27	35-38	1 + 2	25	-1.85	0.064
	Yellow-bellied Eremomela	11	25-30	35-40	3 + 4	33	-1.77	0.076
C	Chestnut-vented Tit-Babbler	18	22-32	36-38	3 + 4	117	-1.41	0.159
	Anteater Chat	21	20-31	35-38	All	183	-9.31	0.352
	Swallow-tailed Bee-eater	15	24-30	36-38	3 + 4	90	-0.91	0.361
	Crimson-breasted Shrike	13	24-30	35-38	2 + 3 + 4	67	-0.87	0.383
	Ashy Tit	24	24-29	35-40	3 + 4	252	-0.73	0.464
	Common Ostrich	14	17-27	34-36	1 + 2	91	-0.30	0.765
	Cape Turtle-Dove	54	22-30	35-40	All	1435	0.14	0.888

\* Microsite ranking: 1 = On-ground in sun; 2 = On-ground out of sun; 3 = Off-ground in sun; 4 = Off-ground out of sun. On-ground = open-ground and grass habitats; off-ground = trees, shrubs and man-made-structures.



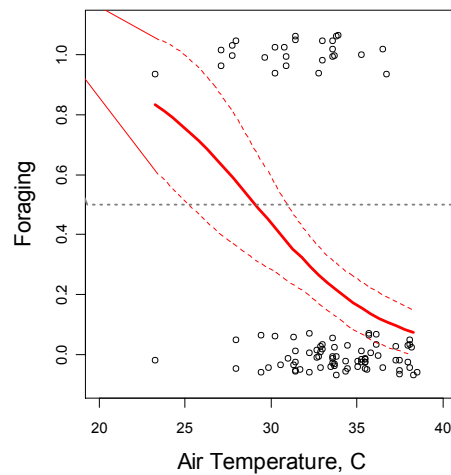


Figure 2: A binomial generalised linear model (with 95% confidence intervals) showing the highly significant reduction in foraging with increased ambient temperature for White-browed Sparrow-Weaver (GLM:  $df = 96$ ,  $p < 0.001$ ).

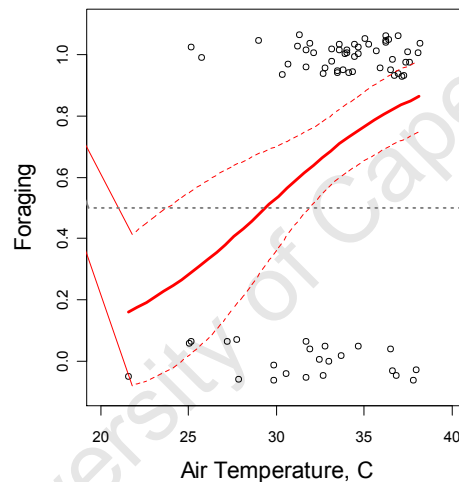


Figure 3: A binomial generalised linear model (with 95% confidence intervals) showing the significant positive relationship between foraging activity and ambient temperature for Chestnut-vented Tit-Babbler (GLM:  $df = 70$ ,  $p < 0.05$ ).

### Physiological thermoregulation and differing methodologies

#### *Type 1 data: Instantaneous scans*

Of the 18 species for which data were available from both Dreghorn and KTFP, a significant increase in heat-dissipation behaviour with increasing temperature occurred in nine species (Appendix E - Table E3). Those with the largest body masses, Common Ostrich and Southern Yellow-billed Hornbill, had the lowest predicted  $HD_{50}$ ; while White-browed Sparrow-Weaver and Marico Flycatcher were at the other end of the heat-stress continuum, with  $HD_{50}$ s exceeding 45 C. Of the nine species that did not display an increase in heat-dissipation with

an increase in temperature, the likely explanation behind two (Sabota Lark and White-backed Vulture) is small sample size. Once again, Chestnut-vented Tit-Babbler did not appear to be affected by the increased temperature. The same was true of other off-ground foragers, including Ashy Tit, Swallow-tailed Bee-eater and Yellow-bellied Eremomela. Among the on-ground foragers, no significant increase in heat dissipation was detected for Scaly-feathered Finch, Crowned Lapwing or Kalahari Scrub-Robin.

The candidate models that were compared with the aim of finding the model best able to explain Type 1 heat-dissipation data are listed in Table 2 in the order that they were tested. Model 1 incorporated only the main effects of each explanatory variable. All coefficients were found to have a significant effect on the response ( $p < 0.05$ ). Model 2 aimed to investigate how interactions affected the response, where once again all coefficients had a significant effect ( $p < 0.05$ ). On comparison, the deviance of Model 1 did not differ significantly from that of Model 2 ( $\chi^2$  test:  $p > 0.05$ ). Model 3 therefore included a combination of main and interaction effects. The interaction between temperature and body mass did not have a significant effect ( $p > 0.05$ ). The main effects of all explanatory variables, as well as the interaction between temperature and guild made up the final model (Model 4).

Table 2: A description of all candidate models used in defining the pattern of Type 1 heat-dissipation behaviour by birds of Dreghorn and KTFP.

Model No.	Description	AIC	Akaike weight (%)	% variance explained
1	HD ~ T + BM + G	1401.44	0.23	15.81
2	HD ~ T : BM + T : G	1534.33	0.00	7.65
3	HD ~ T * BM + T * G	1391.32	36.88	16.78
4	HD ~ T * G + BM	1390.25	62.88	16.73

\*\* HD = heat-dissipation, T = ambient temperature, BM = (log) body mass, G = guild, (~) = as a function of, (+) = main affects, (: ) = interaction, (\*) = main effects and interaction.

Although AIC values of Models 3 and 4 did not differ significantly in terms of deviance ( $\chi^2$  test:  $p > 0.05$ ), all coefficients emerged as having a significant effect on the response in Model 4 (Appendix E - Table E4). This is also the more parsimonious of the two, with less parameters in Model 4 explaining a similar amount of variance in the response (Table 2). The decision to accept Model 4 as the best was also supported by the greatest “weight of evidence” found for Model 4 out of all the candidate models in the form of the highest

Akaike weight (62.88%, Table 2 - Burnham 2004). The model that best explains heat-dissipation (assessed using Type 1 data) is a function of the main effects of temperature, body mass and guild, as well the interaction between temperature and guild. This model explained 16.73% of the variance, with the effect of temperature contributing most to the explanation of the response (11.87% - Appendix E-Table E5).

*Type 2 data: 30-second observations*

Twenty-two species occurring both at Dreghorn and Tswalu were used in this analysis, and a significant relationship between temperature and heat-dissipation was found for 16 species, allowing prediction of HD<sub>50</sub> values (Appendix F - Table F6). Common Ostrich (Fig. 4) and Southern Yellow-billed Hornbill once again emerged with the lowest predicted HD<sub>50</sub> value, with Common Scimitarbill also predicted as having an HD<sub>50</sub> below 36 C. These species represent off- and on-ground foragers, as well as plant- and animal-based diets. They also vary substantially in terms of body mass (32 - 68 000 g). Those species predicted to have the highest HD<sub>50</sub> values were Fawn-coloured Lark, Scaly-feathered Finch, Kalahari Scrub-Robin, and Ant-eating Chat (Fig. 5), with 50% of the populations of these species heat dissipating only when temperatures exceeded 40 C. This group consists of both animal- and plant-eaters, and all except Ant-eating Chat are on-ground gleaners. Body masses range from approximately 10 to 50 g. The species that did not significantly increase heat dissipation with temperature (and for which there was a sufficient sample size) were Crimson-breasted Shrike and Swallow-tailed Bee-eater.

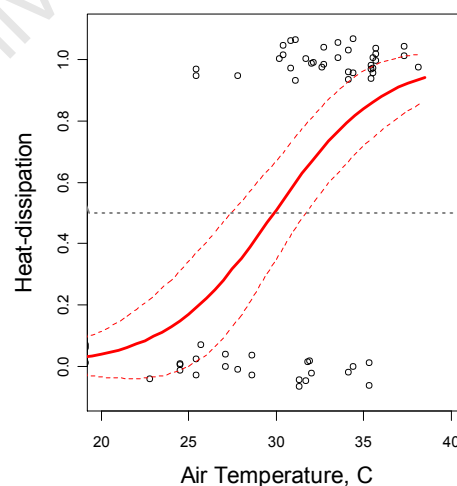


Figure 4: The significant increase in heat-dissipation (with 95% confidence intervals) by Common Ostrich with increasing  $T_a$ , based on a binomial GLM (GLM: df = 60,  $p < 0.001$ ).

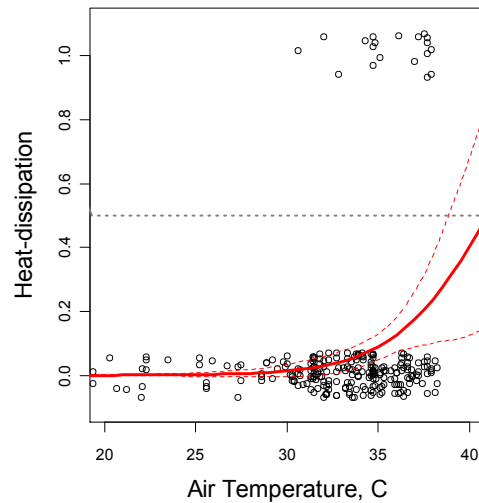


Figure 5: The significant increase in heat-dissipation (with 95% confidence intervals) displayed by Ant-eating Chat with increasing  $T_a$ , based on a binomial generalised linear model (GLM:  $df = 248$ ,  $p < 0.05$ ).

