Taking the heat: integrating behavioural and physiological variables to predict avian responses to climate change in the Kalahari Desert

by

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DECLARATION

I, ...Ben Smit..., declare that the thesis, which I hereby submit for the degree ... Doctor of Philosophy (Zoology)..., is my own work and has not previously been submitted by me for a degree at this or any other tertiary institution.

SIGNATURE:...

DATE:........10 July 2013......................

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DISCLAIMER

This thesis consists of chapters that have been prepared as stand-alone manuscripts. One of these manuscripts has been published and the others are prepared for future submission. As a consequence there may be differences in style and some repetition between chapters.

PUBLICATIONS AND MANUSCRIPTS IN PREPARATION

In the course of this research, one manuscript was published, and the others are in preparation. Chapter 1 is based on this manuscript.

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SUMMARY

Predicting how species will respond to climate change requires an understanding of how temperature affects behaviour, physiological tolerance limits and adaptive capacity. In this thesis, I investigated the temperature-dependency of physiology and behaviour of birds in the Kalahari Desert of South Africa.

I tested predictions that birds in arid habitats should express fine-scale variation in the temperature-dependency of thermoregulation, daily water flux (DWF) and daily energy expenditure (DEE), in response to prevailing climatic conditions. These predictions were tested during summer in a hot, desert site, and a milder, semi-desert site, in the Kalahari Desert, using White-browed Sparrow-Weaver (*Plocepasser mahali*) as a model species. The desert site birds showed higher body temperatures (T_b) and a greater magnitude of daily heterothermy. Whereas birds at the semi-desert site showed significant negative relationships between DWF and DEE, and maximum daily air temperature (T_{air}), conspecifics at the desert site showed lower DWF and DEE independent of maximum daily $T_{air.}$. Together, these findings reveal that populations can vary in their thermoregulatory responses, energy and water demands, and suggest that small changes in T_{air} can have significant effects on thermoregulation in free-ranging desert birds, even when $T_{air} < T_b$.

Water acquisition comprises an important daily activity for birds in arid habitats. I investigated the dependency of species on free-standing surface water by 1) conducting observations at waterholes and 2) using deuterium-enriched water to trace spatial water-use during summer 2011 at Tswalu Kalahari Reserve (TKR). Both methods revealed that only a small portion (~ 25 %) of the avian community at TKR depend on free-standing water sources. The majority of species visiting waterholes were granivorous; a few insectivorous and omnivorous species drank mostly on hot days in small numbers. These findings illustrate how the two methods employed in this study provide complimentary data on the relative value of a water source to the avian community.

Lastly, I carried out assessment of heat dissipation behaviour (HDB) responses as a proxy for vulnerability to heat stress in a Kalahari Desert avian community. Using data from 35 species, I showed that the temperature-dependency of HDB resonses varied greatly at an interspecific level. A phylogenetic independent analysis showed that activity levels played a major role in explaining heat-dissipation behaviours. The heat dissipation patterns observed in the Kalahari species may represent a trade-off between maintaining high activity levels to forage at high temperatures, and being exposed to an increased heat load and elevated demands for evaporative water loss.

In summary, in this thesis I presented novel data on physiological and behavioural responses in free-living birds. Collectively, my findings on thermoregulation, behaviour, water and energy fluxes in sparrow-weavers have important implications for assessing vulnerability of species to climate change, suggesting that sensitivity should be assessed at the population, rather than species level. Future studies should examine not only the impacts of extreme events which lead to sudden mass die-offs, but also longer term, chronic heat stress resulting from warmer average temperatures.

GENERAL INTRODUCTION AND OUTLINE OF THE STUDY

Global climate change will lead to large-scale range shifts among organisms, and increase the extinction risk of many species (Parmesan and Yohe 2003). Up to one million species may become extinct within the next 50 years as a direct result of global warming (Thomas et al. 2004), which will lead to large-scale ecosystem imbalances over a very short time scale (McLaughlin et al. 2002). The increase in the frequency and intensity of extreme heat waves (Meehl and Tebaldi 2004, IPCC 2007, 2011), leading to air temperatures (T_{air}) that exceed the upper limits of organisms' thermal tolerances, is potentially one of the greatest direct short-term threats to biodiversity (Wolf 2000, Welbergen et al. 2008).

Understanding which species are most vulnerable to climate change has emerged as a major challenge facing conservation biologists (Williams et al., 2008). Until recently, most predictions of species' range changes and vulnerability to climate change have relied heavily on climate envelope models (Pearson and Dawson 2003, Huntley et al. 2006). The predictions of these models, however, are based entirely on correlations between species' current distributions and the prevailing climate, and incorporate little or no data on how physiological and behavioural traits are influenced by actual environmental factors. In other words, their biological realism is questionable (Beale et al. 2008).

The short-term bottlenecks (increases in extreme maximum temperatures and heat waves) that climate change imposes on the homeostasis of organisms are important for the direct survival of a species (Humphries et al. 2002, McLaughlin et al. 2002, Welbergen et al. 2008). Among birds, for instance, mass die-offs have been recorded during extreme heat waves when temperatures exceeded 45 °C (Welbergen et al. 2008, Towie 2009, Saunders et al. 2011). To understand and predict the vulnerability of populations, communities and/or ecosystems to climate change, a more detailed assessment is needed of how environmental factors interact with the intrinsic traits and responses of a species, e.g. behaviour and physiology, and how these traits and responses vary among species (Williams et al., 2008).

Physiological and behavioural responses at relatively mild T_{air} (30–40 °C) below avian body temperatures (T_b), i.e. ~ 39–41 °C, are particularly important in the context of predicting responses to climate change. It is at these temperatures that species might experience the greatest trade-offs between activities (such as foraging, preening, territorial maintenance, and breeding), water flux rates and thermoregulation (Tieleman and Williams 2002a, Tieleman et al. 2003, du Plessis et al. 2012). General circulation models used in The Intergovernmental Panel on Climate Change has predicted that the frequency distribution of current maximum T_{air}, as well as record maximum T_{air} will shift upwards by 2–5 °C over the next few decades [see Fig. SPM.3, (IPCC 2011)]. This means that birds will become more vulnerable to longer term, cumulative effects of chronic heat stress (McKechnie et al. 2012).

Williams et al. (2008) proposed that species' vulnerability to climate change should be assessed in terms of sensitivity (i.e. intrinsic traits) and exposure (traits such as climate, habitat and environment). Intrinsic, or organismal traits are defined as physiological limits (determined by thermal physiology, water and energy requirements) and ecological traits (behavioural and ecological interactions), and genetic diversity (i.e. resilience to disturbances, and genetic or phenotypic adaptive capacity) (Williams et al., 2008). A better understanding of the ecological and evolutionary links between thermal physiology, water and energy requirements and behaviour are particularly important for studies on endotherms because of the cost associated with regulating T_b relatively independent of the environment. Genetic diversity is another important factor to take into consideration, as it could increase the probability of adaptive responses (Williams et al., 2008). Although difficult to quantify, adaptive responses (genetic or phenotypic) would be an important factor in determining species' vulnerabilities to climate change. Phenotypic plasticity in physiological, ecological and behavioural traits would be especially important in vertebrates, such as birds, since they are generally long-lived and will have to respond to environmental changes within lifetimes, rather than between generations (Boyles et al. 2011). These predictions suggest that vulnerability should be assessed at the level of populations, rather than species, especially in taxa that occupy wide geographical ranges [sensu Williams et al., (2008)].

Vulnerability of birds in hot subtropical deserts to climate change

Climate change models predict that nearly all the world's hot deserts (those located at subtropical latitudes) will be become significantly hotter during the 21st Century, with maximum T_{air} expected to increase by 3 to 5°C by the 2080s (IPCC 2007). However, the impact of this warming will not only result in record extreme temperatures, but average temperatures will also increase (IPCC 2011) Birds that inhabit hot, sub-tropical desert environments are particularly vulnerable to increasing temperatures because the majority of species are diurnal and make very limited use of thermally well-buffered refugia, such as underground burrows, to escape high temperatures (Williams & Tieleman, 2005; Wolf, 2000). In addition, the scarcity of surface water means that maintaining endogenous water balance may be problematic for birds during hot periods. In extreme instances, the combination of very high maximum temperatures and limited water resources can lead to catastrophic avian mortality events, such as those reported in the deserts of Australia and the south-western United

States (Finlayson 1932, Keast 1960, Miller 1963). More recently in Western Australia, a severe heat wave (temperatures > 45 °C) resulted in thousands of Budgerigars (*Melopsittacus undulates*), Zebra Finches (*Taeniopygia guttata*) and Cockatiels (*Nymphicus hollandicus*) dying of heat stress and dehydration within two weeks (Towie 2009).

Birds normally regulate a relatively high T_b within a narrow range (typically 39–41°C) through endogenous metabolic heat production, irrespective of the environmental temperature (T_e, i.e. combined effects of air temperature, solar heat load, relative humidity and convective heat loss) (Schmidt-Nielsen 1990). Normal avian T_b are near lethal upper limits, and increases in T_b to above 45 °C typically result in the loss of the capacity for coordinated movement, whereas T_b > 46–47° C is almost invariably lethal (Dawson & Schmidt-Nielsen, 1964; Dawson, 1954). The process of maintaining T_b within the normothermic range is expensive in terms of both resources (energy and water) and time (Schmidt-Nielsen 1990, Tieleman and Williams 2002a). Regulation of body heat (H_b) in endotherms can be represented using a simplified heat exchange model:

$$H_b = H_v + H_t - H_e$$

where H_v represents heat produced metabolically (e.g. metabolic processes or locomotor activity), H_t represents environmental heat transfer (heat gained – heat lost, by conduction, convection or radiation), and H_e represents heat lost through evaporation (Schmidt-Nielsen 1990). When $T_{air} > T_b$, heat transfer will be positive and the only avenue to lose heat is through increased evaporative heat loss. In addition birds can further reduce the rate of heat gain when $T_{air} > T_b$ by 1) reducing metabolic production and activity levels, and 2) by decreasing thermal conductance (e.g. by altering insulative properties and body position). Alternatively, birds can simply store heat, by allowing T_b to increase. The respective costs and benefits of thermoregultion in hot desert environments can vary greatly, depending on which of these thermoregulatory mechanisms birds rely on.

In general, a bird's thermoregulatory input is minimal over a range of T_{air} (i.e. the thermoneutral zone, TNZ) (Schmidt-Nielsen 1990). However, at T_{air} above or below the TNZ, behavioural and physiological thermoregulatory responses are initiated to counter heat flux. As temperatures start rising towards or exceed the upper limit of the TNZ (T_{uc}), progressively more time will be spent to counter heat load behaviourally, or to dissipate heat physiologically (Dawson, 1976).

Behavioural thermoregulation under high T_{air} involves, reducing activity levels, seeking cooler microsites (shade, rarely burrows), perching in the wind (to facilitate convective heat loss), wing-drooping (to expose bare skin, a.k.a. thermal windows, to moving air) and ptiloerection (raising dorsal feathers on the back to reduce direct solar heat gain through the skin) (Dawson & Whittow, 2000). Many nesting birds also make use of behavioural responses to regulate egg and nestling temperatures when T_{air} exceeds T_b e.g. shading eggs and nestlings and enhancing evaporating cooling of egg surfaces by wetting the eggs and nest with soaked belly feathers (Grant 1982, Walsberg and Voss-Roberts 1983).

Physiological responses that facilitate heat loss include vasodilation to increase the volume of blood flowing through peripheral body regions where heat loss can be maximized, and/or by taking advantage of the cooling powers of evaporation by allowing body water to evaporate from skin (cutaneous EWL) and respiratory surfaces (Schmidt-Nielsen 1990). To increase the rate of evaporative cooling, many birds make use of panting or gular fluttering behaviours to facilitate the convection of air over moist respiratory surfaces (Schmidt-Nielsen 1990). Although gular fluttering and panting are highly efficient heat dissipation mechanisms, they result in additional heat production through metabolic activity. Cutaneous evaporation (water lost through skin) on the other hand, is used by a number of birds to facilitate heat loss without an increase in metabolic rate (Bernstein 1971, Lasiewski et al. 1971, Wolf and Walsberg 1996, Tieleman and Williams 2002b, McKechnie and Wolf 2004). By altering the skin's waterproofing properties under heat acclimation regimes, White-winged Doves (*Zenaida asiatica*) can increase cutaneous evaporation rates to reduce the demands of respiratory water associated with panting (McKechnie and Wolf 2004).

The relative importance of behavioural and physiological mechanisms of heat dissipation is likely to vary greatly among avian taxa due to interspecific differences in thermal tolerance, thermoregulatory precision, and the demands for energy and water resources (Boyles et al. 2011). In many cases these physiological characteristics are phylogenetically constrained, meaning that their short term adaptive capacity might be limited (Blomberg et al. 2003). For instance, only some avian taxa can make use of gular fluttering (Caprimulgiformes, Galliformes, Pelecaniformes, Cuculiformes, Strigiformes). Passerines seem to rely mostly on panting (Dawson & Whittow, 2000), whereas columbids (doves and pigeons) dissipate most of their heat loads through cutaneous evaporation (Wolf and Walsberg 1996).

Although evaporative cooling is usually the most effective pathway of heat dissipation under very hot conditions, it is expensive in terms of water requirements, and is therefore only be feasible if a bird can maintain an adequately hydrated state during hot periods (Wolf 2000). There are very few data on avian short-term dehydration tolerance limits, but the 7-g Verdin (*Auriparus flaviceps*) can lose approximately 11% of its body mass before losing the ability for coordinated movement (Wolf and Walsberg 1996). Moreover, many desert birds have limited access to drinking water and/or rely largely on their diets to supply them with water (i.e. pre-formed water); their reliance on evaporative water loss (EWL) during extremely hot periods will increase the risk of death when their dehydration tolerance limits are exceeded. Desert species with limited access to water sources should, therefore, either modify behavioural to reduce metabolic rate and EWL, or store heat (Angilletta et al. 2010) by allowing T_b to increase when T_{air} is high to minimize EWL (i.e. facultative hyperthermia) (Tieleman and Williams 1999). Both these alternative strategies could potentially involve additional costs and trade-offs. Behavioural thermoregulation often takes up a large fraction of a bird's time-activity budget, thereby reducing the times allocated to foraging, reproduction and maintenance (Tieleman et al. 2003), whereas facultative hyperthermia increases the risk of reaching lethal levels of T_b (Tieleman and Williams 1999).

The vulnerability of a particular species to climate change, specifically increased maximum air temperatures, will thus be critically dependent on factors such as dehydration tolerance, facultative hyperthermia and ability to dissipate heat loads via evaporative pathways. Understanding these responses will provide a measureable quantitative framework for assessing upper limits of thermal tolerance and the plasticity of physiological and behavioural responses to temperature extremes in the field.

The Kalahari Desert of southern Africa as a model system

Southern Africa's hottest desert, the Kalahari Desert, has a diverse bird community. Most species appear to be largely independent of drinking water (Willoughby and Cade 1967). Most of the Kalahari Basin is dominated by arid savanna on deep sands and immobile dunes, with a general lack of surface water. The rainfall of the region is erratic (100–400 mm/year) and occurs largely as thunder showers during summer (November to March) that are spatially and temporally unpredictable (Lovegrove 1993). Historically, surface water sources were limited to calcrete pans and fossil riverbeds which become inundated only after rains, although the recent sinking of boreholes by stock farmers have resulted in a more or less continuous network of waterholes and drinking troughs throughout most of the Kalahari region in South Africa and Namibia.

The southern Kalahari region, is generally defined as the dune fields covering northern regions of Northern Cape Province in South Africa, south-eastern Namibia and south-western Botswana (Fig. 1). Some regions frequently experience extreme maximum temperatures (> 40 °C) during summer and the average summer maxima is higher (~ 35 °C) than most other regions in southern Africa [Fig. 16 in Harrison et al. (1997)]. It is predicted that the southern Kalahari will experience high levels of warming (Moise and Hudson 2008). For example, Twee Rivieren showed some of the greatest rates of warming in South Africa over the last few decades (Kruger and Sekele 2012). Moreover, climate envelope models of South African bird distributions predict large-scale climate-change-related species loss for the western parts of region, covering the entire Kalahari region of South Africa (Erasmus et al. 2002). The Southern Kalahari desert shows a strong east-west climatic gradient, largely caused by the Kalahari High Pressure Zone (subsiding air masses) and the drying effect of the cold Benguela current of the west coast of southern Africa (Usman and Reason 2004, Reason et al. 2006). Rainfall (falling mainly during the austral summer) is therefore higher in the east, and summer maxima temperatures are milder.

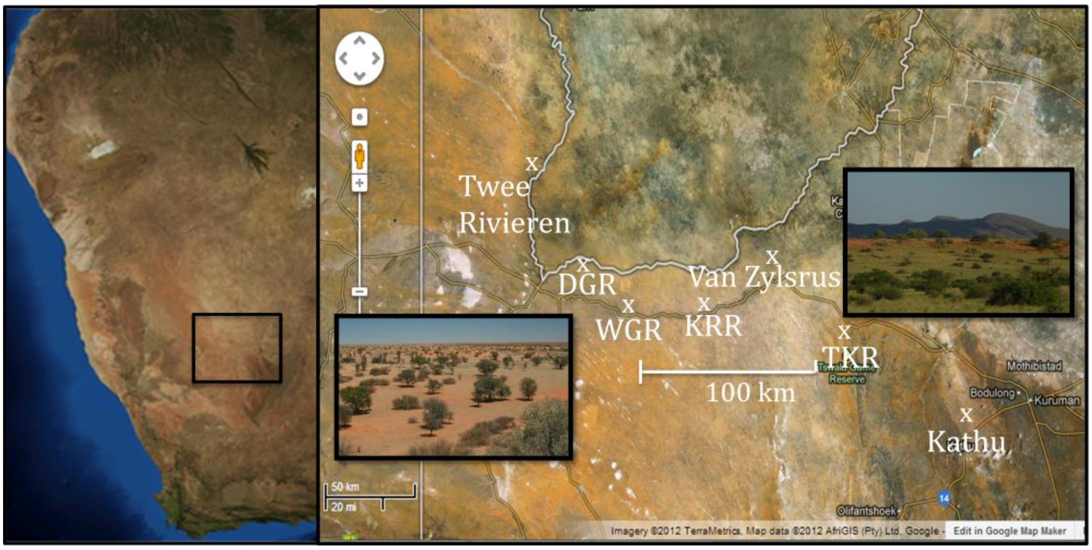

Figure 1: Map of southern Kalahari Desert study sites (satellite images obtained from NASA World Wind and Google Maps for southern Africa and southern Kalahari, respectively, showing Tswalu Kalahari Reserve (TKR), Kuruman River Reserve (KRR), Wildsgenot Game Ranch (WGR), Dreghorn Game Ranch (DGR).

OBJECTIVES AND THESIS STRUCTURE

The over-arching aims of my thesis were to investigate if behavioural (e.g. drinking behaviours, time-activity budgets) and physiological responses (daily water and energy fluxes, facultative hyperthermia) of birds in the southern Kalahari are affected by high air temperature and trade-offs between water and energy balance. In the first two chapters I address specific questions about the temperature dependency of thermoregulation, behaviour, water and energy fluxes, using an arid-zone passerine, the White-Browed Sparrow-Weaver (*Plocepasser mahali*) as a model species. These responses were investigated in both a hot, desert site (Wildgenot Game Ranch) and a milder, semi-desert site (Tswalu Kalahari Reserve) in the souther Kalahari Desert (Fig. 1). In the remaining chapters, I investigate temperature-dependency of drinking patterns and heat dissipation behaviour in Kalahari Desert avian communities at an interspecific level.

In Chapter 1, I tested predictions that birds in arid habitats should express fine-scale variation in their thermoregulatory patterns as a function of prevailing climatic conditions. I tested these predictions on two populations (warm desert and milder, semi-desert population) of White-browed Sparrow-weavers. I hypothesized that 1) birds would store heat on hot days and therefore T_b would be positively correlated to T_{air}; 2) reliance on hyperthermia during warm weather should be greater in the population at the desert site, and/or that this population should express a higher set-point T_b; and 3) the population at the desert site should thermoregulate less precisely during the rest phase than birds from the semi-desert site.

In Chapter 2 I tested whether daily water flux (i.e. water intake) in free-living birds is driven most strongly by 1) the demands for evaporative cooling—i.e. an increase in water flux on hot days, or 2) by activity-related water demands—i.e. a decrease in water flux on hot days correlated with decreased activity patterns. These predictions were tested on two populations (warm desert and milder, semi-desert population) of White-browed Sparrow-weavers (*Plocepasser mahali*). Firstly I hypothesized that water flux will be reduced on hot days since sparrow-weavers obtain most of their water through foraging. I further hypothesized that water flux should be lower in birds inhabiting more xeric habitats, and expected that the population from the arid site should show lower daily water flux and daily energy expenditure than the population from the semi-arid site.

In Chapter 3 I investigated the temperature-dependency of drinking behaviour of the Kalahari avian community. I assessed drinking dependency through two methods: 1) by direct observation through video surveillance at four waterholes at Tswalu Kalahari Reserve, and 2) by establishing the contribution of a water source to the body water pool of the bird community using an isotopically-labelled water source. I predicted that birds should increase drinking frequency on hot days to compensate for elevated evaporative water loss demands. Specifically, I predicted that species that generally do not drink, or obtain most of their water through pre-formed or oxidative water, should rely more on free-surface water sources during hot weather.

The ecology and behavioural patterns of species will greatly affect their thermal heat load and evaporative water loss demands. In Chapter 4, I investigate variation in heat dissipation behaviour (panting/gular fluttering) in the Kalahari Desert avian community, and explore the value of the methodology as a proxy for evaluating heat stress. I tested the effect of temperature on heat dissipation behaviour and activity levels (such as foraging effort) in 35 Kalahari species. I predicted that temperature-dependency of activity-related behaviour show considerable variation at an interspecific level, and that these should correlate strongly with heat-dissipation effort.

Chapter 5 provides a general summary of project and discusses implications of future warming scenarios for Kalahari Desert species.