The candidate models that were compared with the aim of finding the model best able to explain Type 2 heat-dissipation data are listed in Table 3 in the order that they were tested. Model 1 included only main effects and resulted in all coefficients having a significant effect on the response ( $p < 0.05$ ), temperature and guild more so than body mass. Model 2 excluded body mass, attempting to investigate whether this main effect was necessary at all. The exclusion of body mass from the model resulted in a significant increase in the deviance ( $\chi^2$  test:  $p < 0.05$ ). Model 3 then investigated interaction effects, where only the interaction between temperature and guild emerged as having a significant effect ( $p < 0.05$ ). However, the deviance was significantly worsened in Model 3 relative to Model 1 ( $\chi^2$  test:  $p < 0.001$ ), illustrating the importance of main effects for explaining the heat-dissipation response. Model 4 therefore combined main and interaction effects. Even though this model emerged with the lowest AIC, it was not a significant improvement on Model 1 ( $\chi^2$  test:  $p > 0.05$ ). In this model, the interaction between body mass and guild again emerged as having no significant effect on the response. Model 5 then attempted to retain the main effects and interaction between temperature and guild, but remove all effects of body mass. This model was significantly worse than Model 2 with regards to deviance ( $\chi^2$  test:  $p > 0.05$ ). The final model (Model 6) therefore included body mass as a main effect, as well as the main and interaction effects of temperature and guild. There was no significant difference between Model 4 and Model 6 ( $\chi^2$  test:  $p > 0.05$ ), however all explanatory variables emerged as being significantly different ( $p < 0.05$ ) to the null model (i.e. the response in the absence of any explanatory variables - Appendix F-Table F7).

Table 3: A description of all candidate models used in defining the pattern of Type 2 heat-dissipation behaviour by birds of Dreghorn and Tswalu.

Model No.	Description	AIC	Akaike weight (%)	% variance explained
1	HD ~ T + BM + G	1900.68	12.67	22.91
2	HD ~ T + G	1903.74	2.74	22.71
3	HD ~ T : BM + T : G	1902.16	0.00	22.85
4	HD ~ T * BM + T * G	1899.19	26.77	23.30
5	HD ~ T * G	1900.81	11.88	23.07
6	HD ~ T * G + BM	1898.11	45.94	23.26

\*\* HD = heat-dissipation, T = ambient temperature, BM = (log) body mass, G = guild, (~) = as a function of, (+) = main affects, (: ) = interaction, (\*) = main effects and interaction.

Apart from Model 6 having the lowest AIC value, it also emerged with the highest Akaike weight (45.94%) and explained the highest percentage of variance (23.26% - Table 3). Of the latter, the large majority is explained by temperature (21.61% - Appendix F-Table F8). Therefore the model which best explains heat dissipation (based on Type 2 data) is a function of temperature, body mass, guild and the interaction between temperature and guild. By changing the reference guild that was used as the null model, off-ground species with an animal-based diet appeared to respond to high temperatures in the same way as those with a plant-based diet. (Appendix F - Table F7). Off-ground foragers as a group behaved differently to on-ground foragers, but among on-ground foragers, diet appeared to have no influence on heat-dissipation behaviour (Appendix F - Table F9).

*Type 3 data: duration of heat-stress within 30-second observations*

Twenty-eight species observed most commonly at Dreghorn were used in this analysis, and a significant relationship between temperature and the amount of time spent in heat dissipation was found only for Southern Yellow-billed Hornbill and Fork-tailed Drongo (Fig. 6).

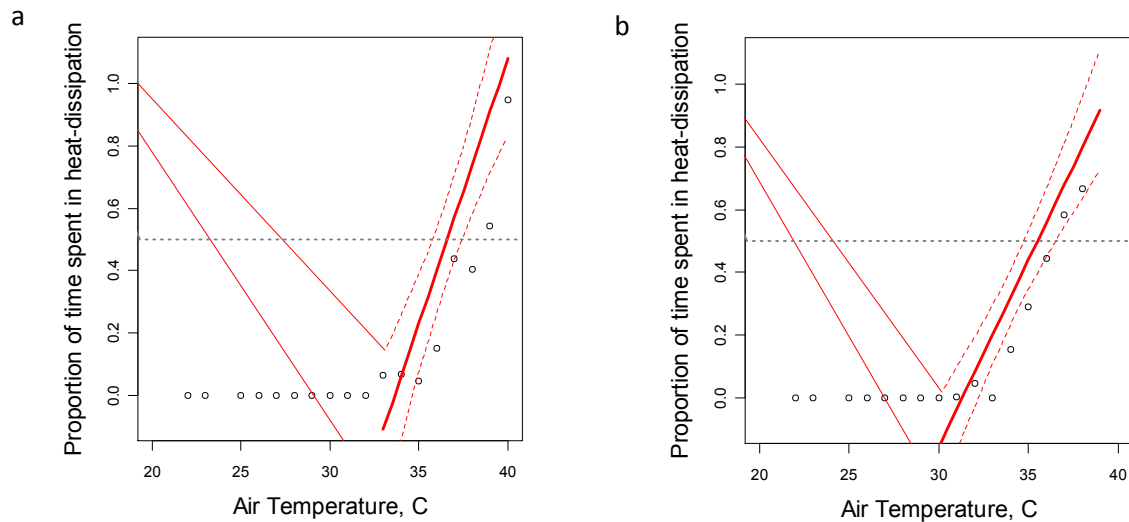


Figure 6: The significant positive relationship between the proportions of time spent heat dissipating with increasing  $T_a$ , illustrated using a linear regression (and 95% confidence intervals) for a) Fork-tailed Drongo ( $F = 33.02$ ,  $df = 6$ ,  $p < 0.05$ ), and b) Southern Yellow-billed Hornbill ( $F = 47.73$ ,  $df = 7$ ,  $p < 0.001$ ).

#### *Comparison of methodologies*

When comparing the  $HD_{50}$  values predicted using different methods (Appendix G - Table G10), Type 1 data predicted significantly higher  $HD_{50}$  values for all species than was predicted using Type 2 data (Wilcoxon Matched-Pairs Test:  $z = 2.37$ ,  $p < 0.05$ ). Even though the same model can best explain Type 1 and Type 2 data (Tables 2, 3), more variance in heat-dissipation response can be explained using Type 2 data (23.26% - Appendix F-Table F8) than using Type 1 data (16.73% - Appendix E-Table E5). This increase is largely due to the almost doubling of variance explained by temperature in Type 2 data (21.61% - Appendix F-Table F8). The probability of detecting heat-dissipation behaviour was also compared between Type 1 and Type 2 data, and between temperatures above and below  $35^{\circ}\text{C}$  (Table 4). For the majority of species, heat dissipation was more likely to be detected from Type 2 data, the exceptions being Crowned Lapwing (under warm conditions) and Crimson-breasted Shrike (under hot conditions). The most important differences regarding detection were at lower temperatures, where 50% of species showing heat-stressed based on Type 2 data were not detected as being stressed using Type 1 data. Even at temperatures above  $35^{\circ}\text{C}$ , the difference between the two was substantial (Table 4).

Table 4: The percentage of observations detected as being heat-stressed using Type 1 and 2, under warm and hot conditions.

<b>Species</b>	<b>Warm (30-35 C)</b>		<b>Hot (36-40 C)</b>	
	<b>Type1</b>	<b>Type2</b>	<b>Type1</b>	<b>Type2</b>
Ashy Tit	0	1.49	21.05	36.36
Cape Turtle-Dove	0.44	2.72	10.10	28.57
Chestnut-vented Tit-Babbler	0	0.00	4.76	31.71
Common Scimitarbill	13.79	17.86	28.57	60.00
Crimson-breasted Shrike	0	0.00	17.86	14.29
Crowned Lapwing	11.86	0.00	14.29	16.00
Fork-tailed Drongo	2.72	4.69	17.82	39.66
Kalahari Scrub-Robin	0	4.85	4.26	16.90
Marico Flycatcher	0	2.17	3.09	21.74
Sabota Lark	7.14	22.22	11.11	25.00
Scaly-feathered Finch	0	2.38	0.31	15.79
Sociable Weaver	0	8.24	15.52	42.59
Southern Yellow-billed Hornbill	10.20	37.25	50.00	50.00
Swallow-tailed Bee-eater	0	3.85	1.56	12.50
White-backed Vulture	13.04	16.67	13.64	15.38
White-browed Sparrow-Weaver	1.04	12.86	6.56	46.15

*Vulnerability indicated by behavioural and physiological thermoregulation*

With the relationship between temperature and heat-dissipation already determined, the effect of the other variables explaining variance in heat-dissipation behaviour were investigated. Under the same temperature conditions ( $> 33$  C), birds with a body mass lower than 150 g were consistently observed to heat dissipate less than larger birds (except at 38 C) (Fig. 7). Foraging location emerged as being the more important aspect of guild than diet in explaining this variation in heat dissipation (Appendix F - Table F7, F9). Obligate ground-foragers heat dissipated more than species belonging to other foraging niches, while the opposite was true for those species that foraged off-ground (Fig. 8). This was the case for all temperature conditions, except the most extreme (i.e. 39 C).