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CHAPTER 1

ADAPTIVE THERMOREGULATION DURING SUMMER IN TWO POPULATIONS OF AN ARID-ZONE PASSERINE

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ABSTRACT

Heterothermy plays an important role in lowering the costs of thermoregulation in endotherms by reducing water and energy requirements. We tested predictions that birds in arid habitats should express fine-scale variation in their thermoregulatory patterns as a function of prevailing climatic conditions. We assessed the effects of air temperature (T_{air}) and water vapor pressure deficit (D) on body temperature (T_b) in free-living white-browed sparrow-weavers (*Plocepasser mahali*) during summer in two arid habitats in the Kalahari Desert, South Africa, using data from a dry period at a hot, desert site ($n = 7$), and a dry ($n = 4$) and a wet period ($n = 5$) at a milder, semi-desert site. The desert birds maintained a significantly ($p < 0.001$) higher set-point T_b (41.5 ± 0.2 °C, mean ± SD) than semi-desert birds (40.2 ± 0.2 °C). During the warmest part of day (12:00 – 18:00 hours), T_b increased significantly during periods of high T_{air} and/or high humidity, and mean and maximum T_b were up to 1.4 and 2.3 °C, respectively, above normal levels. However, as T_{air} increased, birds at the desert site maintained T_b at or below set-point levels for a greater proportion of the time than birds at the semi-desert site. Birds at the desert site also expressed a greater magnitude of daily heterothermy (mean Heterothermy Index, HI = 2.4 ± 0.3 °C) than birds at the semi-desert site: the latter population showed a greater magnitude of heterothermy during a dry period (HI = 2.1 ± 0.3 °C) than during a wet period (HI = 1.6 ± 0.2 °C). Birds continued foraging throughout the warmest part of the day, despite the fact that heat dissipation (% time spent panting and wing-spreading) increased significantly with increasing T_{air}. Our findings reveal that populations can vary in their thermoregulatory responses in both space and time, and suggest that small changes in T_{air} can have significant effects on thermoregulation in free-ranging desert birds, even when $T_{air} < T_b$. These data have important implications for assessing vulnerability of

species to climate change, suggesting that sensitivity should be assessed at the population, rather than species level.

Key words: white-browed sparrow-weaver, *Plocepasser mahali*, thermoregulation, hyperthermia, heterothermy, climate change, heat dissipation

INTRODUCTION

An organism's body temperature (T_b) has far-reaching consequences for its short- and long-term performance, and hence fitness, and many animals have evolved the capacity to regulate an optimal T_b via behavioral and/or physiological mechanisms. For endotherms, T_b regulation occurs continuously often under varying conditions, and sometimes at extreme temperatures that are far outside the thermoneutral zone. In the last two decades, a proliferation of data on daily and seasonal T_b variation in endotherms (especially studies on free-living animals) has revealed T_b to be a dynamic trait, tightly linked to an endotherm's interactions with its environment [reviewed by Angilletta et al. (2010)]. For example, plasticity in T_b regulation both within and among populations has been observed in the Australian bush rat (*Rattus fuscipes*), with set-point T_b (the most frequently regulated body temperature) lower in winter than in summer (Glanville and Seebacher 2010), and lower in populations inhabiting colder climates (Glanville et al. 2012).

Angilletta et al. (2010) argued that thermoregulatory variation in endotherms is largely adaptive, and that T_b should be maintained or varied in response to ecological and energetic costs and benefits associated with thermoregulation. Birds and mammals need to expend considerable amounts of energy on thermogenesis when the effective environmental temperature (T_a) is below the lower bound of the thermoneutral zone (TNZ), and face potentially high rates of water loss (on evaporative cooling) when T_a exceeds the upper bound of the TNZ (Withers 1992). The increased costs or decreased benefits of homeothermy should thus favor either a change in set-point T_b or an increase in the variability of T_b in a direction that increases the benefit to cost ratio (Angilletta et al. 2010).

Compared to the number of studies on rest-phase heterothermy, thermoregulation in small free-ranging endotherms under warm conditions has received comparatively little attention (Fick et al. 2009). An improved understanding of how environmental factors affect the costs of thermoregulation and, more importantly, the abilities of organisms to respond to different climatic conditions, is essential in the face of growing concerns about the vulnerability of endotherms to climate change (Welbergen et al. 2008, Fuller et al. 2010, McKechnie and Wolf 2010, Boyles et al. 2011a, Glanville et al. 2012). One of the main predictions of bioclimatic envelope models is that populations near the climatic extremes of species' distributions, where thermoregulatory costs are presumably high, are performing sub-optimally and are at greater risk of extinction (Thomas et al. 2004). However, if populations are physiologically adapted (genetic variation across generations and/or plastic adjustments) to their respective climates, species may be capable of maintaining high levels of performance throughout their geographic ranges (Chown et al. 2010, Glanville et al. 2012).

Selection pressures on thermoregulatory ability during an animal's rest-phase likely favor reduced energy expenditure brought about through facultative reductions in T_b (Pravosudov and Lucas 2000, McKechnie and Lovegrove 2002), but selection pressures acting during the active phase are likely to favor a T_b range appropriate for high-activity performance and endurance over a range of environmental conditions

(Heinrich 1977, Angilletta et al. 2010). The regulation of an optimal, active-phase T_b will likely influence foraging efficiency, reproductive effort, and ultimately evolutionary fitness (Heinrich 1977). A T_b too far below the optimal range could result in reduced performance (Angilletta et al. 2003, 2010), whereas a T_b above the optimal range carries with it the risk of lethal hyperthermia, since the range of T_b an organism can tolerate above normal T_b is generally narrow (Dawson 1954).

Heat dissipation through evaporative cooling can constitute a major cost of thermoregulation during the active phase, especially when the environmental temperature exceeds T_b (or more specifically, the animal's surface temperature) and because evaporative water loss increases rapidly with increasing T_{air} (Wolf 2000). Many endotherms are thought to reduce this cost by storing heat (facultative hyperthermia) during periods of heat stress, thereby reducing the need for evaporative cooling at high T_{air} [mammals: reviewed by Mitchell et al. (2002) and Cain et al. (2006); and birds: reviewed by Tieleman and Williams (1999)].

Deserts provide ideal environments for examining relationships between thermoregulation and environmental factors (Wolf 2000). The large fluctuations in T_{air} that occur daily can result in endotherms experiencing T_{air} both above and below their TNZs in the space of a few hours. Desert birds are exposed to these T_{air} fluctuations to a greater degree than taxa such as reptiles and small mammals because few diurnal avian species make use of thermally buffered microsites below ground (Bartholomew and Cade 1963, Williams et al. 1999, Wolf 2000). Limited food resources often force desert birds to forage during hot weather (Tieleman and Williams 2002), posing the potential risk of water and energy expenditure rates exceeding intake rates (du Plessis et al. 2012). Moreover, the scarcity of surface water means that balancing water losses associated with high rates of thermoregulatory EWL may become costly during periods of very hot weather.

Birds inhabiting desert environments are thought to benefit greatly from facultative hyperthermia, which contributes to water savings during heat stress (Tieleman and Williams 1999). However, facultative hyperthermia as a physiological adaptation does not appear to be restricted to desert birds. There is no evidence that desert species elevate their T_b more or regulate a higher set-point T_b than non-desert species (Tieleman and Williams 1999). It is noteworthy, however, that all the data used to test this hypothesis were obtained from birds under laboratory conditions. Under natural conditions T_b regulation can be strongly affected by variation in resources (energy and water) and activity patterns. For instance, as heat load increases, hydration state should play an important role in the regulation of T_b [Angilletta et al. (2010); see also Maloney and Dawson (1998)]. Because birds living in hot deserts are more likely to experience water stress than those in cooler, more mesic environments, one might predict that they would maintain a higher T_b (either through facultative hyperthermia or a higher set-point T_b) to dissipate heat via non-evaporative pathways.

We hypothesized that both active- and rest-phase thermoregulatory patterns are tightly linked to environmental conditions in hot, arid habitats, and investigated the influence of T_{air} on thermoregulation in an Afrotropical, arid-zone passerine bird during summer at two sites in arid habitats—a desert site with high T_{air} maxima and low rainfall, and a semi-desert site with cooler and wetter conditions. We tested the predictions that 1) birds would store heat on hot days and that T_b should be positively correlated to T_{air} by both day and night; 2) reliance on hyperthermia during warm weather should be greater in the population at the desert site, and/or that this population should express a higher set-point T_b; and 3) the population at the desert site should thermoregulate less precisely during the rest phase than birds from the semi-desert site.

METHODS AND MATERIALS

We investigated the effect of T_{air} on T_b and behavior of an arid-zone endotherm, the white-browed sparrow-weaver (*Plocepasser mahali*; family: Ploceidae; order: Passeriformes; Appendix A, Fig. A1), at two sites, 100 km apart, in the southern Kalahari Desert of South Africa, over two consecutive summer seasons. During the first summer we collected data from birds at a semi-desert site, Tswalu Kalahari Reserve (TKR, ~1100 m a.s.l., S27°19', E22°25'), over two periods: 1 December 2010 to 28 December 2010 (period 1) and 14 January to 12 February 2011 (period 2). During the following summer we obtained additional data from a more arid site, Wildsgenot Game Ranch (WGR, ~ 890m a.s.l., S 27°04' E21°23'; ~ 100 km due west of TKR) from 21 November to 18 December 2011 (period 3). We subsequently refer to TKR as the semi-desert site and WGR as the desert site (Appendix A, Fig. A2). The desert site is part of the most extreme climatic region occupied by our study species across its southern African range.

During the study, weather data were obtained at both sites using a portable weather station (Vantage Pro2, Davis Instruments, Hayward, CA), set 2 m above ground in the approximate centre of each study site. This weather station has an aspirator fan to ensure air movement over the temperature and humidity sensors. We checked the factory calibration of the weather station against a mercury thermometer for T_{air} and against a regularly calibrated CO_2/H_2O gas analyzer (LI-840A, LI-COR Inc., Lincoln, Nebraska) for humidity. The weather during period 3 at the desert site was similar to period 1 (the dry season at the semi-desert site), whereas period 2 experienced wet, humid conditions, and a less extreme range in temperature (Appendix A, Table A1).

We trapped birds at night (21:00 to 23:00 hours) in their roost nests using a hand net. At the semi-desert site we caught 12 individuals on 28 November 2010 (dry season), 12 individuals on 12 January 2011 (wet season), and we caught 13 individuals at the desert site on 20 November 2011. All the birds were banded with a single aluminium ring and up to three color rings for subsequent identification in the field.

Measurement of body temperature

On the day of capture the birds were transported to a veterinary clinic where a registered veterinarian implanted temperature-sensitive dataloggers intra-peritoneally (iButtons, Model DS1922L, Maxim Semiconductors, Dallas, Texas). The iButtons were modified following Lovegrove (2009), by removing the steel casing to reduce their mass below 1.5 g. However, whereas Lovegrove (2009) soldered the battery onto the circuit board to secure the connection, we found that this method increased the chances of draining the battery, and we therefore glued the battery to the circuit board using an adhesive (Pratley Ezeebond®, Krugersdorp, South Africa). We calibrated the iButtons against a mercury thermometer (accurate to 0.1 °C) at temperatures between 35 and 45 °C at 2.5 °C intervals. We programmed the iButtons to record data every 10 min (0.0625°C resolution), and coated them in biologically inert surgical wax before implantation. The mean body mass of birds was 42.9 g (range = 35.8 – 51 g) and therefore the implanted iButtons (1.76 – 2.05 g) weighed less than 5.5 % of body mass in all individuals—we ensured the lightest iButtons were implanted in the smallest individuals. The birds were fully anesthetized during surgery, initially using 4 % isoflorane (supplied through a facial mask) and subsequently maintained at 2 % isoflorane. We kept the birds in captivity in a cage (1 x 1 x 1 m) constructed of shade-cloth for a maximum of 24 h, providing mealworm larvae and water *ad libitum* to allow them to recover from surgery before releasing them at the site of capture. We attempted to recapture the birds one month after surgery, either by hand from their roosts or during the day using mist nets (Ecotone, Gdynia, Poland) and transported all recaptured individuals to the veterinary clinic where the iButtons where surgically removed, following the same procedure described above. Finally, all individuals were released at the site of capture. We recovered T_b data from four and five birds during the dry and wet season at the semi-desert site, and seven birds from the dry season at the desert site.

Behavioral observations

We monitored individuals implanted with data-loggers between 12:00 and 18:00 hours (i.e. the warmest time of day) to link behavioral patterns to T_b measurements. A single focal observation per day, lasting 10 - 30 min, was made on a randomly chosen, implanted bird. During each focal period we noted behavior at one-minute intervals, and recorded activity state (mobile/stationary), general activity (foraging, resting/scanning, preening, calling, nest maintenance or provisioning chicks). Foraging behavior included running on the ground with intermittent stops to inspect grass-tufts, bushes or plant litter for insects or seeds, pecking at insects, and digging in the ground or plant litter for food. Resting or scanning behavior included perching on the ground, vegetation or an elevated post: individuals often scanned their surroundings (probably vigilance behavior), preened, or communicated vocally with group members at this time. We also recorded microsite use by recording 1) whether the bird was on the ground or arboreal; 2) if it was associated with vegetation and 3) the bird's exposure to direct sun (sun/shade/dappled sunlight). Finally we recorded whether the bird engaged in heat-dissipation behavior during any of the above-mentioned activities, i.e. panting (defined as gaping when breathing) and/or wing-spreading (defined as lifting the shoulder away from body to facilitate air flow over the underwing). We conducted a total of 10, 88 and 11 focal observations during the first, second and third data-collection periods, respectively.

Data and statistical analyses

All statistical analyses were done using R (R Development Core Team 2011). We followed Boyles et al. (2011b) and assumed that modal body temperature (T_{mod}, defined as the most frequently measured body temperature to the nearest 0.1°C), measured at temperatures when the birds were active but unlikely to be experiencing thermal stress, approximated active-phase optimal or set-point T_b. We determined T_{mod} for each bird by pooling all T_b measurements made between 06:00 and 10:00. We used analyses of variance (ANOVA) to compare T_{mod} between dry and wet seasons at the semi-desert site and the dry season at the desert site. To investigate deviations in T_b from T_{mod} during the warmest part of the day (12:00 – 18:00), we calculated mean T_b-T_{mod} and maximum T_b-T_{mod} for each individual over three time-intervals: 12:00 – 14:00, 14:00 – 16:00 and 16:00 – 18:00 (hereafter referred to as early-, mid- and late-afternoon). For each time-interval we calculated mean T_{air} (for each interval maximum T_{air} was normally within 1 °C of mean T_{air}) and mean water vapor pressure deficit (*D*, in kPa). We calculated *D* as the difference in vapor pressure between saturated air (e_s, the vapor pressure of saturated air at T_i) and the actual vapor pressure (e_a, measured by the weather station) (Campbell and Norman 1998). We hypothesized that D should strongly influence the ability of the birds to lose heat through evaporation. However, assessing the role of D in the field is potentially problematic because D is highly dependent on T_{air}. If there was sufficient variation in e_a levels between days, collinearity between D and T_{air} was less severe since there was a greater range of possible D at any given T_{air}. However, if e_a did not vary sufficiently in the data set, the degree of collinearity between D and T_{air} was high in statistical analyses which can result in unstable model estimates and artificially inflated p-values (Zuur et al. 2010). For this reason, before including D as a factor in any of our models, we first assessed the degree of collinearity between T_{air} and D in each data set using a Spearman's rank correlation and variance inflation factors. We excluded D from models when the variance inflation factors exceeded 10 [following Montgomery and Peck (1992)]. We used generalized mixed-effects models to test if T_b and behavior were related to T_{air} and D (if applicable). We used the *nlme* (Pinheiro et al. 2009) and *lme4* (Bates et al. 2007) packages in R to analyze T_b and behavioral data, respectively. For T_b analyses (absolute and T_b-T_{mod} mean and maxima) we included the fixed effects of study period, time of day and gender as categorical factors, and T_{air}, D, and body mass as covariates. The random effects (fitted through model selection) of individual, and date were included in a nested design because T_b measurements for individuals were repeated on 18-28 days. We investigated the extent of daily heterothermy (i.e. T_b variation across the circadian cycle) expressed by each individual by calculating a Heterothermy Index (HI; Boyles et al. 2011b), using 24-hour T_b measurements (midnight to midnight). The HI value quantifies deviation of T_b away from modal T_b, and provides a quantitative index of heterothermy.

HI was calculated as:

$$HI = \sqrt{\frac{\sum (T_{b-\mathrm{mod}} - T_{b-i})^2}{n-1}}$$

where $T_{b\text{-mod}}$ is the modal T_b of an individual, $T_{b\text{-i}}$ is the T_b at time *i*, and n is the number of times T_b is sampled (in our case, 144 during a 24-hour period). We assessed variation in daily heterothermy as a function of mean daily T_{air}, study period, sex, and body mass, using individual and date as random factors in a nested design.

In analyses of behavioral data we calculated the proportion of time (determined by frequency) allocated by each individual to major behavioral activities (i.e. foraging and resting/scanning) for each focal period. Using a binomial model, we evaluated how these behavioral patterns varied as a function of mean T_{air} and time of day as fixed effects, and individual and date as random factors (*D* was highly collinear with T_{air} in this data set and could not be included in the models). Initially we ran the models using two potential link functions, logit or cloglog, and subsequently used the function that provided the lowest Akaike Information Criterion score adjusted for small sizes (AIC_c) (Burnham and Anderson 2002). When ΔAICc for the two logit and cloglog models was < 2, we assumed a logit function.

In all analyses we initially entered all relevant factors in a model, subsequently removing factors which were not important in a stepwise manner using of multi-model inference (Burnham and Anderson 2002), using the R package *MuMIn* (Barton 2010) to select the model which gave the lowest AIC_c weighted score. We included all relevant interactions *a priori* and, when an interaction was not important, it was removed in the final model (Engqvist 2005). For *post hoc* tests of dependent data sets we used a Multiple Comparisons of Means *Post hoc* test (i.e. Tukey Contrasts for mixed-effects models), using *multcomp* (Hothorn et al. 2008) and *mvtnorm* (Genz et al. 2011).

We also investigated the effects of behavior on T_b. Because T_b was measured every 10 min (hereafter referred to as the T_b-interval) we could evaluate the effect of behaviors between consecutive T_b readings on 1) the magnitude and direction of a change in T_b, and 2) T_b-T_{mod} at the end of the interval. We categorized activity levels as zero (completely inactive), low (0%< activity levels ≤ 50%) and high (50%< activity levels ≤ 100%) and compared mean T_b values as a function of activity levels using generalized mixed-effects models with activity level as a fixed effect and individual and day as random effects.

RESULTS

Body temperature

The T_b of white-browed sparrow-weavers was bimodally distributed (Fig. 1), reflecting a circadian cycle with T_b typically maintained between 40 and 41 °C by day and between 35 and 38 °C at night (Fig. 2). However, daily fluctuations in T_b were associated with maximum T_{air} and variation in *D* (see daily traces in Fig. 2, and Appendix B, Fig B1). Furthermore, birds at the desert site had a significantly higher T_{mod} (41.5 ± 0.2 °C, mean ± SD) than birds from the semi-desert site (40.1 ± 0.1°C and 40.2 ± 0.3°C, for the dry and wet season, respectively) ($F_{2,13} = 61.55$, $p < 0.001$; Fig. 1).

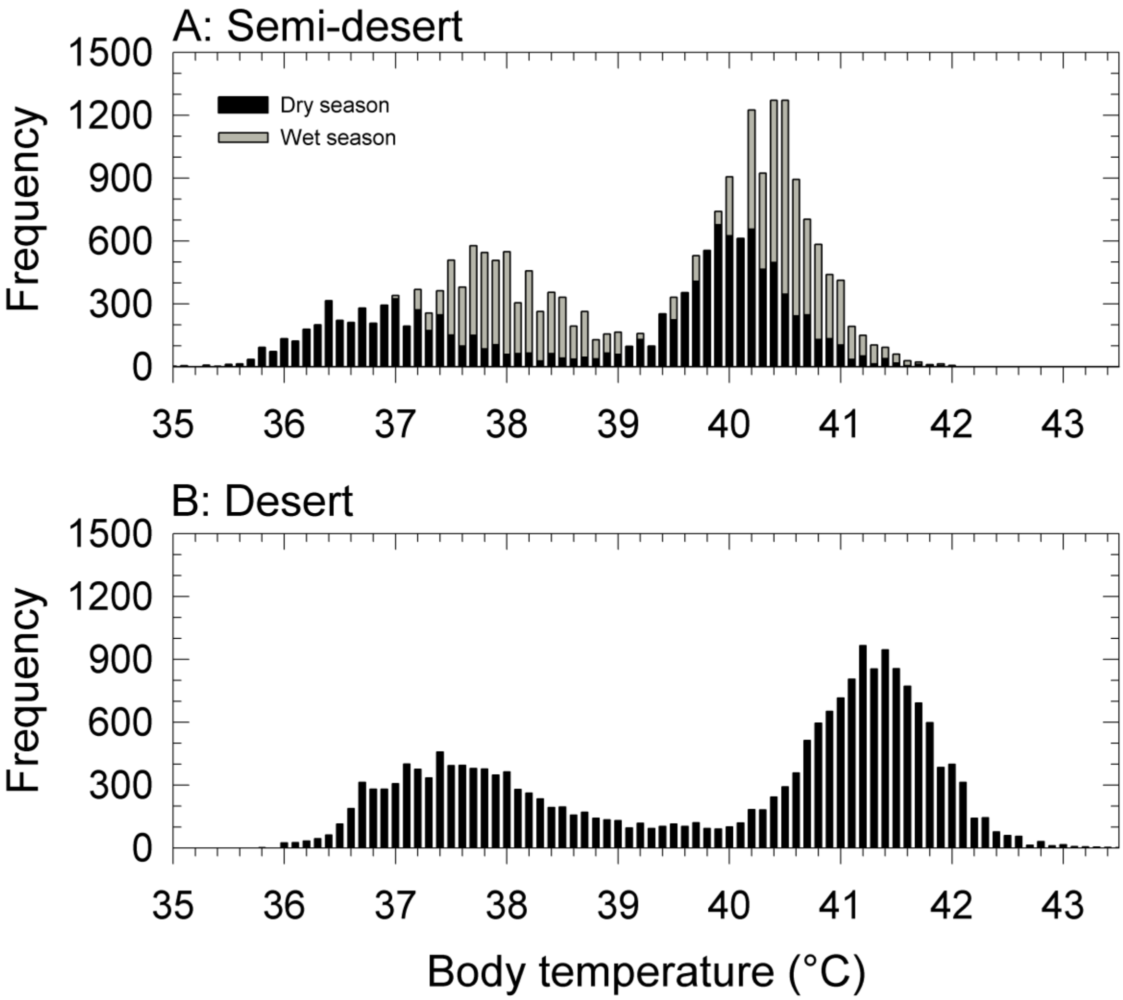

Figure 1: Distributions of summer body temperatures (Tb) in white-browed sparrow-weavers (Plocepasser mahali) at A) Tswalu Kalahari Reserve (semi-desert) during a dry season (black; n = 4), and wet season (dark grey; n = 5), and B) at Wildsgenot Game Range (desert, black: n = 7) during the dry season.