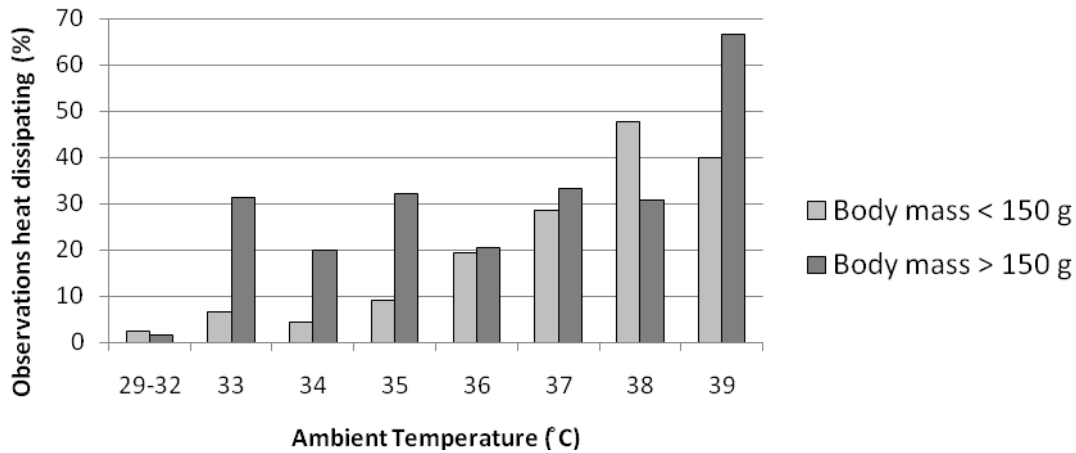


Figure 7: A comparison of the frequency of heat-dissipation behaviour at different temperatures for species with body masses above and under 150 g.

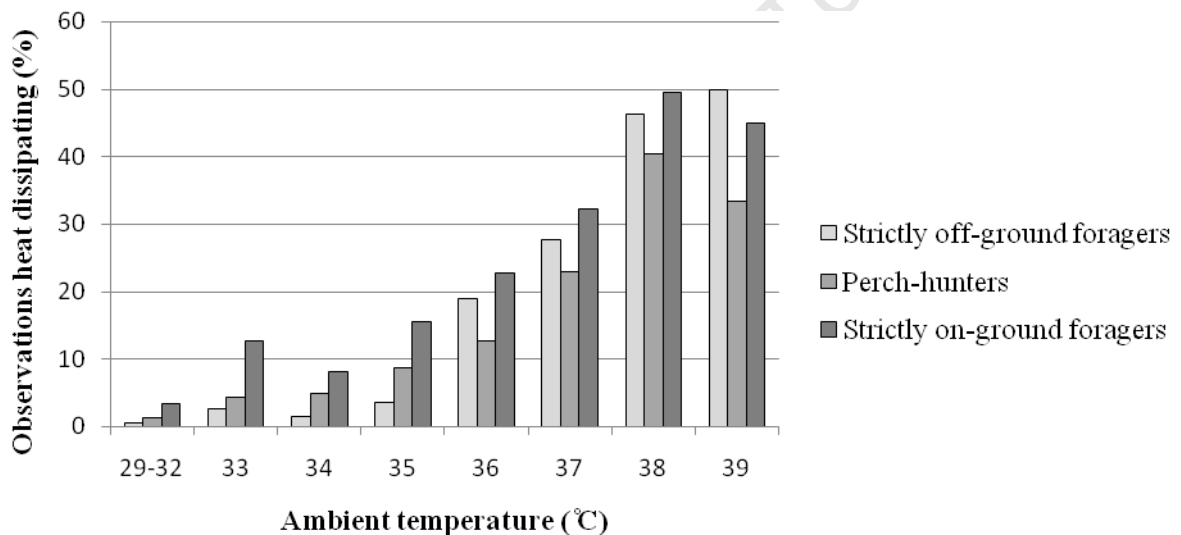


Figure 8: A comparison of the frequency of heat-dissipation behaviour at different temperatures for species that are obligate ground-foragers (e.g. Cape Turtle-Dove), obligate tree-foragers (e.g. Crimson-breasted Shrike), and those that hunt from a perch, but capture their prey on the ground (e.g. Swallow-tailed Bee-eater).

Even though Common Ostrich and Southern Yellow-billed Hornbill emerged as having the lowest  $HD_{50}$  values, neither species significantly reduced their time allocation to foraging (even though Southern Yellow-billed Hornbills changed their microsite use with changing temperature - Table 5). Foraging was also not reduced in any of the other species with an  $HD_{50}$  below 37 C. Of those species with an  $HD_{50}$  between 37 C and 39 C only some used behavioural thermoregulation in addition to physiological thermoregulation (Table 5).



Table 5: A summary of inter-specific patterns of behavioural (based on Dreghorn data) and physiological thermoregulation (based on data from Dreghorn and Tswalu) in response to high ambient temperatures, in the order from lowest to highest HD<sub>50</sub>.

Species	Significant change in microsite use	Significant decr. in foraging	Significant incr.in heat-dissipation	HD <sub>50</sub>
Common Ostrich	0	0	1	28.5
Southern Yellow-billed Hornbill	1	0	1	33.8
Common Scimitarbill	0	0	1	35.2
Ashy Tit	0	0	1	36.7
Cape Turtle-Dove	0	0	1	36.9
Cape Glossy Starling	n/a	0	1	36.9
Marico Flycatcher	1	1	1	37.4
Chestnut-vented Tit-Babbler	0	0	1	37.8
Sociable Weaver	1	0	1	37.9
Fork-tailed Drongo	1	1	n/a	n/a
White-browed Sparrow-Weaver	1	1	1	38.1
Black-chested Prinia	1	0	1	38.6
Crowned Lapwing	0	0	1	38.9
Fawn-coloured Lark	n/a	0	1	40.8
Scaly-feathered Finch	1	1	1	41.3
Kalahari Scrub-Robin	1	0	1	41.6
Ant-eating Chat	0	0	1	41.8
Crimson-breasted Shrike	0	0	0	> 42
Swallow-tailed Bee-eater	0	0	0	> 42

0 = no significant difference with increasing temperature, 1= significant difference

n/a = species was not included in analysis due to small sample size

The species with the highest HD<sub>50</sub> values (> 40 C) were Fawn-coloured Lark, Scaly-feathered Finch, Kalahari Scrub-Robin, Ant-eating Chat, Crimson-breasted Shrike and Swallow-tailed Bee-eater. Of these, only Scaly-feathered Finch and Kalahari Scrub-Robin significantly changed their use of microsites with rising temperatures, and only in the case of Scaly-feathered Finch did this result in a significant reduction in foraging activity (Table 5). Crimson-breasted Shrike and Swallow-tailed Bee-eater were the only species where neither behavioural nor physiological thermoregulation was observed; even at the highest ambient temperature recorded (40 C). An HD<sub>50</sub> could therefore not be established for either species, although it is certainly above 42 C.

## Discussion

### Behavioural thermoregulation

#### *Microsite use*

Solar radiation imposes significant thermal stress on birds by exacerbating the effects of ambient temperature (e.g. Morton & Carey 1971; Lustick *et al.* 1979; Tomback & Murphy 1981; Salzman 1982; Webb & King 1983; Murphy 1985; Battley *et al.* 2003). Direct exposure to the sun will inevitably cause body temperature to rise, thereby bringing species closer to their critical thermal maxima, exposing them to the risk of overheating (Sinervo *et al.* 2010). If temperature alone is responsible for changes in microsite use, we would expect microhabitats would be used at random at temperatures below stress levels and become increasingly non-random as temperatures increase (Ricklefs & Hainsworth 1968). This effect was not detected for the majority of species that live and forage in trees and shrubs. Large savanna trees (e.g. *A. erioloba*) provide resources that are otherwise scarce in the Kalahari, including shade, shelter, and a relatively cooler microclimate (Dean *et al.* 1999), suggesting that species dependent on such trees to provide foraging substrata have little need to move elsewhere as temperatures rise.

The opposite was true for the majority of ground-dwellers, where temperatures exceeding 35 C saw most retreating to shaded (and, where possible, off-ground) microsites. Most desert organisms have a fairly narrow range of temperatures at which they function optimally. For this reason, it is essential that they minimise as far as possible extreme temperature fluctuations within their own bodies (Lovegrove 1993). This form of behavioural thermoregulation (seeking shade) would thus be an attempt at just that. Shade also reduces soil temperatures and evaporation such that moisture levels remain higher beneath canopies (Belsky *et al.* 1989, 1993; Belsky & Canham 1994), an advantage for species that rely on probing in the soil (Clark 1987). There were, however, three obligate ground foragers whose use of microsite did not change with increasing temperature. For Common Ostrich, this can largely be explained by the limited options available to it because of its extreme body size – the largest living bird (Wolf & Walsberg 1996a; Kearney & Porter 2009). There was also no significant difference in microsite use by Cape Turtle-Doves or Crowned Lapwings, both of which largely appear to be sun-intolerant, spending most of their time in shade regardless of temperature or time of day. Other than the extreme case (of Common Ostrich), there was no clear pattern in the use of microsites with regards to being strongly influenced by body mass.

### *Foraging*

Time spent inactive is potentially traded off against time available for foraging or other activities (Tieleman & Williams 2002; Buckley 2008). Based on this, fewer-than-expected species (i.e. four) significantly increased inactivity at the cost of foraging time, suggesting that under current conditions this trade-off is not a costly one. The species where this trade-off was apparent were those that either foraged at the ground surface (White-browed Sparrow-Weaver and Scaly-feathered Finch), or those that scanned the ground for food from an elevated perch (Fork-tailed Drongo and Marico Flycatcher). Thermal environments occupied during foraging are usually hotter than thermal refuges used when inactive (Wolf 2000). The fact that there was a shift by these species into shaded (and where possible, off-ground) microsites suggests that foraging in exposed areas is compromised by the risk of overheating (Ricklefs & Hainsworth 1968; Tieleman & Williams 2002). Shade-seeking by both ground-foraging and perch-hunting guild members is likely to have reduced food availability in the shaded areas as a corollary. For those that have to shelter beneath trees, they are forced into a very small portion of the semi-desert ground environment (because trees are scarce). Similarly, those driven to shaded perches also have spatially reduced hunting options: this has been shown to lead to reduced foraging effectiveness (Walsberg 1993).

Strictly arboreal foragers however, are less constrained by the trade-off between shade and foraging, and, even at high temperatures are able to continue foraging in shaded and relatively cool microclimates (Dean *et al.* 1999). In general, the foraging activity of arboreal foragers in this study was not compromised by the need to seek shade away from favoured foraging sites. Indeed, one species - Chestnut-vented Tit-Babbler - increased its foraging activity as temperatures rose. Ambient temperatures are highest directly above the ground because of the reflection of radiant heat (Kotzen 2003; Tieleman & Williams 2002). Despite this, fewer ground-dwelling species than expected were negatively affected by temperature. Possible explanations for the absence of behavioural adjustments is the alternative diet in the form of seeds and berries that both Kalahari Scrub-Robins and Southern Yellow-billed Hornbills can take advantage of from a cooler microsite away from the ground-surface (Hockey *et al.* 2005). Sociable Weaver also have an advantage over other ground-foragers in terms of access to the cool microclimate inside their large nests that are exploited between foraging bouts (Eloff 1984). This 'shuttling' behaviour between foraging and shade-seeking has also been observed in Common Starlings (*Sturnus vulgaris* - Clark 1987).

## Physiological thermoregulation

### *Best observational methodology for the study of heat dissipation*

The analysis of Type 1 data suggests that the majority of birds are not heat-stressed, except at very high temperatures: such species might thus be considered as well adapted, at least to current conditions. Apart from Common Ostrich and Southern Yellow-billed Hornbill, Type 2 data resulted in a different ordering of species along the heat-stress continuum. A greater proportion of species were recorded as being heat-stressed, and this technique predicted lower HD<sub>50</sub> values for all species relative to those derived from instantaneous scans. The key difference between the two techniques was the greater likelihood of detecting heat stress at relatively low temperatures when using Type 2 data. This effect was thus not only mathematically predictable, but also empirically demonstrated. For this reason, an observation time of at least 30 seconds is recommended over instantaneous scans (unless the latter can guarantee large sample sizes, which in the case of most desert species, is unlikely).

With the exceptions of Fork-tailed Drongo and Southern-Yellow-billed Hornbill, the analysis of Type 3 data suggests that for the majority of species, time spent heat dissipating does not significantly increase with increasing temperature. A significant relationship was found for these same species using Type 1 methodology. This would suggest that in both of these instances, the response to temperature could have been derived from the simplest and lowest resolution data. The fact that the significant relationship found in all other species using Type 1 and 2 were not mirrored in Type 3, suggests that the proportion of time spent heat-dissipating is not interchangeable with the proportion of individuals heat-dissipating. Even with the same observation period, the conclusions drawn from Type 2 differ substantially from Type 3, where temperature appears not to have an effect on the time spent heat stressed.

### *The use of heat dissipation to thermoregulate body temperature*

The fact that most species are using evaporative cooling as a means of physiological thermoregulation under current conditions implies that the frequency and/or duration which they have to do this in the future may increase, elevating their vulnerability to climate change. Based on Type 2 data, it was predicted that a large proportion of the populations of Common Ostrich and Southern Yellow-billed Hornbill would start heat-dissipating at relatively low temperatures (< 34 C). Of all species included in this study, these are at the upper end of the body-mass spectrum. Plumage may also contribute to patterns of evaporative

heat loss in these larger birds, whereby a thicker plumage increases the gradient between the bird's body and the outside air allowing greater evaporation than is possible for smaller birds (Weathers 1981). As a result of lower rates of mass-specific evaporative water loss however, larger species are less at risk of dehydration (McKechnie & Wolf 2010), and can therefore perhaps 'afford' to use this form of thermoregulation at lower temperatures (because their risk of lethal dehydration is proportionally lower).

Unlike the pattern found using Type 1 data, Type 2 data also identified several species with  $HD_{50}$  values below 40 C. This is of some concern, given that temperatures approaching (and exceeding) 40 C occur regularly under current conditions. Of the study species, only six had  $HD_{50}$  values above 40 C. This includes Fawn-coloured Lark, Scaly-feathered Finch, Kalahari Scrub-Robin and Ant-eating Chat. It is interesting to note that, of these, Ant-eating Chat is the only species that does not forage exclusively from the ground surface. Those species that appear to be able to delay losing water for the longest are Crimson-breasted Shrike and Swallow-tailed Bee-eater, suggesting that these species will be among the best adapted to rising temperatures. However it should be noted that even if birds do not show obvious behaviours that enhance evaporative rates, such as panting - large amounts of water may still be lost through cooling via cutaneous evaporation (Wolf & Walsberg 1996a).

#### Vulnerability to rising temperatures

Exposure to solar radiation at even moderate temperatures can elevate body temperatures sufficiently to elicit heat-stress behaviour (such as evaporative cooling - Glassey & Amos 2009). For this reason, shade-seeking may prevent otherwise excessive loss of evaporative water by reducing heat load on the body (Ricklefs & Hainsworth 1968, Barrows 1981; Walsberg 1993; Wolf & Walsberg 1996b). This was seen in a number of species, and used more by those falling at the upper end of the heat-stress continuum. Shade-seeking could therefore play an important role in delaying the onset of water loss. One of the likely explanations for the largest bird being first to suffer heat stress is therefore its limited access to shaded microsites (Wolf & Walsberg 1996a; Kearney & Porter 2009).

Food intake of endotherms is often inversely related to environmental temperatures (Huey 1991), reflecting the trade-offs between water conservation, heat regulation and energy intake (Ricklefs & Hainsworth 1968; Anava *et al.* 2001). However, in order to persist at a given

location, organisms must not only maintain physiologically viable body temperatures but must also acquire sufficient energy, water and nutrients to grow and reproduce (Kearney & Porter 2009). It has been suggested that restriction to thermal refuges could effectively increase the risk of extinction through the negative impacts of reduced foraging on growth, maintenance, and reproduction (Sinervo *et al.* 2010). Although several species in this study did make use of shaded microsites as a means of regulating body temperature at high ambient temperatures, this behaviour was only accompanied by a reduction in foraging in White-browed Sparrow-Weavers, Scaly-feathered Finches, Fork-tailed Drongos and Marico Flycatchers. All other species that made use of shaded retreats did so without having to reduce their foraging efforts. This is similar to the behavioural thermoregulation patterns of Verdins (*Auriparus flaviceps*): these small birds are able to continue to forage at high ambient temperatures by making use of shade (Austin 1976). The fact that a reduction in foraging was found for so few species in this study implies that this form of thermoregulation is not used to any great extent by the Dreghorn bird community (at least in temperatures of up to 40°C).

Like ectotherms (Gillooly *et al.* 2001), absolute energy expenditure and overall resource requirements of endotherms increase with body size (Brown *et al.* 1978; Wolf 2000; Kearney & Porter 2009). In absolute terms, small birds have lower field metabolic rates and rates of heat loss than do larger birds. However, small birds must feed more regularly and are less well buffered against extended periods of food scarcity (Brown *et al.* 1978), making balancing energy gain and thermoregulation more of a challenge than birds that are large in size. The reduction in foraging seen in four species at Dreghorn could be as a result of increased dependency on heat dissipation, as suggested by Root (1988), representing a significant trade-off between heat loss and energy gain. Reduced energy, combined with an increase in water loss, place these species at risk under future climate-change predictions. There were some species (such as Southern Yellow-billed Hornbills and Sociable Weavers) that became heat stressed at relatively low temperatures, even though they opted to retreat to shade. At low wind speeds, the use of shaded microsites by small birds is equivalent to a 12°C decrease in  $T_a$  (Wolf & Walsberg 1996a). However, even with this thermal buffering, small birds that retreat to shaded microsites and/or become inactive (such as Marico Flycatcher, Sociable Weaver, and Black-chested Prinia) can experience rates of evaporative water loss exceeding 5% of their body mass per hour (Wolf & Walsberg 1996a) - conditions under which dehydration would pose a very real threat for these species (McKechnie & Wolf 2010).

All species predicted to have the highest HD<sub>50</sub> values are able to exploit cooler conditions away from the ground surface, as none are obligate ground-dwellers. However, only Ant-eating Chat, Crimson-breasted Shrike and Swallow-tailed Bee-eater are able to continue their foraging efforts in these same cooler microsites, suggesting that they will be least vulnerable to the early loss of water, and to losing energy. The fact that on-ground gleaners (Fawn-coupled Lark, Kalahari-Scrub-Robin and Scaly-feathered Finch) have such high HD<sub>50</sub> values, implies that their behavioural adjustments play an important role in reducing heat-load (Huey 1991). The most dramatic change in the use of microsites was made by Kalahari Scrub-Robins, with microsite choice being random at low temperatures and increasingly non-random as temperatures rose. In concert with this behavioural change, the rate at which stress levels in this species increased with rising temperatures was also fairly slow, as evidenced by the species' high HD<sub>50</sub>. Seemingly the most heat-tolerant species of all were Crimson-breasted Shrike and Swallow-tailed Bee-eater. Not only were these species never observed to employ evaporative cooling, their patterns of microsite use did not change as temperatures rose. The ecological traits shared between these species include an ability to exploit the thermal gradient away from the ground, an animal-based diet and small size (< 50 g).