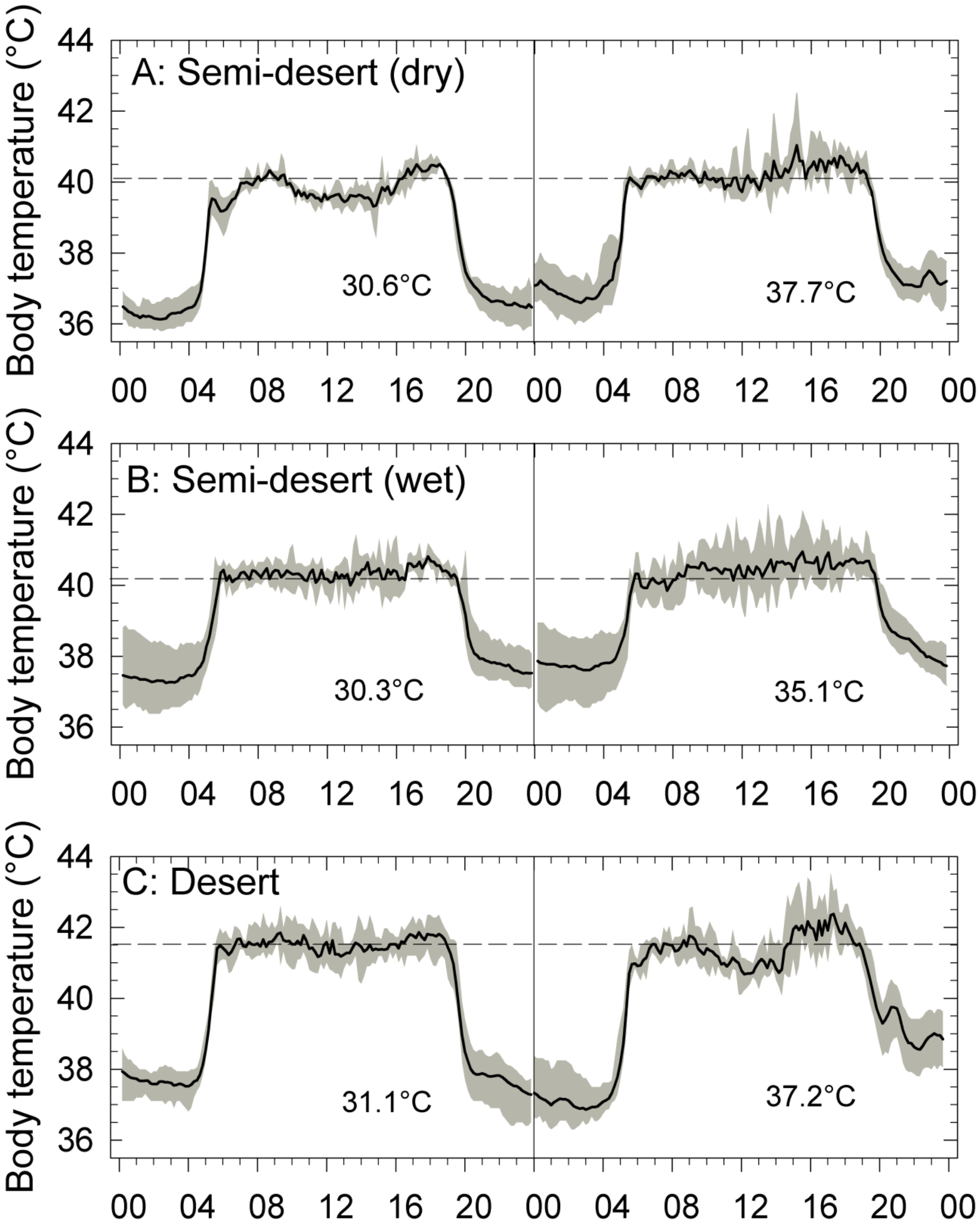

Figure 2: Traces of summer body temperature in white-browed sparrow-weavers (*Plocepasser mahali*) on two representative days (mild and hot) at (A) Tswalu Kalahari Reserve (semi-desert) during a dry season (n = 4, Dec 2010), and (B) wet season (n= 5), and (C) at Wildsgenot Game Range (desert) during the dry season (n = 7). Mean T_b is indicated by the black line and the range in T_b (minimum and maximum) by the grey area. The maximum T_{air} values measured on the representative days are displayed inside each panel and the horizontal dashed line represents the mean modal T_b measured during the respective study period

Air temperature, *D*, time of day, and study period were important predictors of thermoregulatory patterns (Appendix C, Table C1). Mean and maximum T_b, when analyzed as absolute measurements or as deviations from T_{mod}, i.e. T_b-T_{mod}, were linked positively to T_{air} (mean: $\chi^2_{1,819} = 95.13$, $p < 0.001$, maximum: $\chi^2_{1,819} = 173.7$, $p < 0.001$) and negatively to *D* (mean: $\chi^2_{1,819} = 42.59$, $p < 0.001$, maximum: $\chi^2_{1,819} = 56.14$, $p < 0.001$), and the interaction between T_{air} and VPD was significant in all models (mean: $\chi^2_{1,819} = 33.97$, $p < 0.001$, maximum: $\chi^2_{1,819} = 34.51$, $p < 0.001$). During periods of high T_{air} (>36 °C), mean T_b was typically above T_{mod} (Fig. 2&3), whereas maximum T_b exceeded T_{mod} by up to 2.3 °C. Mean and maximum T_b were generally higher than T_{mod} at low *D;* for example, at mild T_{air} (28 - 32 °C) mean and maximum T_b were above T_{mod} at *D* below 3 kPa (Fig. 4). There was also a highly significant difference in both mean and maximum T_b as a function of time of day (mean: $\chi^2_{2,819} = 598.7$, $p < 0.001$, maximum: $\chi^2_{2,819} = 254.0$, $p < 0.001$). Mean T_b was significantly higher during mid- and late-afternoon than during early-afternoon (Tukey HSD, $p < 0.001$), and the interaction between time of day, T_{air} and *D* was significant (mean: $\chi^2_{2,819} = 123.1$, $p < 0.001$, maximum: $\chi^2_{1,819} = 74.09$, $p < 0.001$).

Absolute mean and maximum T_b during the warmest part of the day varied significantly between study periods (mean: $\chi^2_{2,13} = 57.08$, $p < 0.001$, maximum: $\chi^2_{1,819} = 54.76$, $p < 0.001$), and were significantly higher at the desert site compared to the semi-desert site (both in the dry and wet seasons; Tukey HSD, $p < 0.001$; Fig. 3 A,C). In contrast, mean and maximum daily T_b-T_{mod} was significantly higher in birds at the semi-desert site than in birds at the desert site (Fig. 3 B,D; Tukey HSD, $p < 0.001$). In the above models the interaction between study period, T_{air} and *D* was significant (mean: $\chi^2_{2,819} = 6.537$, $p = 0.038$, maximum: $\chi^2_{1,819} = 56.14$, $p = 0.008$).

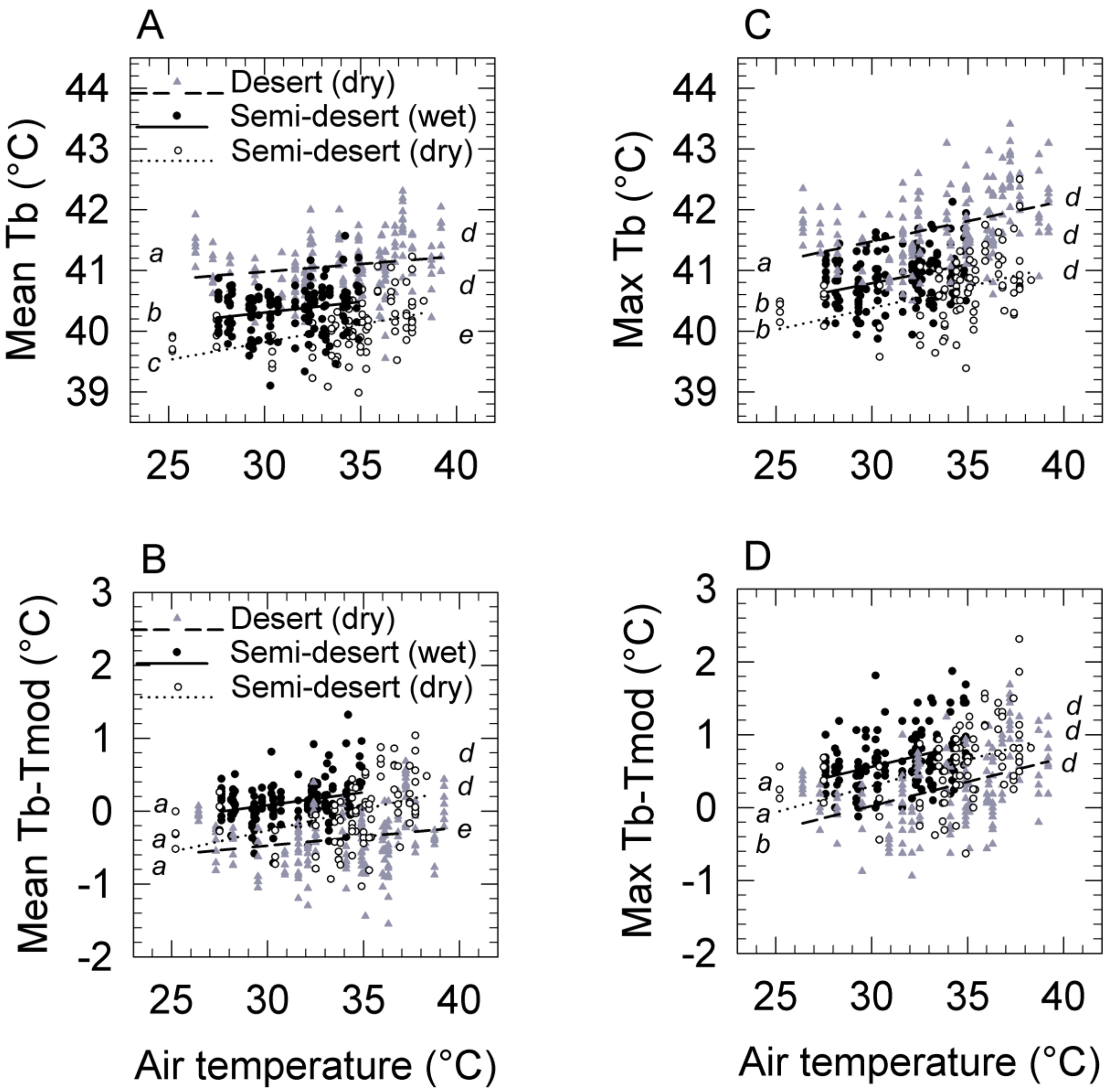

Figure 3: Body temperature (T_b) as a function of air temperature (T_{air}) in white-browed sparrow-weavers (*Plocepasser mahali*) measured between 14:00 and 16:00 hours at Tswalu Kalahari Reserve (semi-desert) and Wildsgenot Game Ranch (desert). Body temperatures are displayed as A) absolute mean T_b; B) mean T_b relative to modal T_b ($T_b - T_{mod}$); C) absolute maximum T_b; and D) maximum $T_b - T_{mod}$. Trendlines indicate a significant relationship ($p < 0.05$), and symbols to left and right of each trendline indicate significant differences ($p < 0.05$) between intercepts and slopes, respectively.

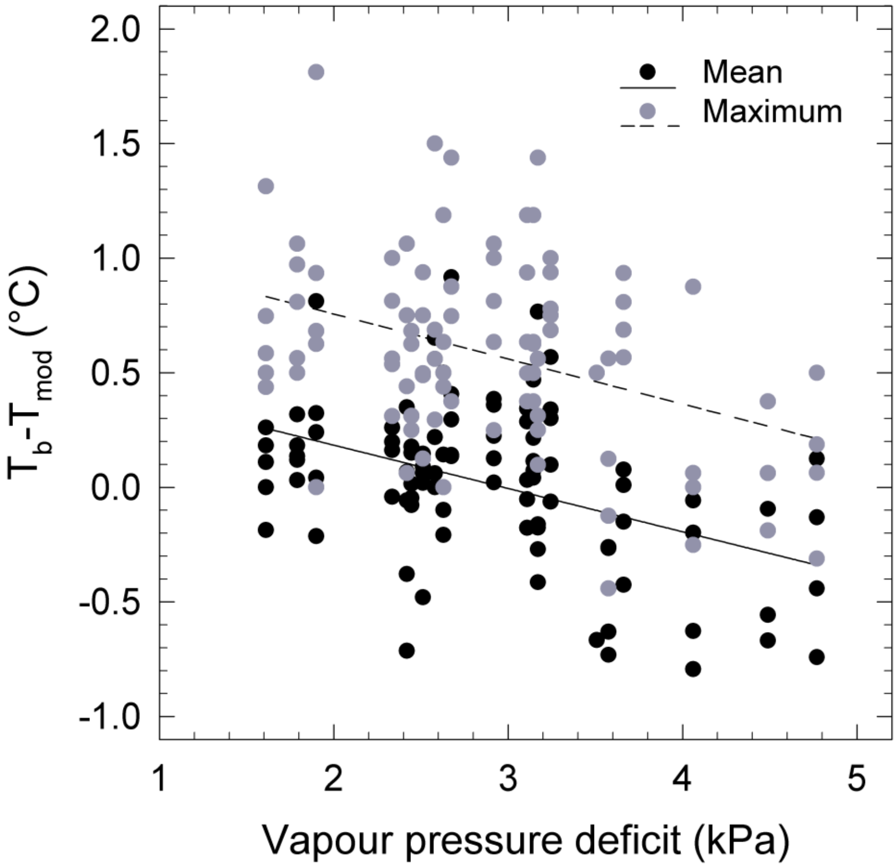

Figure 4: Mean and maximum body temperature (T_b) relative to modal T_b (T_b – T_{mod}) in white-browed sparrow-weavers (*Plocepasser mahali*) at Tswalu Kalahari Reserve (semi-desert dry and wet season data pooled) as a function of vapor pressure deficit (*D*) measured between 14:00 and 16:00 hours, including only days when maximum T_{air} was between 28 and 32 °C. On these days T_b was not related to T_{air} ($p = 0.185$), but showed a significant negative relationship with *D* ($p < 0.001$). In the above model variation in *D* was most strongly driven by day-to-day variation in dew-point temperatures, ranging from 1.4 to 19.5 °C.

The overall mean daily HI value for all birds was 2.1 ± 0.5 °C (mean ± SD) and there was no effect of sex or body mass on HI. However, daily HI was significantly and inversely related to mean daily T_{air} ($\chi^2_{1,394} = 316.8$, $p < 0.001$). There was also a significant effect of study period ($\chi^2_{2,13} = 55.53$, $p < 0.001$; Fig. 5), and a significant interaction between mean T_{air} and study period ($\chi^2_{2,394} = 57.79$, $p < 0.001$). The magnitude of heterothermy was greater in the desert birds (HI = 2.4 ± 0.3 °C), than the semi-desert population in both dry and wet seasons (Tukey HSD, $p < 0.05$ and $p < 0.001$, respectively). The semi-desert population expressed a greater magnitude of heterothermy during the dry season (HI = 2.1 ± 0.3 °C) than during the wet season (HI = 1.6 ± 0.2 °C; Tukey HSD, $p < 0.001$). Whereas there was no significant difference in the slope of HI as a function of mean T_{air} between the dry and wet season the semi-desert site ($p = 0.832$), the slope was significantly higher at the desert site ($p < 0.001$).

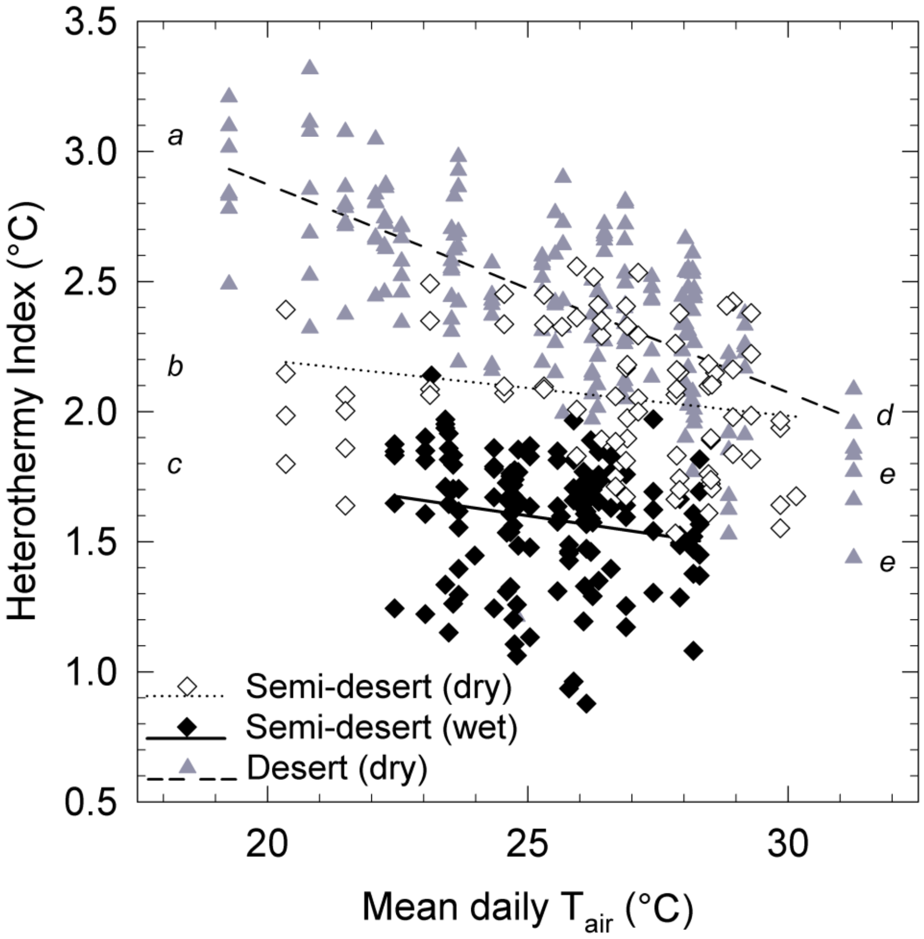

Figure 5: Daily Heterothermy Index (°C) during summer as a function of mean daily air temperature (T_{air} °C) in white-browed sparrow-weavers (*Plocepasser mahali*) at Tswalu Kalahari Reserve (semi-desert), during a dry (n = 4) and wet (n = 5) season, and Wildsgenot Game Ranch (desert) during a dry season (n = 7). Trendlines indicate a significant relationship ($p < 0.05$), and symbols to left and right of each trendline indicate significant differences ($p < 0.05$) between intercepts and slopes, respectively.

Behavior

The number of focal observations during the study was low, especially at the desert site, and therefore study period and *D* could not be included as predictors; the most important factors used in the final model for the behavioral responses are listed in Appendix C, Table C. The average proportion of time spent active during the warmest time of day (12:00 to 18:00 hours) was 40 ± 20 %: more than 95 % of all active behavior involved foraging on the ground for insects and seeds. Time spent foraging was negatively related to T_{air} ($\chi^2_{1,110} = 21.816$, $p < 0.001$), time of day ($\chi^2_{2,110} = 63.238$, $p < 0.001$) and the interaction between time of day and T_{air} ($\chi^2_{2,110} = 14.304$, $p < 0.001$). The birds therefore showed a significant increase in time spent resting as T_{air} increased ($\chi^2_{1,100} = 9.7527$, $p < 0.01$), again depending on time of day ($\chi^2_{2,110} = 29.582$, $p < 0.001$) and the interaction between time of day and T_{air} ($\chi^2_{2,110} = 6.1325$, $p < 0.05$). These behaviors were significantly related to T_{air} during early-afternoon only (Appendix B, Fig. B2), when birds foraged less ($\chi^2_{1,33} = 24.406$, $p < 0.001$) and spent more time inactive ($\chi^2_{1,29} = 8.245$, $p < 0.01$) as a function of T_{air}.

When birds were foraging at high T_{air}, they reduced the time they spent in full sun ($\chi^2_{1,109} = 26.612$, $p<0.001$), depending on time of day and the interaction between time of day and T_{air}. The birds spent significantly less time foraging in the sun at high T_{air} during early- ($\chi^2_{1,29} = 10.982$, $p < 0.001$) and mid-afternoon periods ($\chi^2_{1,47} = 7.1786$, $p < 0.01$): microsite use was unrelated to T_{air} during late-afternoon ($\chi^2_{1,33} = 0.0179$, $p = 0.8934$). As a corollary, birds spent significantly more time in shade vs. sun at high T_{air} during early- ($\chi^2_{1,29} = 12.856$, $p < 0.001$) and mid-afternoon ($\chi^2_{1,47} = 17.545$, $p < 0.001$), whereas microsite use was highly variable late-afternoon ($\chi^2_{1,33} = 0.6836$, $p = 0.4083$) (Appendix B, Fig. B2).

Activity level had a significant effect on both change in T_b during a 10-minute interval ($\chi^2_{2,70} = 19.71$, $p < 0.001$), and T_b at the end of the interval ($\chi^2_{2,70} = 8.823$, $p = 0.012$). When completely inactive, birds reduced T_b on average by 0.46°C (Tukey HSD, $p < 0.01$), whereas the direction of T_b change was generally positive when birds were active. Similarly, T_b was significantly higher (> 0.34 °C on average; Tukey HSD, $p < 0.05$) than T_{mod} when individuals were active. There was no difference in the direction or magnitude of T_b change between high and low activity levels (Tukey HSD, $p = 0.752$ and $p = 0.100$, respectively).

Heat dissipation

Panting behavior started when $T_{air} > 28$ °C (Figure 6A). Time spent panting was positively related to T_{air} ($\chi^2_{1,110} = 37.33$, $p < 0.001$), but was also influenced by time of day ($\chi^2_{2,110} = 19.92$, $p < 0.001$) and the interaction between time of day and T_{air} ($\chi^2_{1,110} = 8.63$, $p < 0.05$). We could not verify the effect of humidity on panting empirically because of a strong correlation between T_{air} and humidity, although most panting behavior below 35 °C was associated with low *D* (Figure 6A). Panting was significantly related to T_{air} during all time-intervals (Figure 6A) but showed the strongest relationship to T_{air} during mid-afternoon (14:00 – 16:00 hours, when daily maximum T_{air} peaked on most days). In a separate model we found that panting was not significantly related to activity levels, but the interaction between activity level, time of day, and T_{air} was significant ($\chi^2_{3,110} = 9.000$, $p < 0.05$), and the birds panted more when active at high T_{air}.

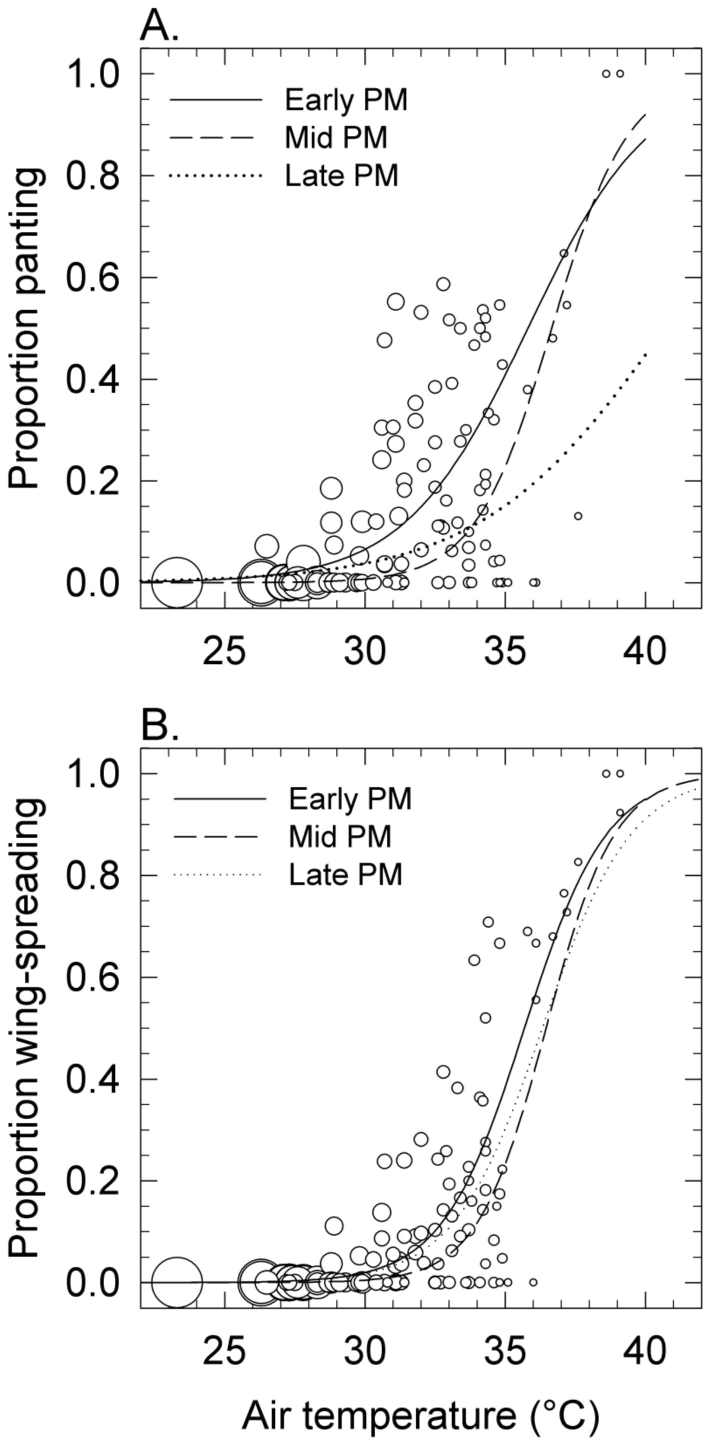

Figure 6: Proportion of time spent A) panting and B) wing-spreading by white-browed sparrow-weavers (*Plocepasser mahali*) as a function of air temperature (T_{air}). The logistic curves represent how heat-dissipation effects varied between early- (12:00 – 14:00 hours), mid- (14:00 – 16:00 hours) and late- (16:00 – 18:00 hours) afternoon (PM). The sizes of circles are indicative of levels of humidity (larger circles indicate lower water vapor pressure deficits).

Wing-spreading behavior was significantly related to T_{air} ($\chi^2_{1,110} = 56.27$, $p < 0.001$) and time of day ($\chi^2_{2,110} = 7.69$, $p = 0.021$), although the interaction between time of day and T_{air} was insignificant in explaining this behavior. Time spent wing-spreading increased at T_{air} above 30 °C (Figure 6B) and was higher during early-afternoon (Tukey HSD, $p < 0.05$), than during mid- and late-afternoon (Tukey HSD, $p<0.05$). In contrast to panting, wing-spreading behavior was unrelated to activity levels ($\chi^2_{1,110} = 0.7120$, $p = 0.3988$).

We linked each individual's T_b to its heat-dissipation behavior during the first five minutes after T_b was measured. This analysis showed that T_b (relative to T_{mod}) was a significant predictor of time spent panting and/or wing-spreading, with birds panting and/or wing-spreading more when $T_b > T_{mod}$ (panting: $\chi^2_{1,111} = 11.129$, $p < 0.001$; wing-spreading: $\chi^2_{1,111} = 12.042$, $p < 0.001$).

DISCUSSION

Our data provide evidence that T_b patterns in white-browed sparrow-weavers are significantly linked to T_{air} during both active and rest phases. When T_{air} approached T_b ($T_{air} > 37$ °C) during the day, T_b was up to 2.3 °C above T_{mod}, these patterns being further influenced by interactions involving humidity, time of day (probably resulting from daily rhythms in activity and thermoregulation) and activity levels. However, we did not find support for the prediction that desert birds were more likely than semi-desert birds to express hyperthermia, i.e., elevations in T_b relative to their T_{mod}. Overall, however, the desert birds had a higher T_{mod} (1.3 and 1.4 °C, for wet and dry seasons, respectively) compared to semi-desert birds, both during cool and warmer periods of the day, supporting the hypothesis that set-point T_b was higher for this population. Although T_b was generally higher in the desert population compared to the semi-desert population during warm periods of the day, T_b levels were more often at or below T_{mod} in the desert population. If we assume that instances when $T_b > T_{mod}$ are indicative of hyperthermia, this suggests that desert birds became hyperthermic less frequently than semi-desert birds. The higher set-point T_b likely reduced the occurrence of hyperthermia. Also consistent with our expectations, desert birds had a larger HI and therefore showed greater variation in daily T_b fluctuations as a function of mean daily T_{air} than semi-desert birds. Thus, within a population, T_b can vary significantly over short time periods as environmental conditions change. These results corroborate other findings that the environment plays an important role in T_b expression at an intraspecific level, both within and between populations (McKechnie et al. 2007, Glanville and Seebacher 2010, Smit et al. 2011, Glanville et al. 2012, Doucette et al. 2012).

These findings challenge the widespread idea that T_b in endotherms is a fixed, species-specific physiological trait (Scholander et al. 1950). For example, sparrow-weavers in this study often showed fluctuations in T_b larger than 3 °C during their active-phase (Fig. 2). The assumption of a constant normothermic T_b set-point is often implicit in models linking the energy and water balance of endotherms to environmental and climatic variables (Anderson and Jetz 2005). Moreover, many bioclimatic models predicting climate change impacts rely strongly on this assumption, usually implicitly (Chambers et al. 2005, Kearney and Porter 2009). A variable T_b could greatly reduce thermoregulatory costs in endotherms, and heterothermic responses should be incorporated in energy and water balance models. However, in order to do this, more empirical data on heterothermic responses are needed, not just at species level, but also at the population level if the species' range stretches across different climatic regions. There is thus a greater urgency to understand the ecological or evolutionary factors driving intra- and interspecific variation in endotherm thermoregulatory responses (Angilletta et al. 2010).

It has often been proposed that desert birds should have a higher T_b to facilitate passive heat loss and conserve water (Withers and Williams 1990, Tieleman and Williams 1999, Williams and Tieleman 2005). Tieleman and Williams (1999) tested this hypothesis by compiling data on 28 species and found that T_b did not differ significantly between desert and non-desert birds when T_{air} was between 25 °C and 45 °C. From this observation, based largely on laboratory studies, they concluded that facultative hyperthermia is probably not an adaptation limited to desert birds. Previously, most field T_b data were obtained from freshly killed birds (Wetmore 1921, Brain and Prozesky 1963), and provided no information on relationships with activity and environmental temperature. The present study is the first of which we are aware to investigate daily T_b in more than one population of free-ranging birds under hot environmental conditions. Our findings contrast with those of Tieleman and Williams (1999), revealing that free-ranging birds in a hot, desert site had a higher set-point T_b than conspecifics in a milder, semi-desert site. Body temperatures measured under laboratory conditions are mostly obtained from captive birds resting in a metabolic chamber under controlled ambient conditions, and arguably would not always be representative of T_b expressed under natural conditions in the same individuals.

The magnitude of the difference (up to 1.4 °C) in set-point diurnal T_b between birds at desert and semi-desert sites was surprising, given that the two populations are only 100 km apart. White-browed sparrow-weavers are highly philopatric and young birds typically delay dispersal for several years, and when adult birds do disperse for breeding purposes they generally relocate to neighboring territories (~200 m) (Lewis 1982). Variation in thermoregulatory patterns (irrespective of whether the driving force is genetic and/or phenotypic) in response to local climate is therefore more likely in this species than in more mobile or nomadic arid-zone species. Our data do not allow us to partition this variation between genetic adaptation and phenotypic plasticity, and common garden experiments are needed to address this question. However, we note that Ribeiro et al. (2011) recently demonstrated using genetic markers that selection for specific physiological traits could occur over small spatial scales (even without any habitat or geographical barriers) across a climatic gradient. Although mean T_{air} during the dry season at the desert and semi-desert sites were similar, in the long term the desert site experiences higher T_{air} extremes (frequently over 40 °C) and is much drier during summer. The desert population is therefore more likely to experience higher water demands for evaporative heat loss. By regulating a higher T_{mod} during the day, birds at the desert site could maintain a larger T_b-T_{air} gradient when $T_{air} < 40$ °C, reducing the demand for evaporative cooling because they can rely more on non-evaporative pathways to dissipate heat (Calder & King, 1974; Tieleman & Williams, 1999). Weathers (1981), for instance, estimated that a 2.3 °C increase in T_b in a 32-g bird (*Cardinalis sinuates*) result in 50 % savings in total evaporative water loss when $T_{air} = 38$ °C. If a higher T_{mod} (normothermic T_b) can contribute to similar water savings in white-browed sparrow-weavers, this would be highly adaptive during hot, dry periods in the Kalahari Desert.

Interestingly, the higher T_{mod} of birds at the desert site meant that this population experienced less hyperthermia (i.e. increases in T_b above T_{mod}). Presumably, having a higher T_{mod}, resulting in a larger T_b-T_{air} gradient, meant that increases in T_b above the set-point were less likely at the T_{air} range recorded in this study. Birds with a higher T_{mod} could potentially be active for longer at high T_{air} before T_b exceeds T_{mod}. This in turn would decrease the demand for panting, thereby decreasing costs of evaporative heat loss. At the desert site, panting was only observed at $T_{air} > 37$ °C, and these birds were also more active than birds at the semi-desert site at $T_{air} > 35$ °C. In a more detailed study on heat dissipation it was found that under similar weather conditions ($T_{air} = 39$ °C) white-browed sparrow-weavers panted 54 % of the time at the semi-desert site, compared to 15 % at the desert site in the Kalahari Desert (Chapter 4)

Thermogenesis during activity can contribute greatly to a bird's body temperature (Bartholomew and Dawson 1958, Dawson and Hudson 1970, Bartholomew 1972, Heinrich 1977, Wilson and Grémillet 1996). Many birds appear to have a high T_b (~ 43.9 ºC) when sustaining high activity levels (Prinzinger et al. 1991). Behavioral observations of white-browed sparrow-weavers implanted with data-loggers showed that activity levels could contribute to T_b changes, although resolution of our T_b measurements was too low to link the type and intensity of activity or immediate microsite selection directly to changes in T_b. During cooler weather T_b was generally below T_{mod} in both populations (Fig. 3) and birds could afford large increases in T_b before T_b exceeded T_{mod}. In addition, when resting follows periods of activity, any heat gained during activity will be readily dissipated through passive heat loss at cool T_{air}. During warmer weather, however, T_b was generally close to or higher than T_{mod}, and further elevations in T_b above T_{mod} could easily result in unregulated, or pathological hyperthermia as a result of further metabolic heat gain during periods of activity (Heinrich 1977). This interaction between external and internal heat loads increases demand for heat dissipation, and likely results in initiation of panting and/or wing-spreading behaviors at a lower T_{air} than if the bird was completely inactive. For instance, under low-humidity conditions in the laboratory, resting white-browed sparrow-weavers only start panting when $T_{air} \approx 40$ –

41 °C; M.C. Whitfield, B. Smit, A.E McKechnie, B.O. Wolf, unpublished data). The potential increase in heat load during periods of activity at high T_{air} is likely to influence a bird's behavioral decisions (Tieleman and Williams 2002). Our behavioral data show that both activity patterns and time spent in shade was dependent on T_{air} and that birds started restricting their foraging behavior to shaded microsites at high temperatures, especially during early afternoon when solar radiation levels are high (Appendix B, Fig. B2). In support of this, heat-dissipation behavior increased significantly when $T_{air} > 30$ °C (Fig. 6), suggesting that birds were experiencing increased heat loads. Panting is an indication of demand for evaporative cooling, but the function of wing-spreading is not well studied. Wing-spreading could facilitate either cutaneous evaporative cooling or dry heat loss though radiative and convective cooling. Further, the interaction effect of T_{air} and *D* suggests that on humid days birds may face a greater risk of uncontrolled hyperthermia at a relatively mild T_{air} when compared to dry days at equivalent temperatures (Powers 1992, Weathers 1997, Walters et al. 2004), and that at a given T_{air}, total EWL would be higher on humid days since the birds are panting more frequently and more intensely than on drier days (see large circles in Fig. 6).

Many authors consider variation in daily fluctuations in T_b that do not meet certain cut-off limits as typical circadian cycles of homeothermy, thereby overlooking the ecological and evolutionary significance of these fluctuations (Boyles et al. 2011b, 2011c). In a previous study Ferguson et al. (2002) argued that white-browed sparrow-weavers are ‘typical homeotherms’ based on the conclusion that these birds showed no evidence of torpor. However, our results show that variation in daily cycles in T_b is strongly influenced by T_{air} and further varies within and between populations. The magnitude of daily HI values in this study was driven by nocturnal reductions in T_b, since these values showed the greatest deviation from modal T_b. The desert population (experiencing the driest conditions) displayed the greatest levels of heterothermy, and birds from the semi-desert population displayed greater levels of heterothermy during the dry season than in the wet season (Fig. 5). These results provide support for predictions made by Angilletta et al. (2010) that heterothermy is related to an increased costs-to-benefit ratio of remaining homeothermic, because birds greater daily variation in thermoregulation patterns during dry periods when food and water availability were likely lower (Seely and Louw 1980). Daily heterothermy levels in the desert birds were also much more strongly related to daily T_{air} than were those of the semi-desert birds. Despite summer diurnal temperatures often exceeding 35 °C, nocturnal temperatures are frequently below 10 °C in the southern Kalahari Desert, especially during dry periods when re-radiation levels are high at night. By allowing T_b to decrease with T_{air}, desert birds would conserve energy on cool nights, which may offset diurnal reductions in foraging performance brought about by low food availability and/or high T_{air} (du Plessis et al. 2012). Daily heterothermy levels in semi-desert birds, on the other hand, showed a stronger relationship to T_{air} during the dry season than during the wet season. This suggests flexibility in thermoregulatory responses of the semi-desert population to environmental conditions. We argue that high primary productivity associated with unusually high rainfall at the semi-desert site after 1 January 2011 (244 mm of rain in less than three weeks) resulted in increased food availability, and probably allowed the birds at this site to regulate a more precise T_b (Angilletta et al. 2010).

Over the last 50 years there has been a sharp increase in temperature extremes around the globe (IPCC 2007). During this period, the Kalahari region in southern Africa, in particular around Twee Rivieren, Northern Cape (which is near our desert study site), has experienced some of the fastest rates of increase in maximum temperatures and the frequency of extreme heat in southern Africa (Kruger and Sekele 2012). We can therefore expect that birds resident in this area are becoming increasingly exposed to temperatures above normothermic T_b. During extreme high-temperature weather anomalies, avoidance of lethal T_b and dehydration become key to short-term survival (McKechnie and Wolf 2010, Boyles et al. 2011a, McKechnie et al. 2012). Because the majority of birds resident in this area do not appear to rely on drinking free surface water (see Chapter 3), at high environmental temperatures we would expect many of these species to make trade-offs between foraging and the need to maintain adequate hydration levels, risking a lethal T_b as a corollary. Tieleman and Williams (2002) showed that nutritional status could play a very important role in this trade off, and birds with low nutritional status will risk foraging at higher T_{air} than well-fed birds. Our field observations are limited to T_{air} below 40 °C, but show that even when $T_{air} < T_b$, T_{air} had a significant effect on thermoregulation, and in a number of cases during warm periods T_b exceeded 43 °C. We predict that at T_{air} above normal T_b, sparrow-weavers will be able to continue foraging by allowing their T_b to increase up to 45 °C, as has been observed in hoopoe-larks (*Alaemon alaudipes*) in the Arabian Desert (B.I. Tieleman and J. B. Williams, personal communications). However, more detailed field studies on how foraging behavior and thermoregulation interact at very high T_{air} are needed to better understand and predict the vulnerability of desert birds to extreme heat events.

CONCLUSION

A key finding of our study was relatively large variation in T_b both within and between conspecific populations. These data suggest that an arid-zone passerine responds differently to prevailing weather conditions in two locations over its range, and that they also respond to seasonal changes in weather conditions. Taken together with the data of Glanville et al. (2012), this suggests that the thermal physiology of endotherms is far more flexible than previously thought, and could potentially contribute to the adaptation of populations under changing climatic conditions (Boyles et al. 2011a). In the past, predictions of species’ vulnerabilities to climate change have relied heavily on the use of bioclimatic envelopes (Pearson and Dawson 2003). These predictions are based entirely on correlations between a species’ current distribution and the prevailing climate experienced within its range. They implicitly assume that physiological responses are species-specific, thereby limiting a species’ current distribution to its physiological tolerances. However, our findings and those of Glanville et al. (2012) suggest that a species' current range may not be an accurate representation of its climatic tolerance. Finally, our data also reiterate that when predicting species’ responses to climate change, their sensitivity (sensu Williams et al. 2008) should be resolved at the population rather than species level (Glanville et al. 2012).

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CHAPTER 2

THE EFFECTS OF TEMPERATURE ON WATER AND ENERGY FLUXES DURING SUMMER IN AN ARID-ZONE PASSERINE BIRD

Abstract

In unproductive arid environments, endotherms are likely to experience mismatches between the demand and supply of water during hot weather. Predicting water demands at air temperatures below body temperature (T_b) in free-living birds is complicated by the fact that many birds may express signs of heat stress but continue to actively forage instead of retreating to shade and ceasing activity. I tested whether daily water flux in free-living birds is driven most strongly by 1) the demands for evaporative cooling—i.e. an increase in water flux on hot days, or 2) by activity related water flux—i.e. a decrease in water flux on hot days. I obtained measurements of daily water flux (DWF, n = 71) and daily energy expenditure (DEE, n = 49) in White-browed Sparrow-Weavers (*Plocepasser mahali*) in a comparatively hot desert site, and in a milder semi-desert site, during summer in the Kalahari Desert of southern Africa. At the semi-desert site sparrow-weavers showed negative relationships between both DWF ($p < 0.001$) and DEE ($p < 0.001$) and maximum daily air temperature (T_{air}). In contrast, conspecifics at the desert site showed no relationship ($p = 0.133$) between DWF and maximum daily T_{air}, and only a weak negative relationship between DEE and increasing maximum daily T_{air} ($p = 0.050$). On warm days (maximum $T_{air} > 37$ °C) DWF was typically equivalent to 20 – 30% of body mass. These data do not provide support for the prediction that water flux is driven primarily by the demands for evaporative water loss in a non-drinking arid zone passerine. My findings instead suggest that activity-related water intake, which could be related to a decrease in foraging success on hot days, is the major determinant of DWF. My data predict that on days when maximum T_{air} exceeds T_b (~ 42 °C), most of a White-browed Sparrow-Weavers' daily water budget will be allocated towards evaporative water loss. On hot days, non-drinking birds may not be

able to increase water intake through foraging alone, and will thus experience strong trade-offs between thermoregulation, hydration state and activity levels as temperatures increase.