Through exploring traits of vulnerability and resilience, an improved understanding regarding the mechanisms by which the effects of temperature arise is achieved (La Sorte *et al.* 2009; Charmantier *et al.* 2010). This study was based on behavioural observations. Microsite choice and foraging activity was used as a measure of behavioural response to stress, and heat-dissipation behaviour was used as a surrogate for physiological stress (rather than being a direct measure of physiological stress). Until we understand how the latter translates into true physiological stress (e.g. rates of evaporative water loss), predictions about the relative vulnerabilities of species must be treated with caution. It is, however, possible to make inferences (which themselves can be treated as testable hypotheses) with regards to likely consequences of future change and which species might be most at risk, and why. The incidence of heat-dissipation behaviour was best explained as a function of ambient temperature, body mass, foraging guild, and the interaction between temperature and guild.

Body mass, although contributing to the model best explaining the pattern of heat-dissipation, explained a very small proportion of the variance. There appears to be a difference in response between birds of relatively small-size (< 150 g) and relatively large-size (> 150 g), with small birds appearing less stressed than larger birds under the same temperature

conditions. Evaporative water loss is highly dependent on body mass, resulting in much larger fractional increases in evaporative water loss in smaller species (McKechnie & Wolf 2010). Maintaining water balance is also most difficult for birds weighing less than 40 g (Bartholomew & Cade 1963). Large species starting to use evaporative cooling at lower temperatures than small birds suggests that these birds at the lower end of the body mass spectrum delay evaporative cooling for as long as possible (perhaps by entering a state of hyperthermia). It has been shown that once heat dissipation is used by small birds, the rate at which evaporative water is lost from the body is much faster than from larger birds (McKechnie & Wolf 2010) – which could thus be the reason behind the later onset of this physiological mechanism in smaller birds. Evidence of the effect of body mass was also expected to be apparent in the proportion of time spent in heat-dissipation behaviour across species, with larger species expected to heat dissipate for a greater proportion of the time (Lovegrove 1993). However, this trend did not emerge from the analysis of Type 3 data.

Species that did not have to make behavioural adjustments to rising temperatures and which lost evaporative water only at the highest temperatures were arboreal foragers with animal-based diets (largely comprising insects). By virtue of their foraging niche, they are able to avoid the extremely harsh conditions experienced by other foraging guilds because much of their foraging takes place in the shade (Dean *et al.* 1999; Tieleman & Williams 2002; Kotzen 2003). Adding to the resilience of off-ground gleaners is their diets. Many insectivorous birds obtain all the water they need from the body fluids of insects, lowering the risks associated with dehydration once evaporative cooling becomes unavoidable (Bartholomew & Cade 1963). The only exception to this heat-related pattern was found at the highest temperature recorded. This may be explained by the easier detection of heat-stress in birds that are resting in trees, compared with ground-dwelling species that often find shelter under dense bushes.

### Conclusions

For several species, shaded (and where possible, off-ground) microsites were favoured over sun-exposed, on-ground microsites at high temperatures, reflecting an increasing need for thermoregulation. This was most evident in ground-foraging species, for which there is limited availability of projected shade. A significant reduction in foraging activity was found for some species, none of which were off-ground foragers. Instantaneous scans underestimated the severity of heat stress and detection proved inadequate at relatively low temperatures. Heat-dissipation behaviour differed between species; in that not all species



displayed heat stress, and amongst those that did, severity differed. The traits that were found to predispose species to being particularly vulnerable to high ambient temperatures were large size and obligate ground-foraging and roosting. Arboreal insectivores– species whose diets are water-rich and whose foraging habitats are largely shaded – are the most resilient.

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### CHAPTER 3: Synthesis

Understanding which species are more adaptable, and how they achieve this adaptability, is extremely helpful in predicting how novel environments and ecosystems produced by climate change will impact on biodiversity (Julliard et al. 2003; Fitzpatrick & Hargrove 2009). Generally, we know very little about the ability of birds (or any other living organism) to undergo the adaptive changes that may be necessary in response to globally increasing temperatures (Berteaux et al. 2004).

Microsite selection, manifest as the seeking out of shaded, cool refuges is an important determining factor behind the successful occupation of deserts by many taxa other than birds (e.g. arthropods: Casey 1976; insects: Heath 1967, Heath & Wilkin 1970; lizards: Sinervo *et al.* 2010). The use of shaded microsites should be most pronounced in endothermic desert mammals and birds, which experience rates of water loss about ten times higher than those of desert ectotherms (Lovegrove 1993). It is largely accepted that organisms do not passively experience their environments but actively select them (Lewontin 2000; Oldling-Smee *et al.* 2003) and microsite selection thus plays a crucial role in determining the body temperature of an animal (Huey 1991). Birds in particular have been found to select relatively cooler microhabitats as ambient temperatures rise (Ricklefs & Hainsworth 1968). There was a substantial change in microsites used by Kalahari birds under hot and cool conditions for a number of species, this being most pronounced in ground-foraging species. Other species for which retreats to shaded microsites have been documented include southwestern quail (*Lophortyx gambeli* and *Cyrtonyx montezuma* - Vorhies 1928), Cactus Wren (*Campylorkynchus brunneicapilla* - Ricklefs & Hainsworth 1968), and Verdin (*Auriparus flaviceps* - Austin 1976). Even at moderate ambient temperatures, retreating from sunlit to shaded microsites greatly increases survival times and could thus be key to birds persisting in increasingly harsh conditions (Wolf 2000). This effect is especially pronounced for small birds, where up to 50-67% of water can be saved through the use of microsites within shaded canopies (Wolf *et al.* 1996, Wolf & Walsberg 1996b).

Intermediate temperatures yield highest net energy gains for desert birds, with resting taking precedence in conditions of high ambient temperature (Goldstein 1984; Carmi-Winkler *et al.* 1987; Williams 2001). Many non-specialist birds are able to thrive in moderately arid regions by avoiding activity during the hottest parts of the day (Bicudo *et al.* 2010). In fact, claims

have even been made of a “universal reduction in activity by desert birds in high temperatures”, associated with a decrease in active foraging (Austin 1976). Those that did significantly reduce foraging effort at high temperatures were those species that foraged at the ground surface. The same pattern was found for the Cactus Wren – an on-ground, insectivorous gleaner (Ricklefs & Hainsworth 1968). This pattern was not evident among arboreal insectivores in the Kalahari, but may become so as temperatures continue to rise. According to Brooke *et al.* (2009), at the level of the individual (and thus, ultimately, the population) the direct effects of weather are as important as the longer term effects of climate. The fact that some species are already reducing their foraging activity at high temperatures may therefore be a harbinger of the future.

It is largely accepted that the thermal environment alone does not dictate activity patterns of desert birds, nor can it explain all variations in behaviour (Clark 1987; Walsberg & Wolf 1996, Tieleman & Williams 2002; Kearney & Porter 2009). This too was found in this study, where although temperature was the variable explaining the greatest amount of variance in the heat-dissipation data, not all species responded to high ambient temperature in the same way. This analysis therefore adds to a growing pool of evidence that species respond individually (e.g. McCarty 2001; Warren *et al.* 2001; Erasmus *et al.* 2002; Mene'ndez *et al.* 2006; Le Roux & McGeoch 2008), and that ecological traits may hold the key to understanding patterns of response (Buckley 2008). It is therefore imperative to detect all signs of heat-stress, particularly at lower temperatures. For this reason an observation time of at least 30 seconds is required; while the most labour-intensive method (Type 3, real-time data), yielding the highest resolution data, adds little insight above Type 2 data.

Body mass has been shown to explain much of the variability in the tolerance of organisms to changing environmental conditions (e.g. Owens & Bennett 2000; Kearney & Porter 2009). On the other hand however, body mass has also failed to predict vulnerability to global change (i.e. climate change, habitat degradation, and direct exploitation - Julliard *et al.* 2003). There is suggestion that that small birds, with short generation times, may be better able to adapt to changes in climate much faster than longer-lived, larger birds (Harte *et al.* 2004). A relatively large bird, the Yellow-billed Magpie (*Pica nuttalli* - 159 g) was found to have limited capacity for evaporative cooling at high temperatures, with death sometimes occurring at temperatures as low as 40°C (Hayworth & Weathers 1984). Larger-bodied species do, however, tend to have broader ecological niches and larger geographical ranges

than smaller-bodied species (Gaston & Blackburn 2000), and tend to be more active dispersers (Jenkins *et al.* 2007). It could therefore be argued that larger-bodied species are in a better position through dispersal capabilities to respond to changing climatic conditions (Warren *et al.* 2001; Mene´ndez *et al.* 2006).

The choice of diet is critical even at moderate temperatures (Bartholomew & Cade 1963), even more so then, at high ambient temperatures where the loss of water is inevitable. With this in mind, granivores that are small in size should be particularly prone to physiological stress, because of the relatively large gap between the metabolic water produced and the total amount lost (Bartholomew & Cade 1963; McKechnie & Wolf 2010). All species that only employ evaporative cooling at high temperatures (> 42 C) have diets that are animal-based, a trait that makes these species more tolerant to high ambient temperatures than are species with relatively water-deficient, plant-based diets (e.g. Doves - Erasmus *et al.* 2002). The study of responses to temperature across a variety of species, allows for inference of the impact at the community level (Helmuth *et al.* 2005). The fact that some species are more vulnerable to high ambient temperature suggests that species composition, and thus functioning of the Kalahari Desert is likely to change (Loreau *et al.* 2001).