INTRODUCTION

Mismatches between the demand and supply of critical resources, such as water and energy, could have deleterious effects on survival and fitness. For endotherms living in unproductive, arid terrestrial environments, the trade-offs between resource acquisition and expenditure may be extreme (Tieleman and Williams 2000, Tieleman et al. 2003). Resource bottlenecks can be strongly driven by temperature, with cold and hot extremes typically affecting energy and water budgets respectively (Carmi-Winkler et al. 1987, Wolf 2000, Ehrhardt et al. 2005, Kam et al. 2012). Information on how endotherms acquire and allocate these resources is thus vital for understanding how they inhabit diverse environments.

Diurnal birds inhabiting subtropical deserts often need to forage under very hot conditions, potentially trading off dietary water intake against elevated thermoregulatory water requirements (Tieleman et al. 2003, du Plessis et al. 2012). The demands for evaporative cooling constitute the greatest thermoregulatory cost during hot weather, and resting rates of evaporative water loss (EWL) in small birds can exceed 5% of body mass per hour during periods of high T_{air} and intense solar radiation (Wolf and Walsberg 1996). Under these conditions, total water losses may exceed dehydration tolerance limits within just a few hours (Wolf 2000, McKechnie and Wolf 2010). Bartholomew and Cade (1956) showed that under conditions of moderate heat stress (~ 39 °C), House Finches (*Carpodacus mexicanus*) typically drink volumes of water equivalent to 40% (but sometimes exceeding 100%) of their body mass daily. To obtain a similar daily water intake, species that rely on preformed or metabolic water will likely incur greater energetic and evaporative cooling costs associated with foraging activity, and consequently reduced body condition during hot weather (Bartholomew and Cade 1956, Walsberg 1993, Wolf 2000, du Plessis et al. 2012).

Current climate change models predict that subtropical desert regions will experience increased warming rates, and heat waves will become more frequent and more intense (IPCC 2007). These conditions will greatly increase the water demands of desert birds, and it is expected that they will become more vulnerable to dehydration and heat stress (McKechnie and Wolf 2010). Under chronic heat stress and dehydration, populations may experience reduced body condition (which could reduce reproductive performance), and during extreme heat events large population-scale die-offs may occur (McKechnie et al. 2012). Understanding how water demands vary with temperature in free-living birds is thus vital for predicting their vulnerability to hotter future conditions and resilience to climate change (Wolf 2000).

Under laboratory conditions, EWL increases with T_{air} above the thermoneutral zone (TNZ), with the rate of increase scaling negatively with body mass (Dawson 1954, Weathers 1981, Tieleman et al. 2002). In contrast, very little is known about how daily water expenditure varies with increasing T_{air} in free-ranging birds inhabiting hot, arid habitats. Webster and Weathers (2000) showed that daily water flux (DWF) in a 6-g desert passerine, the Verdin (*Auriparis flaviceps*), was positively, albeit weakly, related to mean daily operative temperatures. However, in the latter study DWF data were pooled across summer and winter (cooler temperatures represented winter measurements, whereas warmer temperatures represented summer measurements), and seasonal changes in diet, maintenance metabolic requirements and activity levels could confound the apparent temperature dependence of water demands.

When T_{air} exceeds $T_{b,}$ water demands are relatively straightforward to predict, since under these conditions birds are generally inactive in shaded microsites and resting EWL will comprise a major component of DWF. Measurements of EWL in birds resting in metabolic chambers may therefore provide a reasonable approximation of EWL in free-ranging individuals. However, predicting water demands at warm temperatures (30–40 ºC) below avian T_b is more complicated, since birds may express signs of heat stress such as panting and wing-spreading, but nevertheless continue to actively forage instead of retreating to shade and ceasing activity (Tieleman and Williams 2002, Tieleman et al. 2003, du Plessis et al. 2012). Under these conditions birds can still experience periods where environmental temparture exceeds T_b, for example when foraging in full sun (Wolf and Walsberg 1996). Therfore, within this temperature range birds may be expected to experience the strongest trade-offs between foraging and thermoregulation, arising from decreases in foraging efficiency as T_{air} approaches T_b (du Plessis et al. 2012). The latter authors showed that foraging efficiency (but not foraging effort) in Southern Pied Babblers (*Turdoides bicolor*) was significantly decreased when the need for behavioural augmentation of heat dissipation increased above T_{air} = 30 °C (du Plessis et al. 2012). When maximum daily T_{air} exceeded 36 °C, the babblers did not take in enough food to compensate for overnight mass loss, suggesting that $T_{air} \approx 36$ °C constitutes an important abiotic "tipping point" with major implications for body condition, reproduction success and survival over time scales of days to weeks (du Plessis et al. 2012).

There are thus two opposing predictions that can be made concerning the relationship between DWF (which is centred on daily maintaining water balance, assuming constant total body water) and temperature when maximum T_{air} is in the 30–40 °C range (Fig. 1).

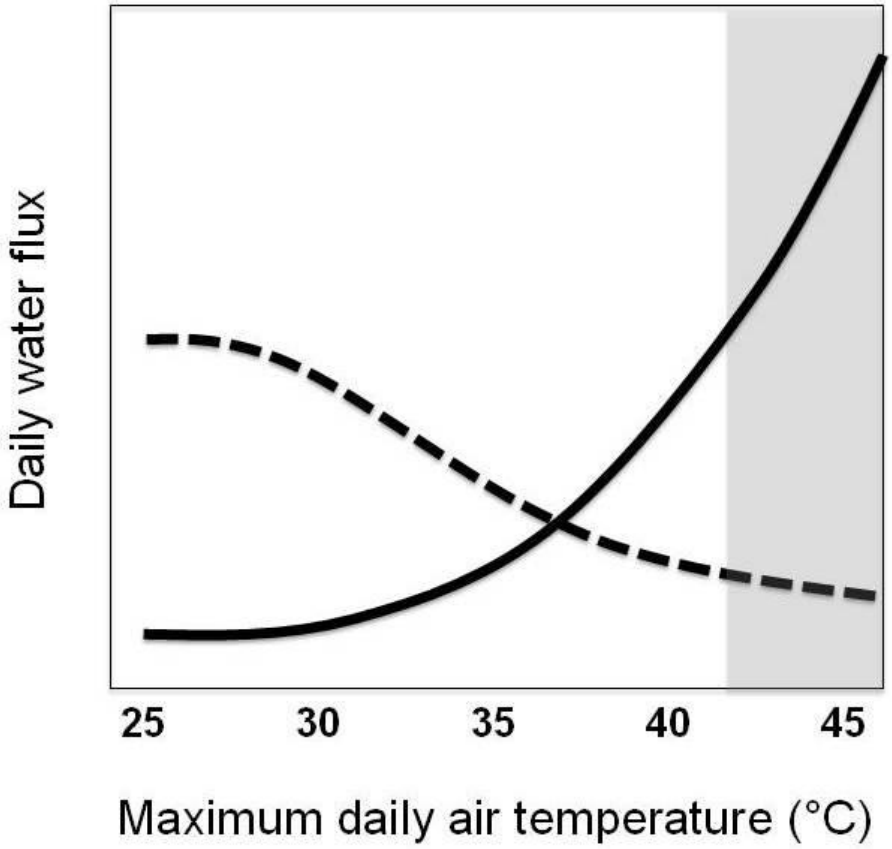

Figure 1: As daily maximum air temperatures approach avian body temperature (grey-shaded area), total daily water flux may be driven primarily by 1) the demands of thermoregulatory evaporative water loss (EWL) which increases with temperature (solid line represents resting EWL requirements), or alternatively 2) by activity-related water intake (dashed line), and as activity and food intake is reduced at higher temperature, so is total water flux. The grey-shaded area represents conditions when T_{air} exceeds avian T_b.

First, thermoregulatory EWL may predominate daily water demands, since many species initiate panting behaviour at $T_{air} > 30$ °C (see Chapter 4); in this scenario I expect an increase in DWF with increasing T_{air}, especially when birds can increase their water intake by drinking. On the other hand, if DWF at these temperatures is dominated by activity-related variables, such as foraging effort and success, I predict a negative relationship as activity and subsequently water intake are reduced on hotter days. The latter relationship would be most likely in non-drinking species which do not have access to free standing water, but obtain their water through food items that must be actively searched for. I tested these alternate predictions in two resident populations of an arid-zone passerine in the Kalahari Desert—one population in a comparatively hot arid site and a second in a milder semi-arid site. In light of the pattern elucidated by Tieleman and Williams (2000), namely that water flux is generally lower in birds inhabiting more xeric habitats, I also expected that the population from the arid site should show lower DWF and daily energy expenditure (DEE) than the population from the semi-arid site.

METHODS AND MATERIALS

Study sites

I investigated the effect of T_{air} on daily water flux (DWF, also referred to as water turn-over or water intake rate) and daily energy expenditure (DEE, also referred to as field metabolic rate) in White-browed Sparrow-Weavers (*Plocepasser mahali*), at two sites 100 km apart in the southern Kalahari Desert over two consecutive summer seasons. During the first summer I collected data from birds at a semi-desert site, Tswalu Kalahari Reserve (TKR, ~1100 m a.s.l. S27°19', E22°25'), from 11 December 2010 to 15 March 2011. During the following summer I obtained additional data during a dry period from a more arid site, Wildsgenot Game Ranch (WGR, ~ 890m a.s.l altitude S 27°04' E21°23'; ~ 100 km due west of TKR) from 21 November to 18 December 2011. The vegetation at both sites is arid savanna on deep, red sand forming parallel fossil dunes dominated by grassland and scattered small shrubs and trees, predominantly camel thorn (*Acacia erioloba*), black thorn (*A. melifera*) and shepherd's tree (*Boscia albitrunca*). Mean annual rainfall is higher at TKR than WGR, mainly because TKR lies closer to the western boundaries of the inter-tropical temperate troughs that bring summer rain to South Africa (Reason, Landman, & Tennant, 2006; Usman & Reason, 2004). Mean ± SD annual rainfall at TKR was 295 ± 172 mm (coefficient of variation, CV = 58.3%) over a 30-year period (unpublished data, Tswalu Kalahari Reserve). Mean ± SD annual rainfall at WGR was 190 ± 125 mm (CV = 66%) over a 60-year period (GHD Scholtz, unpublished data). Hereafter I refer to TKR and WGR as the semi-desert and desert sites, respectively. The climate at the desert site is more extreme (both hotter by day and colder at night) and less humid than at the semi-desert site.

Weather data were obtained at both sites using a portable weather station (Vantage Pro2, Davis Instruments, Hayward, CA), set 2 m above ground at a central location at each study site. This weather station has an aspirator fan to ensure air movement over the temperature and humidity sensors. I checked the factory calibration of the weather station against a mercury thermometer for T_{air} and a regularly calibrated CO_2/H_2O gas analyzer (LI-840A, LI-COR Inc., Lincoln, Nebraska) for humidity. Warm and arid conditions prevailed at the semi-desert site during December 2010, but after 1 January 2011 rainfall events were frequent and primary productivity increased dramatically. Rainfall during the study at the desert site was overall lower, and night-time temperatures were colder and daily maxima were slightly higher. The data collection period at the semi-desert site therefore stretched from the end of the annual dry cycle to the peak wet season. Most of the data at the semi-desert site (85 %) were collected during the peak wet season. The data collection period at the desert site took place before the end of the annual dry cycle. Both sites did not receive any significant rainfall for at least seven months prior to the sampling periods, and the few months before rains are generally considered the harshest, since primary productivity and insect activity is lowest (Seely and Louw 1980).

Study species

White-browed Sparrow-Weavers (35–50 g) breed co-operatively, living in family groups of 2–10 individuals, where only the dominant pair breeds (du Plessis 2005). White-browed Sparrow-Weavers occur in the arid savanna regions of southern and eastern Africa (du Plessis 2005). These birds are omnivorous and feed on insects (80 % of diet), seeds and fruit (du Plessis 2005). They are not dependent on drinking water and family groups often occur far away from free-standing water. At my study sites, only individuals with home-ranges surrounding a free-standing water source seem to drink (see Chapter 3).

Water flux and energy expenditure measurements

I trapped birds at night (21h00–23h00) in their respective roost chambers and obtained a blood sample (50–100µL) from the brachial vein of each individual to establish baseline ratios of stable hydrogen and oxygen isotopes in the body water. Each individual then received an intramuscular injection of doubly labelled water (DLW), consisting of approximately one part 99.9 atom% deuterium oxide and five parts 97.0 atom% ^{18}O (Sigma-Aldrich, Kempton Park, South Africa). However, some birds were injected with only 99.9 atom% deuterium oxide, which enriched the body water δ^2H but not δ^{18}O. The birds were injected at a dosage of 65 µg per 100g body mass for DLW, or 10µg per 100g body mass for deuterium oxide, estimated to enrich body water δ^2H by approximately 1000 ‰ VSMOW and δ^{18}O by approximately 400 ‰ VSMOW. Doubly labelled water was used to determine both DWF and DEE, although during the 2010/2011 study at the semi-desert site only about a third of the birds were injected with DLW, and the majority were injected with 99% deuterium to estimate only DWF. Approximately one hour (equilibration time = 1hr ± 7 min) after injection, a second blood sample (50–100µl) was taken from the brachial vein to estimate initial isotope enrichments. Whenever the roosting chambers were within reach I placed the birds back in their roosting chambers. However, at the desert site roosting chambers were too high above the ground to safely place birds back in chambers and most of these birds were kept for the remainder of the night (from approximately 24h00–5h00) in cloth bags suspended under a sheltered veranda, and released at dawn at the roost tree. Given the short time the birds spent in holding bags (during which they were calm) this procedure is unlikely to have affected total daily water demands. Ferguson et al. (2002) demonstrated that the insulatory properties of White-browed Sparrow-Weaver roost nests could confer energy savings on cold nights (generally below 10 °C). However this was unlikely to be an over-riding affect on daily energy expenditure since night-time T_{air} during my study period was seldom below 10 °C.

The initial enrichment levels were used to estimate total body water (TBW) (Speakman 1997). Each individual was re-trapped approximately 24 hrs (mean 23 hrs 50 min, range 22 hr 41 min to 24 hr 58 min) later, weighed and a final blood sample was collected. One of the main assumptions of the DLW method is that birds maintain water and energy balance and body condition during the release period (Speakman

1997). Birds in my study on average lost 3 % of their body mass during the 24-hr period between blood samples, and % mass loss was random, showing no relationship with daily temperature or variation between sites. Birds often defecated after being trapped or weighed and faeces could be as much of 5 % of a bird's body mass (personnel observation). I obtained TBW estimates from 85 individuals (34 and 51 from the semi-desert and desert sites, respectively), DWF estimates from 71 individuals (31 and 40), and DEE estimates from 49 individuals (9 and 40).

Immediately following collection, I transferred each blood sample to a 150µl micropipette and flame sealed both ends of the pipette (Speakman 1997). The blood was stored between 2 and 5 °C until further analysis. I separated pure water from blood samples by cryogenic vacuum distillation, and measured the δD and $\delta^{18}O$ of the water samples using a PAL autosampler and DLT-100 liquid water isotope analyser (Los Gatos Research, Mountain View, CA, USA). Samples were bracketed with standards spanning the ranges of -79.00 to 1950.69 ‰ VSMOW (δD) and -11.54 to 466.72 ‰ VSMOW ($\delta^{18}O$). A minimum of 10 1-µL replicates were analyzed per sample or standard, with values for the first five replicates typically being discarded in order to avoid isotopic memory effects.

The respective washout rates for labelled hydrogen and oxygen were then used to estimate water turnover and CO_2 production (Lifson and McClintock 1966, Nagy 1980), using equation 7.15 for the two-sample technique in Speakman (1997). Rates of CO_2 production were converted to energy expenditure using the assumed diet of White-browed Sparrow-Weavers (following Gessaman and Nagy 1988, Weathers and Sullivan 1989, Tieleman et al. 2003). I assumed that seeds contain 13.5 % protein, 5.1 % lipid and 81.4 % carbohydrate (Macmillen 1990) and that insects contain 62.0 % protein, 14.9 % lipid and 15.0 % carbohydrate (Williams and Prints 1986). I assumed sparrow-weavers consumed a diet of 80 % insects and 20 % seeds (du Plessis 2005), and calculated a conversion factor of 24.59 kJ L^{-1} CO_2 based on the conversion factors of protein, fat and carbohydrate metabolism (Gessaman and Nagy 1988).

Data analyses

All statistical analyses were conducted in R (R Development Core Team 2011). I performed a general linear model in R to test for the effect of temperature, site, sex and body mass on DWF and DEE. Mean day-time T_{air} (7h00 to 19h00, corresponding to the bird's active phase) was on average 4.1 ± 0.7 °C lower than daily maximum T_{air}, and these measures were highly positively correlated ($r^2 = 0.96$). I therefore used daily maximum T_{air} to test the effect of temperature on daily DWF and DEE. I initially entered all factors and their interactions into the model and subsequently removed non-important factors in a stepwise manner to obtain the lowest Akaike Information Criterion score adjusted for small sizes (AIC_c) (Burnham and Anderson 2002).

RESULTS

I obtained DWF measurements for days varying in maximum T_{air} from 27.5 °C to 37.4 °C at the semi-desert site, and 27.6 °C to 39.2 °C at the desert site. I obtained DEE data on days varying from 27.5 °C to 34.9 °C at the semi-desert site, and 27.6 °C to 39.2 °C at the desert site. Body mass was significantly different between sites ($F_{1,94} = 6.240$, $p < 0.050$) and sexes ($F_{1,94} = 8.900$, $p < 0.010$); the interaction between site and sex was not significant and was subsequently removed from the model. Body mass was significantly higher in males than in females, and significantly higher in the semi-desert birds (males = 44.0 ± 2.6 g; females = 42.9 ± 3.2 g) than in the desert birds (males = 43.1 ± 2.7 g; females = 40.8 ± 2.8 g). Total body water was significantly higher for the semi-desert population ($F_{1,77} = 13.39$, $p < 0.001$); TBW was 71.9 ± 3.6 % in the semi-desert population and 68.7 ± 3.30 % in the desert population.

Mean DWF was 48.2 % higher in the semi-desert population (whole animal = 17.5 ± 3.4 mL day^{-1}; and mass-specific = 0.41 ± 0.08 mL g^{-1} day^{-1}), compared to the desert population (whole animal = 11.8 ± 2.8 mL day^{-1}; mass-specific = 0.28 ± 0.06 mL g^{-1} day^{-1}). Daily water flux differed significantly between sites ($F_{1,59} = 63.41$, $p < 0.001$), and was significantly negatively related to maximum T_{air}. However, interactions between site and maximum daily temperature, and site and body mass were significant. Whereas DWF decreased significantly with increasing maximum daily temperature in the semi-desert population ($R^2 = 0.521$, $F_{1,26} = 30.36$, $p < 0.001$), it showed no relationship with maximum daily temperature in the desert population ($F_{1,34} = 2.364$, $p = 0.133$) (Fig. 2A). Daily water flux did not vary with body mass in the semi-desert population ($F_{1,26} = 0.125$, $p = 0.727$), but showed a weak positive relationship with body mass in the desert population; although the latter was not significant ($F_{1,35} = 3.083$, $p = 0.083$) (Fig. 2B).

Daily energy expenditure was 39 % higher in the semi-desert population (whole animal = 101.7 ± 17.1 kJ day^{-1}; and mass-specific = 2.3 ± 0.3 kJ g^{-1} day^{-1}) compared to the desert population (whole animal = 73.1 ± 9.0 kJ day^{-1}; and mass-specific = 1.7 ± 0.2 kJ g^{-1} day^{-1}). The difference in daily energy expenditure between sites was significant ($F_{1,41} = 72.37$, $p < 0.001$), and also showed a significant negative relationship with maximum air temperature ($F_{1,41} = 11.20$, $p < 0.010$) and positive relationship with body mass ($F_{1,41} = 14.02$, $p < 0.001$) (Fig. 3). The interaction between site and maximum daily air temperature was significant ($F_{1,41} = 18.26$, $p < 0.001$), and the relationship between DEE and maximum daily air temperature was much stronger in the semi-desert population ($R^2 = 0.811$, $F_{1,7} = 35.27$, $p < 0.001$) than in the desert population ($R^2 = 0.343$, $F_{1,34} = 4.146$, $p = 0.05$)—decreasing at 6.5 kJ day^{-1} C^{-1} versus 0.7 kJ day^{-1} C^{-1} (Fig. 3A).

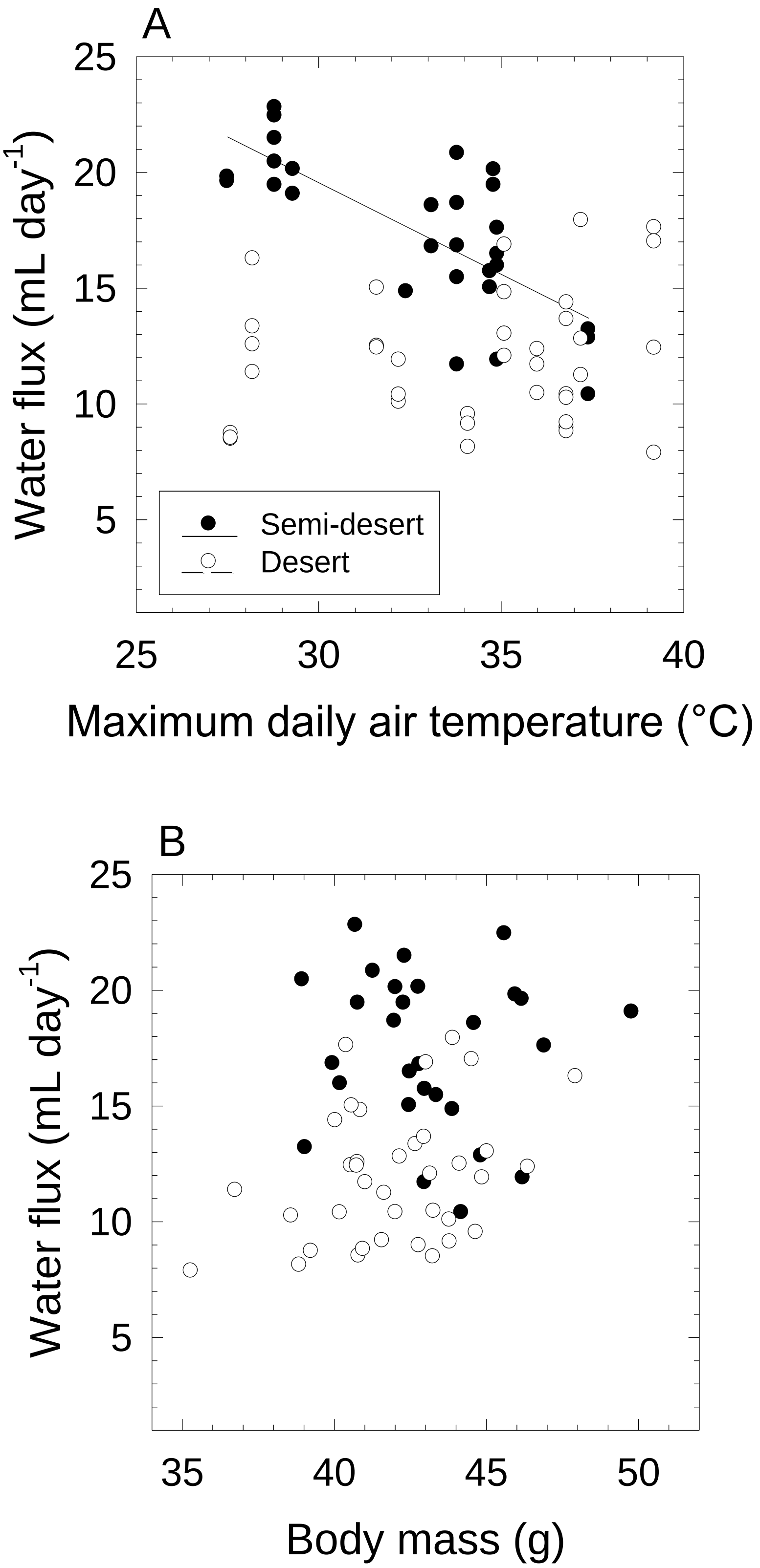

Figure 2: Daily water flux as a function of A) maximum daily air temperature and B) body mass in two populations of White-browed Sparrow-Weavers (*Plocepasser mahali*). The black dots and clear circles represent measurements obtained at a semi-desert and desert site, respectively. A trendline indicates a significant effect ($p < 0.05$).

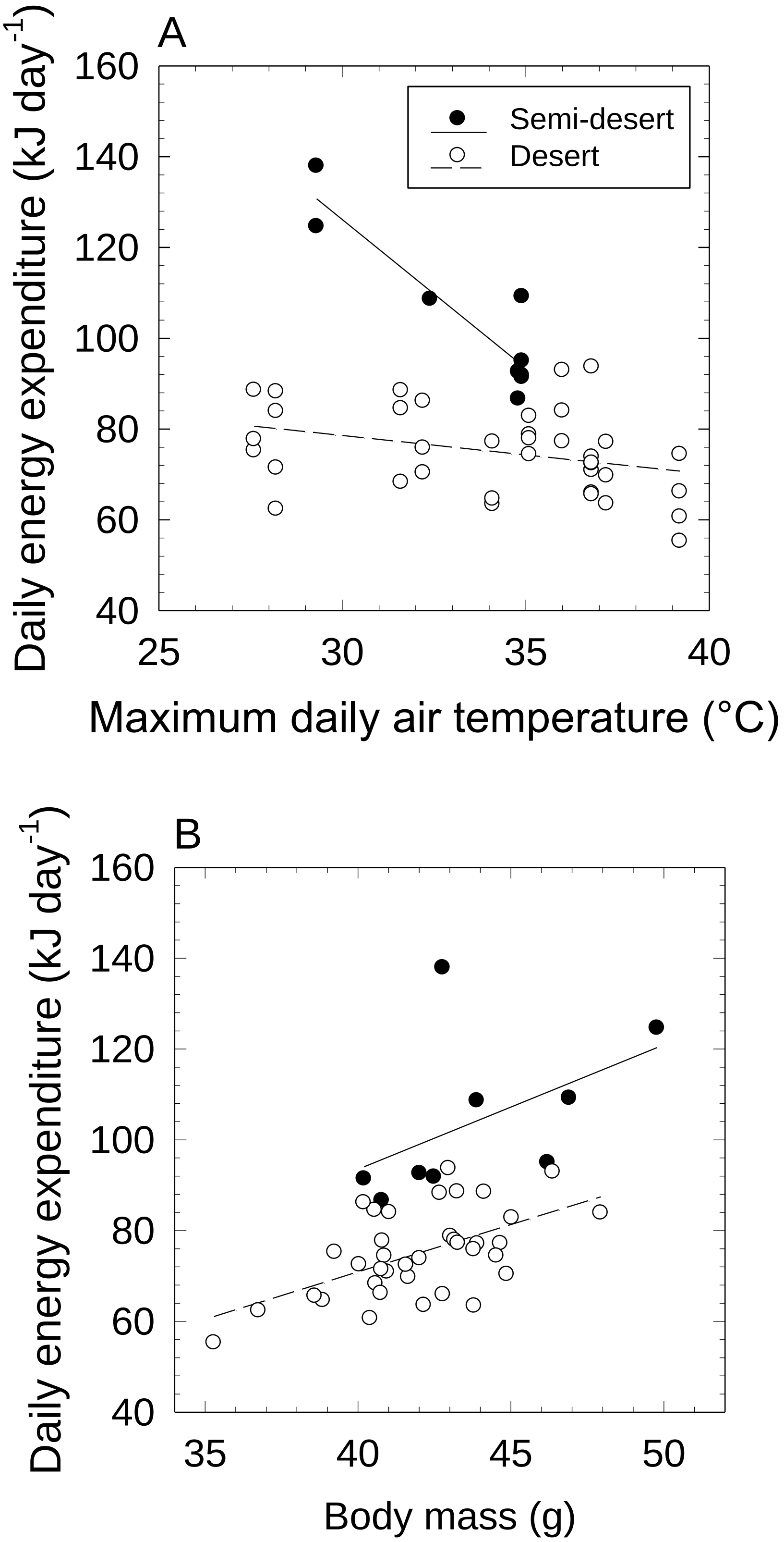

Figure 3: Daily energy expenditure as a function of A) maximum daily air temperature and B) body mass mass in two populations of White-browed Sparrow-Weavers (*Plocepasser mahali*). The black dots and clear circles represent measurements obtained at the semi-desert and desert site, respectively. A trendline indicates a significant effect ($p < 0.05$, see text for statistics).

DISCUSSION

My data show that both water and energy turnover varies with daily air temperature in an arid-zone passerine. Daily water flux did not increase on hot days. Instead, I observed either no relationship (desert population) or a significant decrease (semi-desert population) in DWF with increasing daily maximum T_{air}. These findings provide little support for the argument that thermoregulatory EWL demands drive DWF in the T_{air} range of 30–40°C, but suggest rather that activity levels and/or foraging success was the most important determinant of daily water flux (Fig. 1). Relatively few previous studies have examined the effects of temperature on avian energy and water requirements, with those that have investigated the temperature-dependence of DEE generally focusing on cooler temperature ranges [see table 3 in Weathers et al. (2002)]. To the best of my knowledge, my study is the first to investigate the temperature-dependence of DWF and DEE within a single season in warm environments.

Water fluxes were lower in the desert population and showed no change with increasing maximum T_{air}. In contrast, water flux levels in the semi-desert population were almost 100% higher compared to those of the desert population on the coolest days (27 °C), but decreased significantly on warmer days. However, on the hottest days experienced during the study (> 37 °C), DWF in the two populations converged (Fig. 2A). Daily water flux on the hottest days was on average equivalent to 20–30 % of the body mass of the sparrow-weavers. Other drinking-independent birds from hot desert environments where mean daily maximum T_{air} exceeds 40 °C during summer show slightly lower DWF values as a percentage of their body masses. For example, Hoopoe Larks (*Alaemon alaudipes*) and Arabian Babblers (*Turdoides squamiceps*) take in about 23 % and 20 %, respectively, of their body mass in water daily during summer (Anava et al. 2000, Tieleman et al. 2003). Daily energy expenditure in the sparrow-weavers, on the other hand, was about 39 % lower in the desert population than in the semi-desert population on cool days, and although both populations showed a decrease in DEE with increasing air temperature, the semi-desert birds showed a more pronounced decrease. These findings indicate that both water and energy requirements can be highly dependent on daily T_{air}, even when T_{air} does not exceed avian T_b.

Compared to the allometric predictions of DWF and DEE in Tieleman and Williams (2000) for all birds, my observed mean DWF values for the desert and semi-desert sparrow-weavers were equivalent to 80 % and 92 % respectively of the expected values of all birds, and 101% and 116% of predicted values for desert birds. Mean DEE in desert and semi-desert birds, respectively, was 88 % and 94 % of predicted values for all birds, and 100 % and 106 % of the values predicted for desert birds. White-browed Sparrow-Weavers in this study therefore showed comparatively low DWF and DEE, in general agreement with the trend observed in other desert birds (Tieleman and Williams 2000).

Daily variance in T_{air} accounted for the higher DWF and DEE values in the semi-desert birds, with these being highest on the coolest days (min T_{air} = 21.3 °C, max T_{air} = 29.3 °C); although DEE data on the coolest day represents just two individuals. Minimum T_{air} was around 20 °C on cooler days at the semi-desert site and the higher DEE is thus unlikely to represent thermogenic metabolism (see Ferguson et al. 2000). I suggest two possible explanations, which are not necessarily mutually exclusive, for higher DWF and DEE in the semi-desert birds. First, higher primary productivity at the semi-desert site during the study could mean that birds were taking in more food with a higher water content, especially on the cooler days, compared to the population at the desert site. Second, many White-browed Sparrow-Weaver groups at the semi-desert site were involved in nesting activities during the study period (D. Cram personal communication), which could lead to increased activity levels of group members that were taking part in these activities, even if they were not actively involved in breeding (Anava et al. 2002). Although none of the females I sampled showed brood patches, I could not verify the breeding status or cooperative breeding behaviour of the individuals from which I obtained data at the semi-desert site. The higher DWF and DEE patterns at the semi-desert site are thus probably the combined result of higher water content of food and higher activity levels on cooler days. In contrast, during the study at the desert site, none of the groups showed any breeding behaviour, and these data therefore reflect non-breeding DWF and DEE measurements during a dry and warm period. Anava et al. (2002) have shown that in Arabian Babblers, DWF and DEE are generally higher during the breeding season than the non-breeding season in summer.

Presumably, the higher levels of DWF and DEE observed on the cooler days at the semi-desert site could not be maintained at higher temperatures, when foraging efficiency is likely to decrease (du Plessis et al. 2012) and the potential for increased heat load further limits activity levels. This would potentially explain why DWF and DEE were lower on hotter days in the semi-desert site. The observed temperature-dependent pattern in the semi-desert population provides the best support for my predictions that the relationship between activity and foraging success drive water fluxes. White-browed Sparrow-Weavers studied in the Kalahari Desert generally reduce foraging as a percentage of daily activity from ~ 40 % at 30 °C, to ~10 % at 39 °C, although this depends largely on the time of day (Chapter 1). In contrast, the desert population had low DWF, irrespective of daily T_{air}, whereas DEE was reduced by < 15 % on the hottest days. The study at the desert site was conducted towards the end of the dry season, and since the region was largely devoid of any green plant cover at ground level I suspect that the abundance of insects was likely very low. The desert birds would therefore be subject to lower foraging success, irrespective of daily temperature.

Considering the strong positive relationship between evaporative water losses and T_{air} typically observed in endotherms exposed to high temperatures under laboratory conditions (Wolf 2000, McKechnie and Wolf 2010), the negative relationship between water flux and T_{air} in my study is somewhat surprising. Birds elevate EWL rates as T_{air} approaches T_b, and when T_{air} exceeds $T_{b,}$ EWL rates can increase by around seven fold compared to those at thermoneutral temperatures (Wolf and Walsberg 1996). Although my data are limited to T_{air} below the active-phase set-point T_b of White-browed Sparrow-Weavers [40–41.5 °C; see Chapter 1], I expected that water fluxes would increase as T_{air} approaches T_b for two reasons. First, the operative temperatures experienced by the birds in the sun over the recorded range of daily T_{air} are likely to exceed T_b at times (Wolf and Walsberg 1996, R. Martin, pers. comm.). Secondly, White-browed Sparrow-Weavers spend most their time panting when T_{air} approaches 40 °C (Chapter 1), which would result in increased respiratory EWL. Moreover, under laboratory conditions total resting evaporative water loss demands in White-browed Sparrow-Weavers start increasing significantly with increasing temperatures above 35 °C (M.C. Whitfield, B. Smit, A.E McKechnie, and B.O. Wolf, unpublished data). Since this species if often active at warm temperatures, water demands are likely to be higher than DWF which is an approximation of the birds' daily water intake rate.

Nagy and Peterson (1988) suggested that desert animals that rely predominantly on preformed water need to be highly efficient in the way they expend water while foraging. These authors developed the water economy index (WEI), measured as the water (mL) used per kJ of energy metabolized (i.e. WF/DEE), to quantify the effectiveness of an animal's water conservation mechanisms. To conserve water, desert endotherms with limited water sources should use the minimum water possible to maintain energy balance, and one would expect low WEI values in these organisms. The hyper-arid adapted Dune Lark (*Calendulauda erythrochlamys*), for example, consumes a low-water diet of seeds (occasionally supplemented with insects), and expresses the second-lowest WEI known in vertebrates, 0.06 mL kJ^{-1} (Williams 2001). It has therefore been argued that the Dune Lark has highly efficient water saving mechanisms (Nagy 2004). Tieleman and Williams (2000) showed that desert birds expressed mean WEI (0.16 mL kJ^{-1}) significantly lower than non-desert birds (0.20 mL kJ^{-1}), providing support for the notion that water may dictate energy expenditure in desert environments. In the present study, White-browed Sparrow-Weavers showed a WEI of 0.16 mL kJ^{-1} and 0.17 ml kJ^{-1} in the desert and semi-desert sites, respectively, corroborating the general trend observed in non-drinking desert birds.

Webster and Weathers (2000) found that WEI in Verdins showed a positive correlation with temperature, although it is difficult to rule out seasonal effects in their study. I fitted a simple linear regression through daily WEI as function of daily maximum T_{air} in White-browed Sparrow-Weavers, and found a significant ($p = 0.015$), slightly positive (Beta = 0.004) relationship (Fig. 4). For example, on the hottest day (max T_{air} = 39.2 °C) recorded during the study at desert site, WEI was 0.21 ml kJ^{-1} compared to 0.11 ml kJ^{-1} on the coolest day (max T_{air} = 27.6 °C). This pattern suggests that the sparrow-weavers were becoming less efficient at conserving water on the hottest days recorded during the study, potentially providing support for the prediction that EWL was becoming a larger component of DWF with increasing T_{air}. However data from hotter days (i.e. maximum T_{air} > 40 °C) are needed to verify the significance of the emerging pattern.

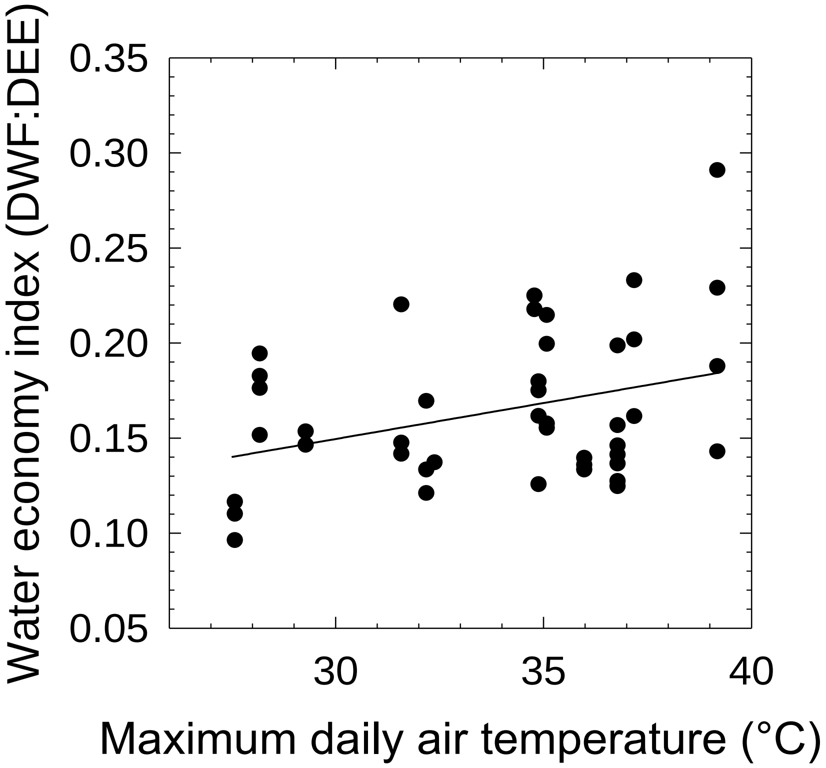

Figure 4: Water economy index (WEI, i.e. water flux/daily energy expenditure mL.kJ^{-1}) as a function of maximum daily air temperature for White-browed Sparrow-Weavers (*Plocepasser mahali*) at semi-desert and desert sites, with data for birds at the two sites pooled ($R^2 = 0.107$, $F_{1,44} = 6.385$. $p = 0.015$).

It has been argued that desert birds can reduce water demands by expressing facultative hyperthermia or regulating a higher set-point T_b. A higher T_b increases the gradient for dry heat transfer and reduces the demands for evaporative cooling (reviewed by Tieleman and Williams 1999). In Chapter 1 [see also Smit et al. (2013)], I have shown that White-browed Sparrow-Weaver populations at both the semi-desert and desert site express elevations in T_b at higher temperatures, and moreover, the desert population regulated a higher set-point body temperature (1.3 °C higher than the semi-desert population). White-browed Sparrow-Weavers also spent more time panting at the semi-desert site compared to the desert site (Chapter 1 and Chapter 4), suggesting that the semi-desert birds will have higher water demands on hot days. Variation in thermoregulatory and behavioural patterns could therefore play an important role in explaining differences in daily water demands between the two populations, if the higher set-point T_b contributed to water savings.

Collectively, the findings on variation in body temperature, heat dissipation, and water and energy fluxes between populations of White-browed Sparrow-Weaver at two sites in the Kalahari Desert (present study and Chapter 1) reveal that birds show complex adjustments in both physiological and behavioural traits to their respective environments. These findings further strengthen the argument that an organism's responses to high temperatures might be different across its distribution (Glanville et al. 2012, Smit et al. 2013) , and that vulnerability to climate change should be assessed at the population, rather than species, level.

This study has important implications for predicting the vulnerability of desert birds to climate change, especially small non-drinking species. Sparrow-weavers at my study site take in only 25–30 % of their body mass in water on hot days where T_{air} approaches avian T_b. These general patterns suggest that sparrow-weavers might not be able to increase daily water intake above these levels on hot days, unless free-standing water sources are available. Daily water loss will include a combination of excretory, respiratory and cutaneous evaporative water loss, although on hot days birds would need to allocate a greater proportion of DWF towards thermoregulatory EWL. I used data on total evaporative water loss as a function of temperature for White-browed Sparrow-Weavers (M.C. Whitfield, B. Smit, A.E. McKechnie, and

B.O. Wolf, unpublished data) to demonstrate how daily resting EWL will become a greater component of total daily water demands as daily temperatures increase. Assuming that the sparrow-weavers cannot increase water-rich food intake on hotter days, these birds need to reduce water demands and/or re-allocate avenues of water loss. I combined the above-mentioned EWL data and the water flux data obtained in the present study to model daily water budgets as a function of daily maximum T_{air} in White-browed Sparrow-Weavers. Based on the DWF data, I assumed two scenarios of total DWF where birds do not drink and dietary water is the only source of water intake: 1) where birds have high foraging success on milder days (maximum $T_{air} < 30$ °C) but where food intake and activity levels are reduced significantly on hotter days, and 2) where foraging success is low and shows no change with daily temperature (probably as a result of limited food availability in the environment). For both these scenarios I estimated mean daily water flux values from linear relationships with daily T_{air} obtained in this study.

This model predicts that on a day in the Kalahari Desert when maximum T_{air} = 39 °C, the birds will need to allocate about 76 % of their DWF budget towards resting EWL (Fig. 5). On days when maximum T_{air} approaches 42 °C, the majority of a sparrow-weaver's daily water budget will be spent on resting EWL. Given that activity levels and foraging effort will likely elevate EWL demands above these levels on hot days, these birds are likely to undergo severe pressure to maintain water balance in these environments over the next few decades.

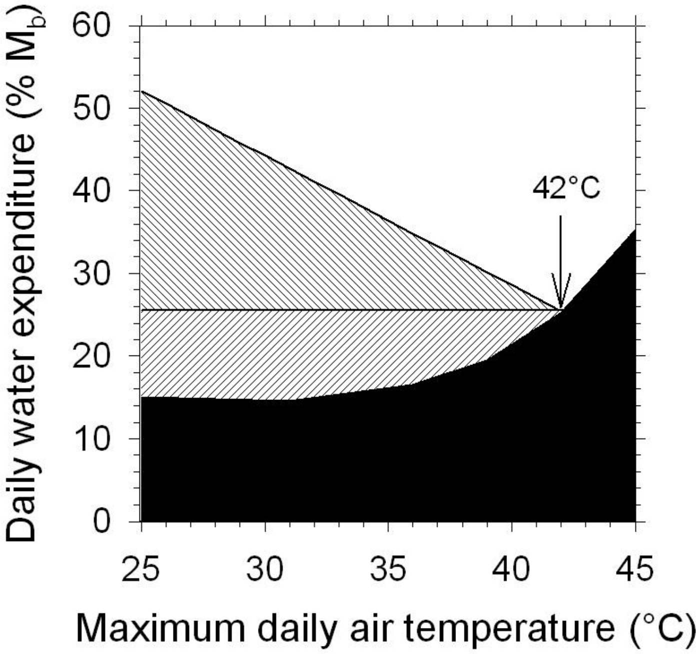

Figure 5. Daily water expenditure (% of body mass, Mb) as a function of maximum daily air temperature in White-browed Sparrow-Weavers (*Plocepasser mahali*). The black area represents total resting evaporative water loss demands (i.e. 24hr-period values calculated from hourly rates as a function of temperature), estimated from data on resting EWL under laboratory conditions (M.C. Whitfield, B. Smit, A.E. McKechnie and B.O. Wolf unpublished data). The forward hatched area represents daily water flux rates under conditions where foraging efficiency is high on mild days, and decreased significantly on days where T_{air} approaches T_b. The backward-hatched area represents conditions where daily water flux rates are low and shows no change with increasing temperature. On days when maximum T_{air} exceeds 42°C evaporative water loss demands are likely to exceed daily water intake.