Most birds are characterised by high mobility. Mobility can act to buffer the impact of rising ambient temperature by allowing short- or medium-term escape from local conditions (Dean 2004; Huey & Tewksbury 2009) and allowing them to seek out remote and isolated water sources (Bartholomew & Cade 1963). This has been observed in the Kalahari, where, in hot conditions, bird populations undertake mass movements from drier to wetter areas (Herremans 2004). Species are also responding by adapting to heat both behaviourally and physiologically (Austin 1976; Reeve & Sherman 1993; Sinervo *et al.* 2010). Rapid acclimation to a changing thermal environment is critical in maintaining thermoregulatory competence at high ambient temperatures (McKechnie & Wolf 2004b). Indeed, the ready response of many species to recent climate change indicates a phenotypic plasticity to cope with such change (Crick 2004), with the greatest resilience to high-temperature anomalies being among those species with broad thermal ranges (Jiguet *et al.* 2006).

It has been predicted that the makeup of desert bird communities will change (Wolf 2000) under the future climate predictions for southern Africa of higher temperatures, less

predictable rainfall and higher humidity (IPCC 2001; Kruger & Shongwe 2004). A major point of concern is that, when other options for losing heat (such as convection and conduction) are no longer available, there is increased dependency on evaporative cooling - a mechanism relying completely on access to water (Lasiewski & Seymour 1972). This reliance on water will only increase under future scenarios: by as much as 95% in small birds (McKechnie & Wolf 2010). If the water demands of birds cannot be met, the consequences are inevitable (Wolf 2000), especially if preformed water in insects proves inadequate in meeting future demands (Ricklefs & Hainsworth 1968). For small birds, ambient humidity (another variable predicted to increase under future climate change scenarios) can be lethal at temperatures that the birds could tolerate under more moderate humidities (Lasiewski *et al.* 1966a). The lethal limits of body temperature for birds are known to be around 46-47°C (Williams & Tieleman 2005) and, although some adaptation may be possible, the natural response capacity of many species may be exceeded (Wolf 2000; Hannah *et al.* 2002). The pattern of future extinctions therefore depends on a) how quickly species can respond to change (McCarty 2001; Bicudo *et al.* 2010), and b) whether or not conditions change to a point where adaptation is no longer possible (Angilletta 2009). Therefore, even those species emerging as super-tolerant to high ambient temperature may be at serious risk, at the rate at which climate is changing.

#### Limitations of the study

Just as instantaneous scans proved inadequate in detecting heat-dissipation behaviour at all but the hottest temperatures, foraging behaviour is also probably best investigated at a higher resolution. This might include more detailed measures allowing the assessment of whether shade-seeking and foraging are traded off against one another. A key weakness of this study, however, was the need to lump together data from sites across a thermal gradient, even though acclimation was corrected for as best as possible. The analyses did, however, highlight this one important point. The data strongly suggest that birds at 'hot' sites are better acclimated to heat than are individuals of the same species living in cooler sites. The implications of this for modelling changing distributions are profound (and disconcerting) because it appears that species' thermal attributes differ across sites, rendering extrapolation from one site to another difficult. Another shortcoming is the possible bias towards recording heat-stress in larger individuals. Natural hypothermia of animals (including hibernation) can be far more conspicuous than natural heat stress (Feder & Hofmann 1999). Detection is made

even more challenging in small birds, with both behavioural and physiological responses more easily detectable in birds of larger body mass.

This study also took no account of variation in plumage across species. It has been argued that the plumage of a bird significantly influences its thermal biology (Walsberg 1988a, 1988b; Battley *et al.* 2003); although others contend that the main barrier to water loss across the body wall is the skin rather than the plumage (Webster *et al.* 1985). Another shortcoming is the generalisation of species' responses. A number of studies have found differing patterns of plasticity among individuals (e.g. Battley *et al.* 2001a; Battley *et al.* 2003; Charmantier *et al.* 2008). However this was hopefully combated through a large sample size per species and sampling across more than one area. An unavoidable shortcoming was that extreme temperatures (close to 40°C) were rarely reached during the study period. According to Gillooly *et al.* (2010), temperatures up to 40°C are the range in which organisms commonly operate; and therefore do not present the optimal conditions in which to study heat-stress. Time did also not permit the conduction of a habitat survey which would have given insight into microsite availability as well as site selectivity; an important aspect of behavioural flexibility that is critical for survival in a warming world (Huey & Tewksbury 2009).

#### Further study

The detection of population change in response to climate change is likely to be affected by the masking effects of density-dependent population regulation (Clark 1987). Populations will often tend to regulate themselves to a certain level after transient or longer term changes (Newton 1998). Furthermore, the changes that are occurring on small scales are less predictable than global thermal change (Walther *et al.* 2002). It is for these reasons that research should continue at local scales in order to determine the underlying impacts of climate change. Not only may impacts be masked, but climate change might result in unexpected ecological consequences (La Sorte *et al.* 2009). This reinforces the importance of maintaining long-term ecological monitoring programmes in order to document the ongoing impacts of global change and predict the long-term consequences for biodiversity, especially in areas such as the Kalahari that are predicted to undergo extensive changes in climatic conditions. The continued evaluation of responses to change is important in ensuring that conservation efforts are directed at not only the appropriate sites, but also the correct species (McCarty 2001; Julliard *et al.* 2004a; Hulme 2005; Jiguet *et al.* 2006; Kearney *et al.* 2010).

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Appendix A – A descriptive summary of all bird observations

Table A1: A summary of 67 species observed at Dreghorn Kalahari Game Ranch. The table includes scientific names, number of observations (n), body masses (Hockey *et al.* 2005), foraging guilds, the minimum temperatures where heat-dissipation was displayed (HD<sub>min</sub>), the temperatures at which 50% of the population are predicted to be heat-stressed (HD<sub>50</sub>), and the maximum temperatures where no heat-dissipation was observed (NHD<sub>max</sub>).

<b>Spp. Name</b>	<b>Scientific name</b>	<b>n</b>	<b>Av. body mass (g)</b>	<b>Foraging Guild</b>	<b>HD<sub>min</sub></b>	<b>HD<sub>50</sub></b>	<b>NHD<sub>max</sub></b>
Acacia Pied Barbet	<i>Tricholaema leucomelas</i>	5	31	Off-ground gleaner Frugivore	29.21		35.47
African Grey Hornbill	<i>Tockus alboterminatus</i>	3	155	On-ground gleaner Insectivore	37.59		29.43
African Hoopoe	<i>Upupa africana</i>	7	53	On-ground gleaner Insectivore	35.47		35.69
African Pipit	<i>Anthus cinnamomeus</i>	2	24.5	On-ground gleaner Insectivore			35.47
Anteater Chat	<i>Myrmecochla formivora</i>	84	47.6	Perch & pounce Insectivore/Carnivore	32.79	41.82	37.93
Ashy Tit	<i>Parus cinerascens</i>	98	20.4	Off-ground gleaner Insectivore	37.82	36.71	38.49
Black-chested Prinia	<i>Prinia flavicans</i>	65	8.9	Off-ground gleaner Insectivore	38.49	38.6	39.50
Brubru	<i>Nilaus afer</i>	20	24	On-ground gleaner Insectivore			38.83
Cape Glossy Starling	<i>Lamprotornis nitens</i>	35	82.5	On-ground gleaner Insectivore	29.66	36.93	38.04
Cape Penduline-Tit	<i>Anthscopus minutis</i>	1	7.5	Off-ground gleaner Insectivore			29.43
Cape Sparrow	<i>Passer melanurus</i>	5	26	On-ground gleaner Granivore			29.10
Cape Turtle-Dove	<i>Streptopelia capicola</i>	214	130.3	On-ground gleaner Granivore	37.37	36.92	39.50
Capped Wheatear	<i>Oenanthe pileata</i>	2	25	On-ground gleaner Insectivore			35.81
Cardinal Woodpecker	<i>Dendropicos fuscescens</i>	5	30	Off-ground gleaner Insectivore	35.47		33.01
Chat Flycatcher	<i>Bradornis infuscatus</i>	7	37	Perch&Pounce Insectivore/Carnivore			38.27
Chestnut-backed Sparrowlark	<i>Eremopterix leucotis</i>	1	22	On-ground gleaner Granivore			38.27
Chestnut-vented Tit-Babbler	<i>Parisoma subcaeruleum</i>	72	15.7	Off-ground gleaner Insectivore	38.09	37.78	38.21
Common Fiscal	<i>Lanius collaris</i>	6	40.8	Perch&Pounce Insectivore/Carnivore			38.38
Common Ostrich	<i>Struthio camelus</i>	54	68700	On-ground gleaner Generalist	24.62	28.48	35.25
Common Scimitarbill	<i>Phoeniculus cyanomelas</i>	40	32.5	Off-ground gleaner Insectivore	32.23	35.19	38.27
Crimson-breasted Shrike	<i>Laniarius atrococcineus</i>	53	48.3	Off-ground gleaner Insectivore	38.04		38.04