It has been predicted that the frequency distribution of current maximum temperatures, as well as record maximum temperatures will shift upwards over the next few decades [see Fig. SPM.3, (IPCC 2011)]. Whereas acute, short-term mismatches during hot extremes could result in large-scale die-offs such as those recently documented in Australian birds (Finlayson 1932, Towie 2009, Saunders et al. 2011), overall warmer temperatures could result longer term and chronic mismatches in water supply and demands. Although these smaller scale mismatches might not be lethal, it could be manifested as reduced body condition when, for example, foraging efficiency and water acquisition is compromised at T_{air} approaching T_b (du Plessis et al 2012). During prolonged warm periods when birds are chronically in negative water balance they are likely suffer reductions in lean body mass as a result of plasma volume conservation [sensu Gerson and Guglielmo (2011)]. It can therefore be predicted that non-drinking species should become more dependent on free-standing water sources, which will have profound effects on avian community structure in the Kalahari, and potentially other hot, subtropical deserts.

In summary, this study has shown that water and energy use are comparatively low in two populations of an arid-zone passerine. Whereas DWF and DEE decreased strongly on hot days in a semi-desert population, desert birds expressed low DWF, independent of temperature, and low DEE that decrease only slightly on hot days. Non-drinking species that do not have the capacity to increase water intake through foraging will thus experience strong trade-offs between thermoregulation, hydration state and activity levels as temperatures increase.

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CHAPTER 3

THE EFFECTS OF TEMPERATURE ON DRINKING PATTERNS AND WATER DEPENDENCY IN KALAHARI DESERT BIRDS

ABSTRACT

Water acquisition comprises an important daily activity for birds in arid habitats. Birds face a trade-off between travelling long distances to isolated free-standing water sources at the cost of elevated energy expenditure and predation risk. Alternatively, birds can obtain most of their water by foraging for food with high water content, but potentially face reduced foraging success on hot days that could result in miss-matches between water demand and intake. In this chapter I evaluated the temperature-dependency of drinking behaviours in the Kalahari avian community. I investigated the dependency of species on free-standing surface water by 1) conducting observations at waterholes and 2) using deuterium-enriched water to trace spatial water-use during summer 2011 at Tswalu Kalahari Reserve (TKR). More than 50 % of the species comprising the avian community at TKR were never observed to drink. I found that the majority of species visiting waterholes were granivorous and only a few of these (for example, doves and sandgrouse) were daily drinkers. I collected blood samples from 42 species along a 2.4-km transect radiating away from an enriched waterhole, and found that 11 of these species showed evidence of drinking at the waterhole, based in the stable hydrogen isotope ratios of their body water. Interestingly, none of the regular-drinking species showed a significant increase in drinking events on hot days. Very few insectivorous and omnivorous species drank, and in those that did, drinking occurred mostly on hot days, and involved small numbers of individuals. Presumably, individuals of these species that occupy territories far from free-standing water will be under pressure to take in more water-rich food to make up for evaporative water losses during very hot weather. Several species were observed drinking surface water frequently, although the hydrogen isotopic signatures of their body water pools suggested that the waterhole

contributed minimally to their daily water turnover. These findings illustrate how the two methods employed in this study could provide complimentary data on the relative value of a water source to the avian community. In summary, my data reveal that artificial waterholes are vital for only a few species (mainly granivores) in the Kalahari Desert. The majority of resident species (especially insectivores) are independent of drinking water, and obtain their water through food. Nevertheless, drinking patterns on the hottest days suggest that free-standing water might become more important for some of these species.

INTRODUCTION

All terrestrial vertebrates regulate water uptake to maintain an adequately hydrated state. Small animals inhabiting arid terrestrial environments can experience high rates of evaporative water loss if they are exposed to extremes and due their limited capacity to store body water, they frequently need to regulate water intake over time scales of minutes to hours to maintain homeostasis (Hill et al. 2004). Daily water demands are especially high in small endotherms, such as birds, since their high mass-specific metabolic and evaporative water loss (EWL) rates can result in high rates of total body water loss (Williams and Tieleman, 2005; Wolf, 2000) . For example, daily water fluxes often exceed 50% of body mass in a small bird (the Verdin, *Auriparis flaviceps*) (Webster and Weathers 2000).

Water acquisition plays an important role in a bird's daily activity budget. Birds can obtain water through drinking surface water, food (preformed water) and metabolic water (i.e., oxidative water) (Bartholomew and Cade 1963, Macmillen 1990). Water intake is therefore a function of foraging effort and success for birds that rely on preformed water sources. In contrast, birds that drink water daily must allocate time to travelling to water sources, and drinking free-standing water therefore constitutes a separate component of their time-activity budgets. In warm environments where activity levels become constrained by high environmental temperatures coupled with increasing rates of EWL, water acquisition efforts can present birds with ecological, energetic and thermoregulatory challenges in the maintenance of a hydrated state.

One trade-off is that, when traveling long distances to water sources, birds accumulate energetic costs; e.g. sandgrouse are known to fly up to 80 km to water sources daily (Lloyd 2005a). Secondly, flying under hot conditions also increases a bird's heat load and body temperature can reach lethal limits (Aulie 1971, Torre-Bueno 1978, Hudson and Bernstein 1981). Thirdly, EWL rate during flight in hot weather is elevated (Tucker 1968, Torre-Bueno 1978, Hudson and Bernstein 1981) and birds could conceivably lose most of the water gained during a drinking event as evaporation during the flight to and from the water source. Fourthly, in many cases, predation risk is higher around water sources (especially isolated water sources) since there is generally a greater concentration of predators (Cade 1965; Ferns and Hinsley 1995; Fisher et al. 1972; Rosenstock et al. 1999). Finally, birds are likely to be exposed to very high environmental temperatures when free-standing water sources are in full sun (Wolf and Walsberg 1996, McKechnie et al. 2012). The spatial distribution of species that rely on drinking water daily will, therefore, be constrained to the availability of free-standing water sources, or alternatively, they have to cover large distances daily to drink water.

In contrast, birds that feed on diets with a high water content (e.g. animals and fruit) could obtain most, if not all, of their water while foraging. For example, in the

Sonoran Desert, Arizona, water-rich saguaro cactus (*Carnegiea gigantea*) fruit is the dominant source of water for white-winged doves (*Zenaida asiatica mearsnii*) during the peak saguaro fruit production period in mid-summer (Wolf et al. 2002; Wolf and Martinez del Rio 2000). In addition to pre-formed water, some birds rely largely on metabolic water to maintain water balance (Macmillen and Baudinette 1993; Macmillen 1990; Williams 1999). The hyper-arid adapted Dune Lark (*Calendulauda erythrochlamys*), consumes a low-water diet of dry seeds (only very occasionally supplemented with insects), presumably because the gains from metabolic water production exceeds EWL (Williams 1999, 2001).

By being independent of surface water, species can therefore utilize habitats where surface water is unavailable (e.g. sandy deserts). However, one potential disadvantage is that foraging efficiency or success could greatly affect hydration state. If these birds experience reduced foraging efficiency on hot days, they are likely to face hydration bottlenecks when evaporative water loss demands exceed water intake. On hot days when maximum air temperature > 36°C, for example, Pied Babblers (*Turdoides bicolor*) cannot obtain enough food (insects) to compensate for overnight mass loss, because of a temperature-dependent reduction in foraging efficiency and increased heat dissipation effort (du Plessis et al. 2012). Similarly, species that rely on metabolic water generally maintain positive water balance at temperatures below their lower limit of thermal neutrality, although at warmer temperatures, EWL rates start exceeding metabolic water production (Macmillen 1990). It can therefore be argued that it would be advantageous for these birds to drink during hot weather conditions.

Birds inhabiting subtropical desert environments are likely to experience intense trade-offs between water acquisition efforts, thermoregulation and ecological factors (e.g. predation) during high temperatures. Free-standing water is usually a scarce resource in desert habitats and the presence of surface water could be an important determinant of avian community structure and diversity. Desert birds show considerable interspecific variation in their drinking requirements, and a large proportion (60–70%) of species in desert bird communities of Australia and the Namib Desert are considered to be independent of free water, either being never observed to drink water or only visiting water very occasionally (Willoughby and Cade 1967, Fisher et al. 1972). However, these patterns are likely to be strongly temperature dependent. In Chapter 2 I have shown that a non-drinking arid-zone passerine in the Kalahari Desert, the White-browed Sparrow-Weaver, has low water intake rates on hot days. In fact, at Tswalu Kalahari Reserve, these birds significantly reduced water intake rate on hot days, suggesting that birds are at risk of experiencing hydration bottle necks on hot days (~ 42 °C) when most of their daily water budget will be taken up by resting evaporative water loss demands. On hot days there would therefore be strong pressure to start taking advantage of free-standing water, most likely because foraging success is reduced and water intake will not be sufficient to compensate for the demands for evaporative water loss.

In this study I investigated the temperature dependency of drinking requirements in a desert avian community. I predicted that birds would increase their dependency on free-standing water during hot weather, and specifically, species which generally rely on water sources other than drinking, i.e. preformed water and oxidative water. Here I present data from a semi-desert site where other than artificial water holes, natural free-standing surface water is largely unavailable and thus I expected the majority of the avian community to rely on preformed water. These predictions were tested using both direct observations at water holes, and testing whether birds utilise a particular water source by artificially enriching the hydrogen stable isotope ratios of the source and then analysing the composition of birds' body water pools.

METHODS AND MATERIALS

Study site

I examined interspecific variation in drinking dependency within a Kalahari Desert bird community at Tswalu Kalahari Reserve (TKR), Northern Cape Province, South Africa during the austral summers of 2009/2010 and 2011/2012 (~1100 m a.s.l. S2719', E2225'). TKR covers approximately 100 000 ha of semi-arid Kalahari savanna on vegetated red sand dunes. Mean annual rainfall over a 30-year period at TKR was 295 ± 172 mm (coefficient of variation, CV = 58.3%) (unpublished data, Tswalu Kalahari Reserve). With the exception of seasonal dams at the foothills of the Koranna Mountain range (1400-1600 m a.s.l., forming the eastern border of TKR), and a few isolated calcareous pans in the far west of the reserve, no natural surface water occurs in the dunes (even during the rainy season). Artificial waterholes have been established throughout the reserve (generally more than 4 km apart), primarily to supply drinking water to large ungulates.

I assessed drinking dependency using two methods: firstly, by monitoring drinking patterns at four artificial waterholes directly, and second, by investigating the importance of a specific body of free-standing water by enriching a water hole with a stable isotope label and sampling body water of the bird community at distance of 0–2.5 km from the water source. I argue that these two methods provide complimentary data on drinking dependency rather than duplications of one another. Many previous studies have investigated the potential benefits from artificial water developments to desert avian communities (Brien, Waddell, Rosenstock, and Rabe, 2006; Broyles, 1995; Lynn, Chambers, and Rosenstock, 2006; Lynn, Rosenstock, and Chambers, 2008; Simpson, Kelley, and Bleich, 2011; Smyth and Coulombe, 1971; Williams and Koenig, 1980). However, whereas direct observations provide qualitative data on which species are observed drinking and their drinking frequency, isotope data provide quantitative data of the importance of a water source to an animal's water body water pool.

Weather data

Weather data were obtained using a portable weather station (Vantage Pro2, Davis Instruments, Hayward, CA), set 2 m above the ground at a central location in the study site. This weather station has an aspirator fan to ensure air movement over the temperature and humidity sensors. I checked the factory calibration of the weather station against a mercury thermometer (resolution 0.1 °C, accuracy traceable to the South African Bureau of Standards) at a range of temperatures (5 to 50 °C).

Observations of drinking patterns

Avian drinking patterns were assessed using video-cameras (Sony Handycam, DCR-SR45E, Sony Corporation, Tokyo, Japan) to record drinking behaviour continuously from sunrise to sunset during mid-summer (November to December 2009), at four waterholes (referred to as Kukama, Gosa 5, Gosa 6 and Donderkamp waterholes) in TKR. All four waterholes were in the dunes, > 3km away from neighbouring waterholes and artificially maintained by boreholes. Kukama and Donderkamp waterholes were circular (~ 3 m in diameter), whereas Gosa 5 and 6 were keyholeshaped (~ 1 m x 2 m). All waterholes were fully exposed to the sun and nearest vegetation was > 5 m away. I placed video cameras in rain- and baboon/rhinoceros-proof steel boxes next to waterholes at Gosa 5 and 6, and in nearby trees at Kukama and Donderkamp water holes. Video cameras were set to cover the maximum area over the water hole to ensure birds would be visible when drinking at any edge of the water. However, on a some days water spilled over the rim of the water hole during the course of the day, resulting in water collecting outside the area visible to the camera. Recordings commenced between dawn and sunrise, i.e. 5h00 and 6h00, respectively (variation due to the 45-min travel time between the first and fourth cameras). The cameras were set to record continuously throughout the day, and in most cases batteries lasted until sunset. I downloaded video footage and recharged batteries on days following recordings and therefore video recordings were repeated on alternate days. I obtained video recordings over a total of 9, 13, 13 and 16 days at Donderkamp, Gosa 5, Gosa 6 and Kukama waterholes, respectively (~ 660 hours of video recordings). I subsequently viewed play-backs of each waterhole's recording at 30-minute intervals for 10 minutes (i.e. two 10 minute periods per hour per waterhole). I recorded species and estimated the number of individuals utilising the waterhole during each 10-minute period. If it was obvious that a particular individual utilised the waterhole more than once during a 10-minute period (for instance, when the bird is disturbed from first drinking attempt) it was counted as a single event. I categorised time of day into seven two-hour intervals, starting at 5h00 and ending and 19h00, and estimated mean visitation rate per hour per species for each time interval (all four water holes pooled). I compared avian species composition and density estimates obtained from sub-sampled video footage (18 x 10 minute intervals) to continuous observations (video or manual) at one waterhole for an entire day, and found that only two species were missed during interval counts compared to a full day of observation.

Water resource use inferred from stable isotope labels

Water resource use by organisms can be assessed using stable hydrogen isotopes, especially if the hydrogen or oxygen isotope ratio of a prominent water sources is enriched above natural levels (McKechnie 2004; McKechnie et al. 2004). The presence of enriched isotope ratios in the body water pool of an individual are used to infer the percentage of an animal's body water pool derived from a particular water source, thereby giving a quantitative estimate of dependence on a free-standing water source (McCluney and Sabo 2010).

I assessed the use of a specific waterhole by an avian community during a wet (23 February to 6 March 2011) and a dry period in summer (21 October to 3 November 2011), by enriching the hydrogen stable isotope ratio (δD) of a relatively isolated water hole (> 5 km from nearest neighbouring water source) by ~ 250 ‰ VSMOW by adding 99.99 % deuterium oxide. The waterhole system consisted of a shallow (20 cm) waterhole (3 m diameter), which was supplied by a ~ 22800 L reservoir (diameter = 4.3 m, depth = 1.57 m). Although large mammals frequently made use of the water source, I estimated that the reservoir took more than 4 weeks to run completely dry. I therefore emptied the reservoir to approximately 14 000 L (1 m deep) and closed the main inlet to prevent the labelled water from being diluted by inflow. I subsequently added 585 mL 99.99 ‰ deuterium oxide to the reservoir, estimated to enrich the waterhole by 200-300 ‰ VSMOW, and mixed the water for at least two minutes. I then emptied the waterhole, before allowing labelled water from the reservoir to fill the waterhole. I collected water samples before the enrichment and subsequently every 1 to 2 days for two weeks after enrichment. I collected blood samples from birds trapped 1) around a non-enriched waterhole (up to 2 km away from the water waterhole) and 2) around the enriched waterhole at increasing distances (<100 m to 2.5 km). I used mistnets (10 per trapping site) and occasionally spring traps baited with tenebrionid larvae to trap birds. Trapping sites around the enriched waterhole were selected along a radius from the waterhole in a direction devoid of waterholes/surface water sources for at least 6 km. I selected trapping sites starting at the first shrubs and trees from waterhole (10 m) at intervals of about 500 m up to a distance of 2.4 km. The latter site was the furthest I could trap from the enriched waterhole without being nearer to neighbouring waterholes. I spent at least one day at each trapping site and carried out 132 trapping hours (80 during Feb and 52 during Oct 2001), trapping a total of 333 birds (196 and 137, respectively). I trapped birds during the morning, from 06h00 (sunrise) until about 11h00, and in the afternoon (depending on temperature) from 15h00 till 19h00 (sunset). I obtained blood from each bird soon after capture, or held trapped birds in cotton bags suspended in full shade until they could be processed. No birds were held for longer than 3 hours.

I obtained blood samples (10-150µl) from the brachial vein of individuals using heparinised microcapillary tubes. I transferred each blood sample immediately to a 150 µl micropipette and flame sealed both ends of the pipette (Speakman 1997). I stored the blood between 2 and 5 °C until further analyses. I separated pure water from the samples by cryogenic vacuum distillation, and measured δD and δ^{18}O of the water samples obtained from bird blood and waterholes, using a PAL autosampler and DLT-100 liquid water isotope analyser (Los Gatos Research, Mountain View, CA, USA). Samples were bracketed with standards spanning the ranges of -79.00 to 978 ‰ VSMOW (δD) and -11.54 to 260.82 ‰ VSMOW (δ^{18}O). A minimum of ten 1-µL replicates were analysed per sample or standard, and values for the first five replicates were typically discarded in order to avoid isotopic memory effects.

Avian communities around waterholes

I assessed the species composition of the bird community in TKR by conducting 62 points count along eight transects (~ 3 km each) (Ralph et al. 1993). Points were on average 500 m apart and ranged from the habitat surrounding a waterhole up to 4 km from the nearest water source. During each point count (lasting 10 minutes) I identified and estimated numbers of all species, seen or heard within a radius of ~ 200 m. I assumed that detectability did not vary with distance from the observer (as typically happens in more closed habitats such as forests) (Reynolds et al. 1980). This assumption was reasonable at TKR because of the open nature of the habitat.

Data analyses

I performed chi-square test to establish if the presence (% days observed drinking) at waterholes of different feeding guilds were representaive of their relative abundance (% reporting rate). I further investigated the temperature-dependency of drinking patterns by performing simple regression analyses of the number of drinking events of 19 species most frequently observed drinking between 12:00 and 19:00 (i.e. hottest part of day and subsequent daylight hours) as a function of daily maximum air temperature (T_{air}). To establish whether daily temperature could affect drinking patterns, especially in infrequent drinkers, I also averaged the maximum T_{air}, linked to each drinking event (hereafter referred to as Max T_{drink}) for each species. I then performed a simple linear regression to investigate the relationship between Max T_{drink} and the percentage of days each respective species was observed drinking.

Water molecules (irrespective of source) are naturally composed of both light and heavy isotopes of hydrogen and oxygen. However the relative abundance of these isotopes varies widely in the environment because of chemical and physical processes, for example rapid fractionation of lighter isotopes through evaporation (McCluney and Sabo 2010). Because of these fractionation processes, heavy hydrogen (D) and oxygen (^{18}O) isotopes co-vary largely at both local and global scales (Clark and Fritz 1997). The ratios of D and ^{18}O isotopes in water sources in any given environment will depend on the degree of fractionation (dependent on temperature and humidity at local scale) that took place from the original water pool (McCluney and Sabo 2010). Based on this principle δD and $\delta^{18}O$ of body water of organisms at the community level will vary linearly—depending on the organisms' prime water source. This relationship was then used to establish a predictive equation of δD and $\delta^{18}O$ values within the bird community—thereby incorporating physiological and natural variation at a local scale. The two-end point mixing model (Kline et al. 1990, Gannes et al. 1997) can then be used to estimate the proportion of an animal's body water pool derived from an artificial water source enriched with δD. By artificially enriching δD levels of a water source, i.e. δD ratios will fall significantly away from the local physiological line (that is baseline δD versus $\delta^{18}O$ relationship). The proportion of a bird's body water derived from an enriched source (P%) can then be estimated using the following equation,

$P\% = [\delta D_{bird} - \delta D_{baseline}]/[\delta D_{spike} - \delta D_{baseline}]$

where δD_{spike} is the value of the enriched source (in ‰ VSMOW), $\delta D_{baseline}$ is the expected δD value of the sample based on the regression of $\delta_{18}O$ and δD for all non-users, and δD_{bird} represents the measured δD value for the bird sample. For each individual's calculations I used the δD_{spike} and $\delta D_{baseline}$ for each respective season. I calculated P% only for individuals in which δD_{bird} values fell to the right of the 95% predictive interval of the appropriate baseline regression line. When δD values fell to the right of prediction intervals for the baseline regressions they were significantly different from the expected δD and $\delta^{18}O$ relationship along the natural physiological line.

Values are presented as means ± SD, unless otherwise stated. I used a paired t-test to establish if P% was different between seasons in two species (Namaqua Dove and Scaly-feathered Finch) from which I obtained representative samples in both seasons (each species was tested separately). In these tests I could assume equal variances across groups in Scaly-feathered Finches, but because of I heteroscadisticity in Namaqua Doves I had to assume non-equal variances across groups. I used regression analyses to test and the relationship between drinking frequency and P%, including only species that were observed drinking and sampled more than three times during the study.