Crowned Lapwing	<i>Vanellus coronatus</i>	39	195	On-ground gleaner Insectivore	38.84	38.38
Diderick Cuckoo	<i>Chrysococcyx caprius</i>	1	30	Off-ground gleaner Insectivore		37.48
Dusky Sunbird	<i>Cinnyris fuscus</i>	1	8	Off-ground Nectar-feeder and Insectivore		31.56
Eastern Clapper Lark	<i>Mirafra fasciolata</i>	2	30	On-ground gleaner Generalist		33.68
European Nightjar	<i>Caprimulgus europaeus</i>	1	67	Aerial Insectivore		35.13
Familiar Chat	<i>Cercomela familiaris</i>	10	22	Perch & pounce Insectivore		38.27
Fawn-coloured Lark	<i>Calendulauda africanoides</i>	30	23.3	On-ground gleaner Granivore	33.68	40.78 39.50
Fiscal Flycatcher	<i>Sigelus silens</i>	3	26	Perch & pounce Insectivore		38.04
Fork-tailed Drongo	<i>Dicrurus adsimilis</i>	227	44	Perch & sally Insectivore/Carnivore	32.79	38.94
Great Sparrow	<i>Passer motitensis</i>	1	32	On-ground gleaner Generalist		32.67
Grey-backed Sparrowlark	<i>Eremopterix verticalis</i>	2	17	On-ground gleaner Granivore	37.48	37.48
Groundscraper Thrush	<i>Psophocichla litsitsirupa</i>	12	76	On-ground gleaner Insectivore	33.35	38.04
Kalahari Scrub-Robin	<i>Cercotrichas paena</i>	78	19.7	On-ground gleaner Insectivore	39.94	41.56 38.82
Kori Bustard	<i>Ardeotis kori</i>	3	8500	On-ground gleaner Granivore		32.79
Lappet-faced Vulture	<i>Torgos trachilotis</i>	3	6700	Scavenging Carnivore		32.34
Laughing Dove	<i>Streptopelia senegalensis</i>	7	98.8	On-ground gleaner Granivore	36.92	36.92
Lesser Grey Shrike	<i>Lanius minor</i>	2	46	Perch & pounce Insectivore/Carnivore		35.02
Lilac-breasted Roller	<i>Coracias caudatus</i>	40	107.5	Perch & pounce Insectivore/Carnivore	37.93	38.49
Marico Flycatcher	<i>Bradornis mariquensis</i>	248	26.2	Perch & pounce Insectivore/Carnivore	35.25	37.35 39.38
Namaqua Dove	<i>Oena capensis</i>	6	39.9	On-ground gleaner Granivore		37.48
Northern Black Korhaan	<i>Afrotis afraoides</i>	18	739	On-ground gleaner Insectivore	35.81	36.48
Pearl-spotted Owlet	<i>Glaucidium perlatum</i>	3	76	Perch & pounce Insectivore/Carnivore		36.03
Pin-tailed Wydah	<i>Vidua macroura</i>	2	15	Off-ground gleaner Insective/Granivore	37.82	38.60
Pirit Batis	<i>Batis soror</i>	24	9.3	Off-ground gleaner Insectivore		39.38
Pygmy Falcon	<i>Polihierax semitorquatus</i>	28	60.5	Perch & Pounce Insectivore/Carnivore	36.81	38.71
Red-crested Korhaan	<i>Lophotis ruficrista</i>	17	674.5	On-ground gleaner Insectivore		39.50
Red-faced Mousebird	<i>Urocolius indicus</i>	1	56.5	Off-ground gleaner Frugivore		23.95
Red-headed Finch	<i>Amadina erythrocephala</i>	2	23	Off-ground gleaner Insective/Granivore		33.01
Rufous-cheeked Nightjar	<i>Caprimulgus rufigena</i>	1	60	Off-ground gleaner Insectivore		33.68

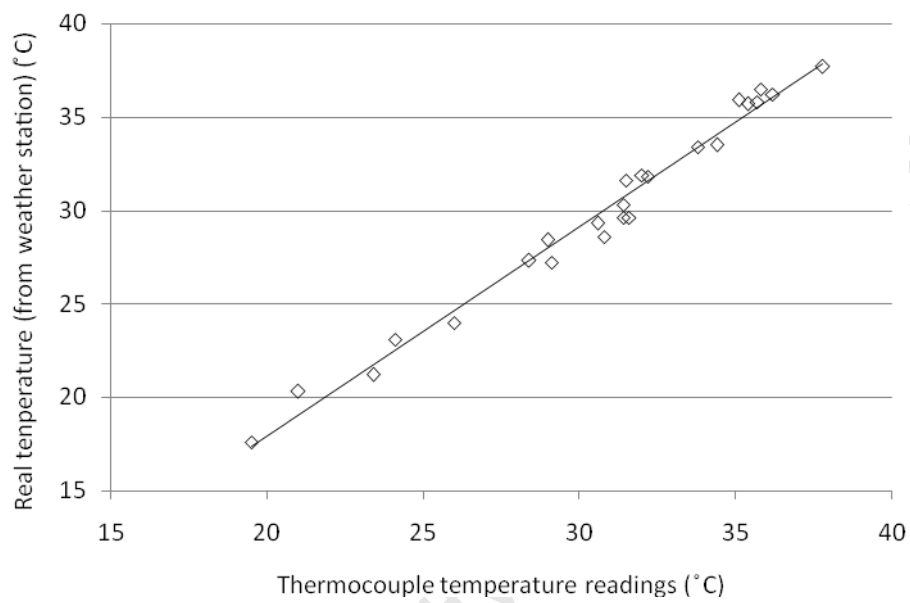
Sabota Lark	<i>Calendulauda sabota</i>	22	23	On-ground gleaner Granivore	34.35		38.60
Scaly-feathered Finch	<i>Sporopipes squamifrons</i>	77	11.1	On-ground gleaner Granivore		41.27	38.83
Shaft-tailed Whydah	<i>Vidua regia</i>	1	14	Off-ground gleaner Granivore			36.59
Sociable Weaver	<i>Philetairus socius</i>	166	27.4	On-ground gleaner Granivore	37.59	37.86	38.49
Southern Pale Chanting Goshawk	<i>Melierax canorus</i>	8	768	Perch & pounce Carnivore			38.27
Southern White-faced Scops-Owl	<i>Ptilopsis granti</i>	1	210	Perch & pounce Insectivore/Carnivore			29.10
Southern Yellow-billed Hornbill	<i>Tockus leucomelas</i>	94	189.5	On-ground gleaner Insectivore	31.44	33.79	38.15
Speckled Pigeon	<i>Columba guinea</i>	1	344	On-ground gleaner Granivore			33.23
Spotted Eagle-Owl	<i>Bubo africanus</i>	5	700	Perch & pounce Carnivore/Insectivore			37.37
Spotted Thick-knee	<i>Burhinus capensis</i>	3	465	Off-ground gleaner Insectivore			35.02
Swallow-tailed Bee-eater	<i>Merops hirundineus</i>	59	23	Perch & sally Insectivore/Carnivore	36.14		38.27
Violet-eared Waxbill	<i>Granatina granatina</i>	1	12	Off ground gleaner Insectivore/Granivore			37.48
White-backed Vulture	<i>Aegyptius occipitalis</i>	32	5500	Perch & pounce Insectivore/Carnivore	34.69		38.38
White-browed Sparrow-Weaver	<i>Plocepasser mahali</i>	98	47.5	On-ground gleaner Granivore	32.79	38.08	38.49
Yellow Canary	<i>Crithagra flaviventris</i>	13	17.5	Off-ground gleaner Granivore			38.82
Yellow-bellied Eremomela	<i>Eremomela icteropygialis</i>	43	7.9	Off-ground gleaner Insectivore			39.94

\*HD<sub>50</sub> values based on Type 2 data (i.e. binary response in a 30-second observation period)



## Appendix B - Calibration of thermocouple temperature measurements

Figure B1: The calibration of temperature readings taken with the thermocouple against those measured simultaneously at the weather station. The equation describing the linear regression is  $y = 1.1182x - 4.4498$  ( $R = 0.99$ ).



Appendix C – Correcting for methodological differences between Dreghorn and Kgalagadi

Figure C2: The calibration of temperature readings taken with the thermocouples used at KTFP against those taken simultaneously at the weather station at Dreghorn. The equation describing the linear regression (based on an average of all three thermocouples) is  $y = 1.128x - 6.037$  ( $R = 0.97$ ).

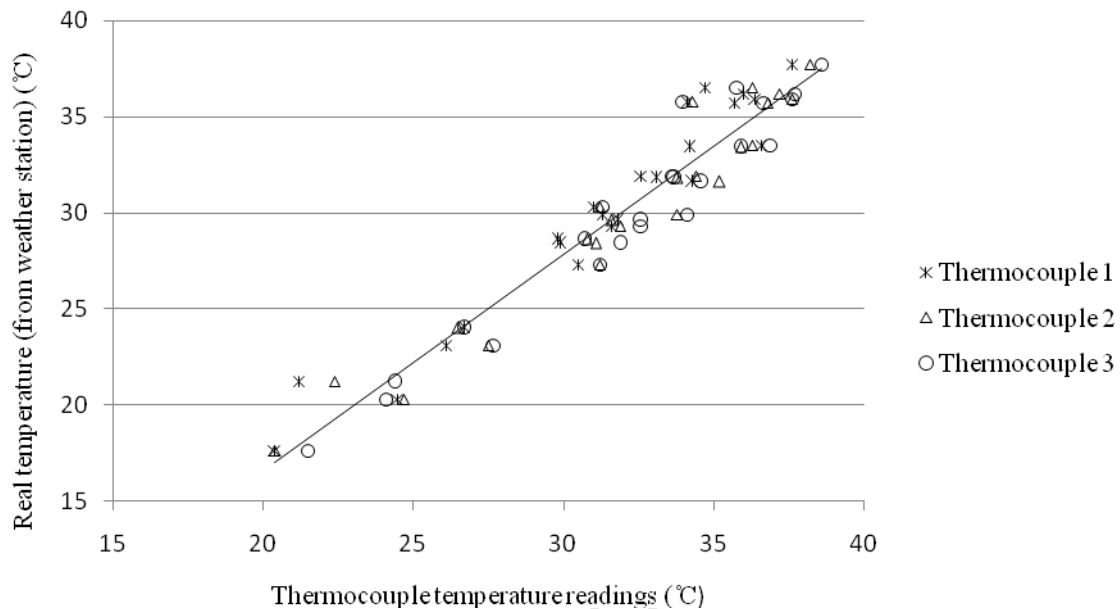
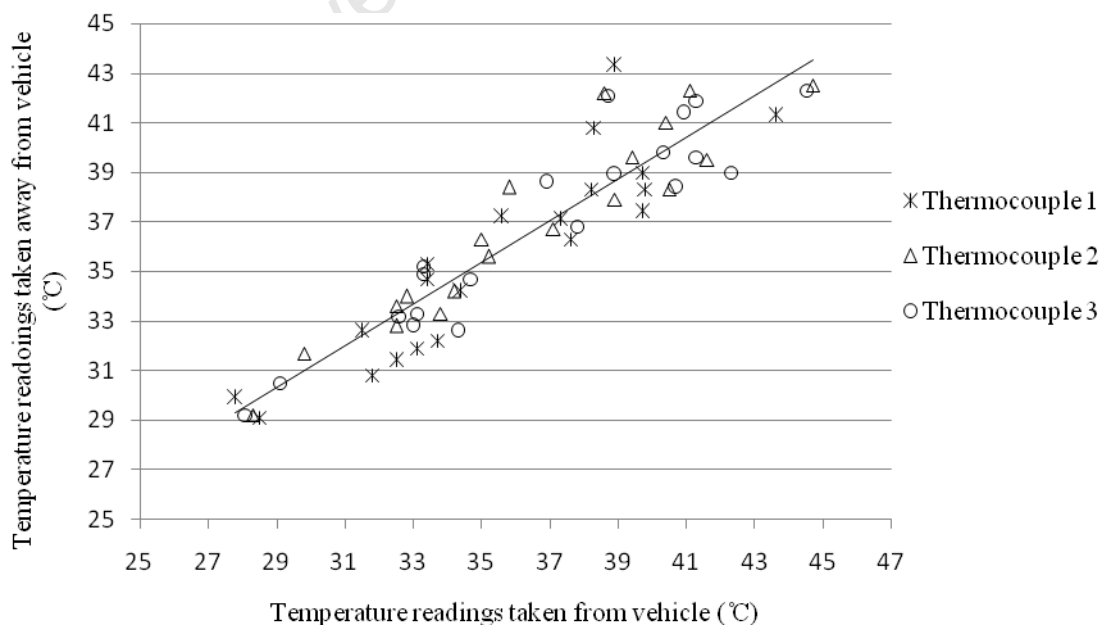


Figure C3: The calibration of temperature readings taken from the vehicle with thermocouples used at KTFP against those taken with the same thermocouples away from the vehicle. The equation describing the linear regression (based on an average of all three thermocouples) is  $y = 0.844x + 5.799$  ( $R = 0.92$ ).



Appendix D – Correcting for site differences between Dreghorn and Tswalu

Table D2: The model species used to correct the HD<sub>50</sub> values calculated for the combined data sets from Dreghorn and Tswalu to account for possible acclimation effects.

Species	HD <sub>50</sub> at Dreghorn ( C)	HD <sub>50</sub> at Tswalu ( C)	Difference between HD <sub>50</sub> values ( C)
Cape Turtle-Dove	38.312	36.635	1.677
Marico Flycatcher	40.494	36.091	4.403
Sociable Weaver	38.109	35.878	2.231
White-browed Sparrow-Weaver	40.607	35.794	4.813
			Average difference = 3.281

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Appendix E - Type 1 model output

Table E3: The temperature at which 50% of the population are predicted to be heat-stressed ( $HD_{50}$ ) based on fitting a binomial generalised linear model to Type 1 heat-dissipation data.

Species	n	$HD_{50}$ ( C)
Common Ostrich	54	30.40
Southern Yellow-billed Hornbill	94	36.63
Sociable Weaver	166	38.50
Crimson-breasted Shrike	92	40.58
Common Scimitarbill	59	41.17
Cape Turtle-Dove	627	41.64
Fork-tailed Drongo	575	42.07
White-browed Sparrow-Weaver	291	46.94
Marico Flycatcher	719	47.70

Table E4: A summary of the effects of each explanatory variable on heat-dissipation behaviour across 18 species (Type 1 data), based on the best-fitting model which includes temperature, body mass and guild, and the interaction between temperature and guild.

Coefficients	Estimate	Std. Error	z value	p	Significance
Intercept	-16.146	1.453	-11.12	0.00	***
Temperature	0.324	0.037	8.64	0.00	***
Body mass	0.362	0.054	6.76	0.00	***
On-ground, animal diet	8.108	2.271	3.57	0.00	***
On-ground, plant diet	-4.084	2.499	-1.63	0.10	
Interaction: Temp. + On-ground, animal diet	-0.205	0.061	-3.35	0.00	***
Interaction: Temp. + On-ground, animal diet	0.096	0.065	1.49	0.14	

\*\*\* = denotes a highly significant effect ( $p < 0.001$ )

Intercept = off-ground forager, with an animal-based diet (i.e. reference guild)

Table E5: Analysis of deviance table for the best model explaining Type 1 heat-dissipation behaviour, displaying the percentage of total deviance explained by each sequentially added factor, and the associated p-values ( $\chi^2$ -test).

Explanatory variables	Df	Deviance	Residual df	Residual deviance	p	% variance explained
None			4228	1652.7		
Temperature	1	196.132	4227	1456.6	0.000	11.87
Body mass	1	53.998	4226	1402.6	0.000	3.27
Guild	2	11.171	4224	1391.4	0.004	0.68
Interaction: Temp. + Guild	2	15.182	4222	1376.2	0.001	0.92
Total						16.73

## Appendix F - Type 2 model output

Table F6: The temperature at which 50% of the population are predicted to be heat-stressed ( $HD_{50}$ ) based on fitting a binomial generalised linear model to Type 2 data, in order from the lowest to the highest predicted  $HD_{50}$ .

Species	n	$HD_{50}$
Common Ostrich	62	28.480
Southern Yellow-billed Hornbill	99	33.793
Common Scimitarbill	57	35.191
Ashy Tit	117	36.713
Cape Turtle-Dove	281	36.915
Cape Glossy Starling	61	36.925
Marico Flycatcher	310	37.348
Chestnut-vented Tit-Babbler	149	37.781
Sociable Weaver	325	37.859
White-browed Sparrow-Weaver	272	38.075
Black-chested Prinia	189	38.602
Crowned Lapwing	85	38.835
Fawn-coloured Lark	163	40.778
Scaly-feathered Finch	194	41.273
Kalahari Scrub-Robin	212	41.558
Ant-eating Chat	250	41.815

Table F7: A summary of the effects of each explanatory variable on heat-dissipation behaviour across 22 species (Type 2 data), based on the best-fitting model which includes temperature, body mass and guild, and the interaction between temperature and guild.

Coefficients:	Estimate	Std. Error	z value	p	Significance
Intercept	-25.22	2.10	-11.99	0.00	***
Body mass	0.12	0.06	2.20	0.03	*
Temperature	0.64	0.06	11.12	0.00	***
Off-ground, plant diet	11.85	13.23	0.90	0.37	
On-ground, animal diet	9.21	3.11	2.96	0.00	**
On-ground, plant diet	5.74	2.61	2.20	0.03	*
Interaction: Temp. + Off-ground, plant diet	-0.35	0.38	-0.92	0.36	
Interaction: Temp. + On-ground, animal diet	-0.24	0.09	-2.82	0.00	**
Interaction: Temp. + On-ground, plant diet	-0.14	0.07	-1.98	0.05	*

\*= greater number denotes higher significance

Intercept = off-ground forager, with an animal-based diet (i.e. reference guild)

Table F8: Analysis of deviance table for the best model explaining Type 2 heat-dissipation behaviour, displaying the percentage of total deviance explained by each sequentially added factor, and the associated p-values ( $\chi^2$ -test).

	Df	Deviance	Res. df	Dev	p	% variance explained
Null model			3379	2450		
Temperature	1	529.53	3377	1910.9	0.000	21.61
Guild	3	22.18	3374	1888.7	0.000	0.91
Body mass	1	9.57	3378	2440.4	0.002	0.39
Interaction: Temp. + Guild	3	8.58	3371	1880.1	0.035	0.35
Total						23.26

Table F9: A summary of the effects of each explanatory variable on heat-dissipation behaviour across 22 species (Type 2 data), based on the best-fitting model which includes temperature, body mass and guild, and the interaction between temperature and guild, with on-ground foragers with plant-based diets as the reference guild.

Coefficients:	Estimate	Std. Error	z value	p	Significance
Intercept	-19.48	1.58	-12.34	0.00	***
Body mass	0.12	0.06	2.20	0.03	*
Temperature	0.50	0.04	11.43	0.00	***
Off-ground, animal diet	-5.74	2.61	-2.20	0.03	*
Off-ground, plant diet	6.12	13.15	0.47	0.64	
On-ground, animal diet	3.47	2.78	1.25	0.21	
Interaction: Temp.+Off-ground, animal diet	0.14	0.07	1.98	0.05	*
Interaction: Temp.+ Off-ground, plant diet	-0.21	0.38	-0.55	0.58	
Interaction: Temp.+On-ground, animal diet	-0.10	0.08	-1.30	0.19	

\*= greater number denotes higher significance

Appendix G – A comparison between Type 1 and Type 2 predictions

Table G10: A comparison of HD<sub>50</sub> values predicted for Type 1 and Type 2 data using a multiple logistic regression.

Species	Type 1 HD <sub>50</sub>	Type 2 HD <sub>50</sub>
Common Ostrich	30.399	28.480
Southern Yellow-billed Hornbill	36.625	33.793
Common Scimitarbill	41.169	35.191
Cape Turtle-Dove	41.644	36.915
Marico Flycatcher	47.704	37.348
Sociable Weaver	38.501	37.859
White-browed Sparrow-Weaver	46.94	38.075

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