RESULTS

Weather during study periods

Mean daily maximum T_{air} on the days for which I obtained video recordings varied over an 11 °C range, from 26.4–37.4 °C (two days > 35 °C). Mean daily maximum T_{air} during the stable isotope study was 32.7 ± 2.7 °C (25–35 °C) during the wet season and 30.6 ± 4.2 °C (26–37 °C) during the dry season, respectively.

Drinking patterns - observational data

I observed 76 species during the study at Tswalu Kalahari Reserve (Appendix D, Table D1). The most commonly observed species (reporting rates > 50 %) were White-browed Sparrow-Weaver (reporting rates = 81.0 %), Black-chested Prinia (66.1 %), Fawn-coloured Lark (64.5 %), Scaly-feathered Finch (62.9 %), Namaqua Dove (59.7 %), Ant-eating Chat (56.5 %) and Kalahari Scrub-Robin (54.8 %). The avian community at TKR is dominated by insectivores (49.3 % of species) and granivores (32.8 %); birds of prey, omnivores, frugivores and nectarivores make up 10.4, 10.4, 9.0 and 1.5 %, respectively.

I observed a total of 36 species drinking at the waterholes during the study (Appendix D, Table D1). The majority of these species (19 species) were granivores and 86 % of all granivores recorded at TKR were observed drinking from waterholes (Fig. 1A). In contrast, only 18 % (6 out of 33 species) of insectivorous species were observed to drink (Fig. 1A). Granivores, frugivores and omnivores were the most frequent drinkers (although species varied greatly), and I observed them drinking on 55.0 ± 40.1 %, 64.1 ± 34.4 % and 52.1 ± 44.3 % of days, respectively (Fig. 1B). The insectivores and birds of prey were observed drinking on 24.0 ± 14.5 % and 16.7 ± 9.5 % of days, respectively (Fig. 1B). The drinking frequencies of the respective foraging guilds were statistically different to what I expected based on their abundance. Whereas granivores, frugivores and omnivores were significantly over-represented ($\chi^2_{1,15} = 385.9$, $p < 0.001$, $\chi^2_{1,3} = 173.6$, $p < 0.001$, $\chi^2_{1,2} = 84.8$, $p < 0.001$, respectively), insectivores were significantly under-represented at the waterholes based on their abundance ($\chi^2_{1,4} = 95.4$, $p < 0.001$).

Three species of Columbiformes (Namaqua Dove, Laughing Dove and Cape Turtle Dove), two Pteroclidiformes (Namaqua and Burchell's Sandgrouse) and one passerine (Southern Masked Weaver) were recorded drinking on every day, whereas a further eight species were observed drinking on more than 50 % of days (Appendix D, Table D1). Namaqua Doves and Cape Turtle Doves showed the largest numbers drinking at waterholes per day (average of 387.3 ± 131.8 and 156 ± 83.9 drinking events per day, respectively for the four waterholes pooled). Sociable Weavers also showed relatively large, but highly variable, numbers drinking per day (69.3 ± 110.7 per day). Many of the irregular drinkers (drinking < 50 % of time) showed low numbers drinking per day (Appendix D, Table D1).

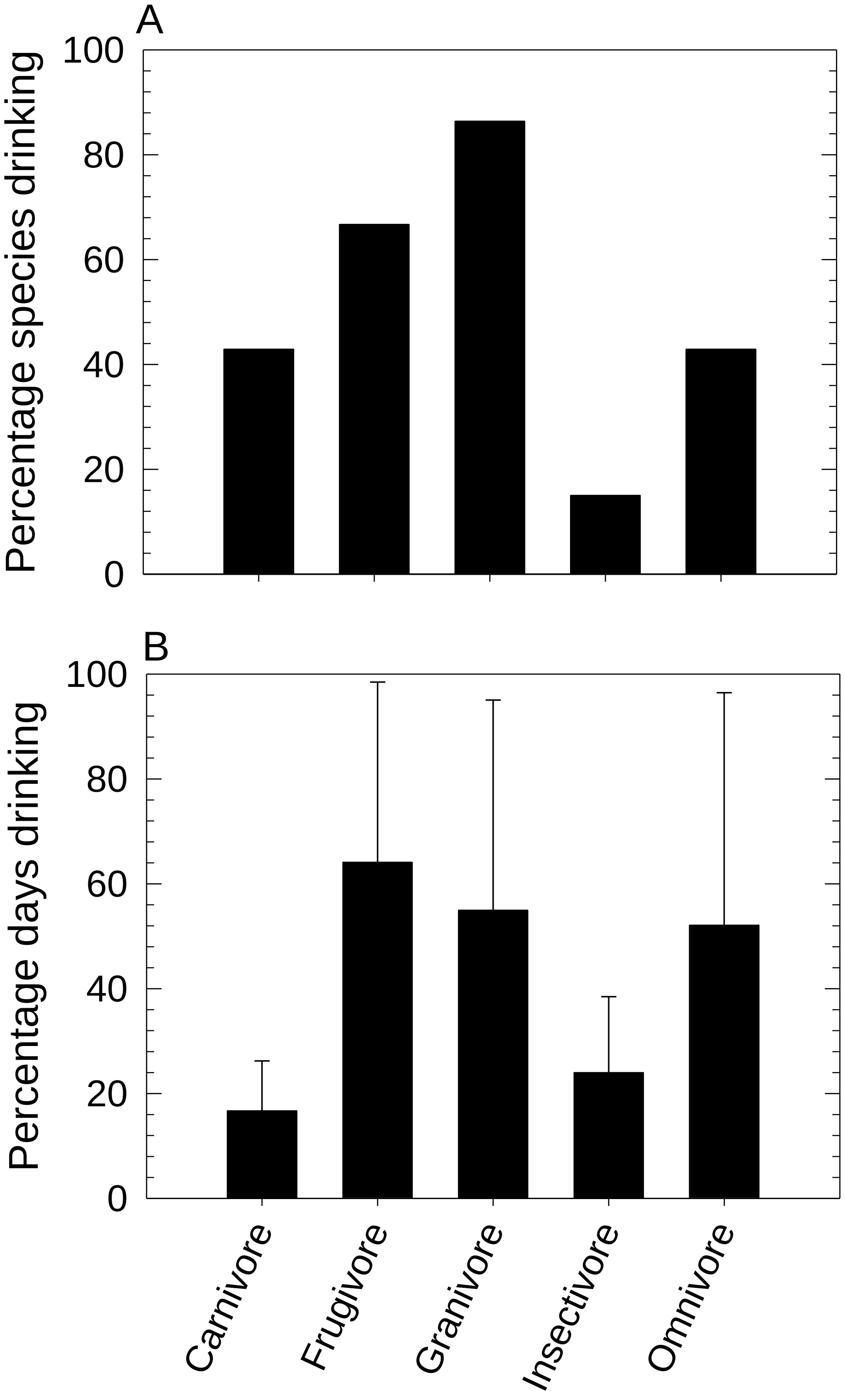

Figure 1: Summary of drinking dependency and frequency (% days observed drinking) as a function of dietary guild in the avian community observed at Tswalu Kalahari Reserve during the summer (November to December 2009).

Drinking patterns as a function of time and temperature were analysed for 19 species that drank most frequently (i.e. drinking on > 30 % of days). The vast majority of species showed a bimodal drinking pattern, with drinking events concentrated during early morning (between 6h00 and 10h00) and late afternoon to evening (16h00 to 19h00) and birds avoiding waterholes during midday (Fig. 2). Namaqua Doves, and to a lesser extent, Violet-eared Waxbills, focussed their drinking around midday (Fig. 2). Laughing Doves and Cape Sparrows showed no particular drinking pattern and drank throughout the day (Fig. 2). Namaqua Sandgrouse, Burchell's Sandgrouse, Larklike Bunting and White-backed Mousebird drank mostly in the morning, whereas White-browed Sparrow-Weaver, African Red-eyed Bulbul and drank mostly late afternoon or evening (Fig. 2).

Drinking during the warmest part of the day (12:00 to 18:00) was not significantly related to maximum daily air temperature in any of the species observed during the study (Fig. 3). Namaqua Sandgrouse, Southern Masked Weaver and African Red-eyed Bulbul showed the smallest change in afternoon drinking patterns and these species drank on most days irrespective of maximum T_{air} (Fig. 3). Most other drinking species appeared to increase the number of drinking events with maximum daily temperature (although not significantly) (Fig. 3), and the patterns were similar when species were pooled within dietary groups (i.e. no significance).

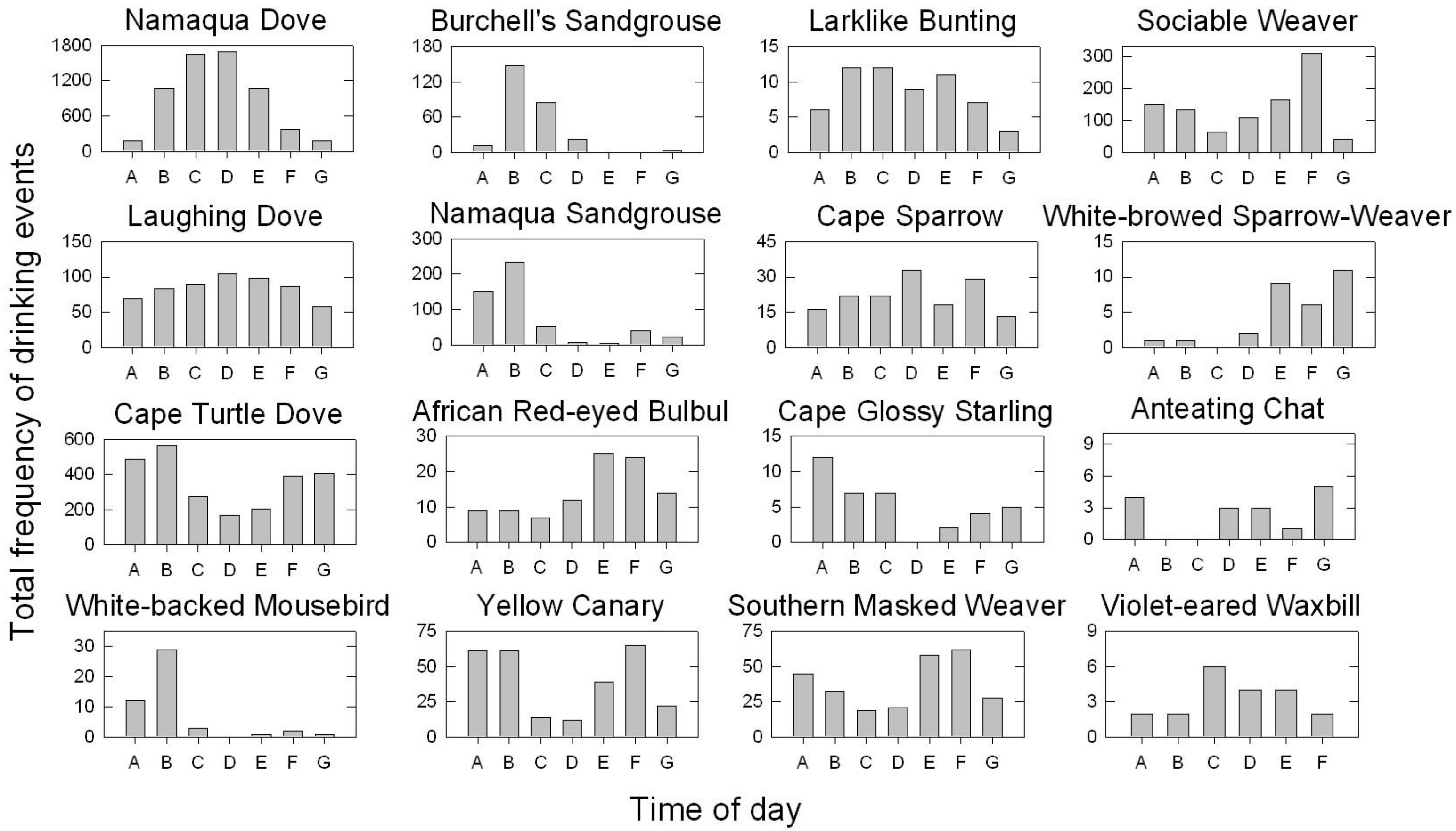

Figure 2: Frequency of drinking events pooled across all four waterholes as a function of time of day in 16 species that drank more than 40% of days during summer in Tswalu Kalahari Reserve (November to December 2009). Times are categorized as A = 05h00 – 07h00; B = 07h00 – 9h00; C = 9h00 –11h00; D = 11h00 – 13h00; E = 13h00 – 15h00, F = 15h00 – 17h00, G = 17h00 – 19h00. Sunrise and sunset times averaged 05:40 and 18:40 respectively during the study period.

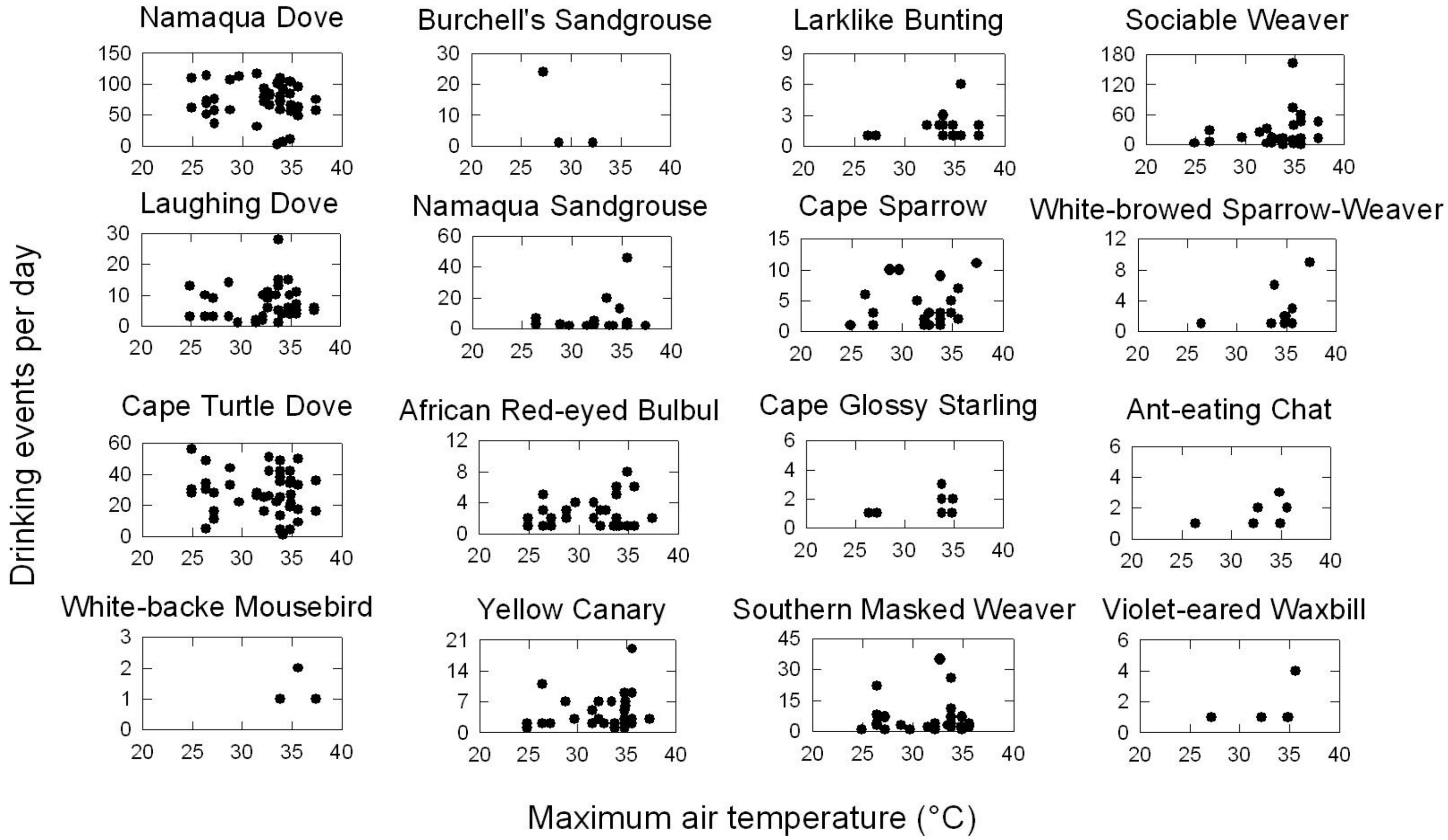

Figure 3: Drinking events pooled across all four waterholes as a function of maximum daily temperature in the 16 species that drank on more than 40% of days during summer in Tswalu Kalahari Reserve (November to December 2009)

Mean maximum daily temperature linked to each drinking event (Max T_{drink}) was significantly related to the overall frequency of drinking events ($r^2 = 0.47$, $F_{1,31} = 27.39$, $p < 0.001$) (Fig. 4A). Max T_{drink} was similar to the average daily maximum T_{air} (31.7 °C) in species that drank frequently (e.g. doves), whereas species that drank infrequently had a higher Max T_{drink} since they generally drank on hot days only (Fig. 4A). In general, insectivorous species showed the highest max T_{drink}, and drinking events in granivorous and frugivorous species were least dependent on temperature (Fig. 4B). Omnivorous species showed a wide range of Max T_{drink} (Fig. 4B). For example, whereas Cape Glossy Starling, Wattled Starling and Southern Masked Weaver showed low Max T_{air} (32.7, 31.5 and 31.9 °C, respectively), and White-browed Sparrow-Weaver and Sociable Weaver showed higher Max T_{drink} (35.4 and 34.6 °C, respectively) since they generally drank only on hotter days (Appendix D, Table D1).

Drinking inferred from isotopically labelled water sources

I obtained blood samples from a total of 303 birds representing 42 species. I obtained 247 of these samples within a 2.4 km radius of the enriched Donderkamp waterhole, and the remaining 55 were obtained at distances of 0 and 2km around two non-enriched waterholes. The δD and δ^{18}O values for the two non-enriched water sources were -47.2‰ and -7.6 ‰ VSMOW respectively (large reservoir), and -24 ‰ and -0.9 ‰ VSMOW respectively (small shallow waterhole). Samples obtained from the three species of dove were the most depleted (δD and δ^{18}O < 20 ‰ and 5 ‰ VSMOW, respectively) and resembled non-enriched waterhole values most closely (Fig. 5). Most of the remaining groups showed large overlap in δD and δ^{18}O values (Fig. 5).

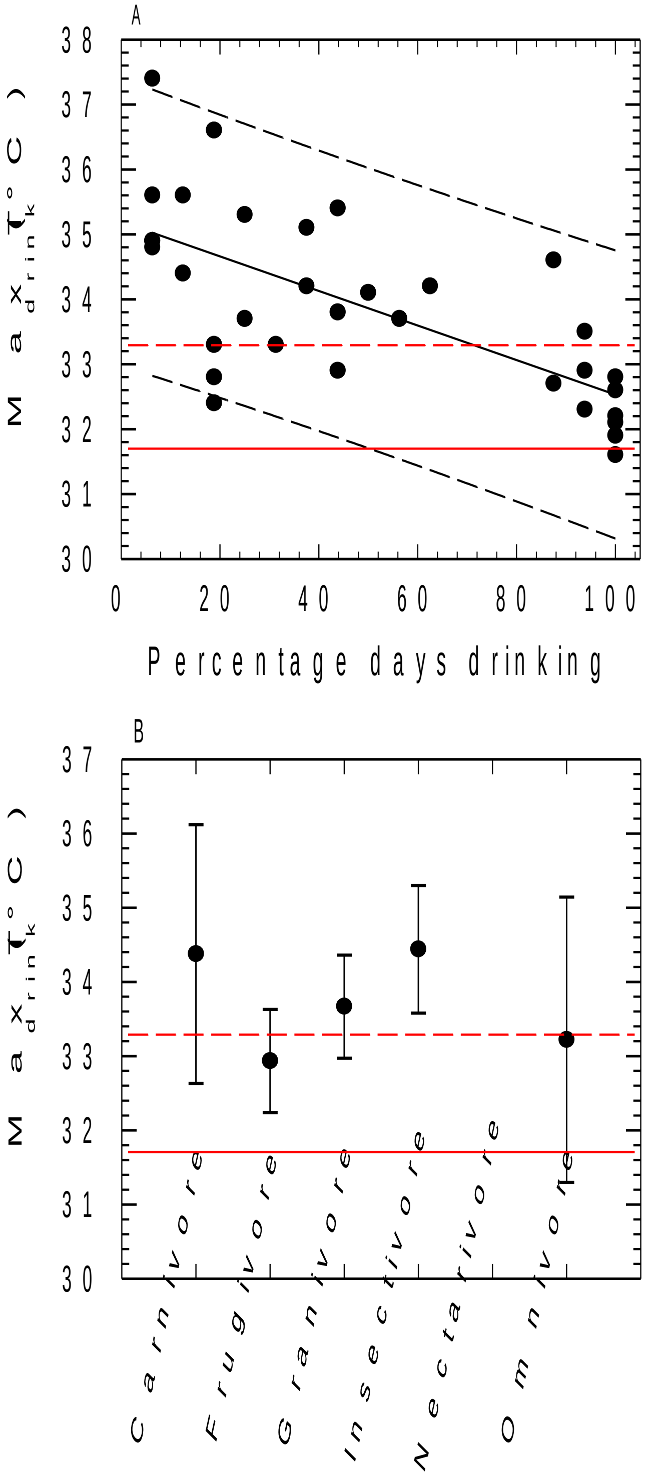

Figure 4: A) Mean maximum daily temperature (Max T_{drink}) linked to each drinking event for each species as a function of drinking frequency (% of days observed drinking) during summer (November to December 2009) at Tswalu Kalahari Reserve (TKR), with the trendline (solid line) representing the significant negative relationship with 95% prediction intervals (PI). B) Mean Max T_{drink} ± 95% confidence interval (CI) as a function of dietary guild. In both panels the solid and dashed red line represents mean and 95% CI of maximum daily air temperature (Max T_{air}), respectively, over the study period at TKR.

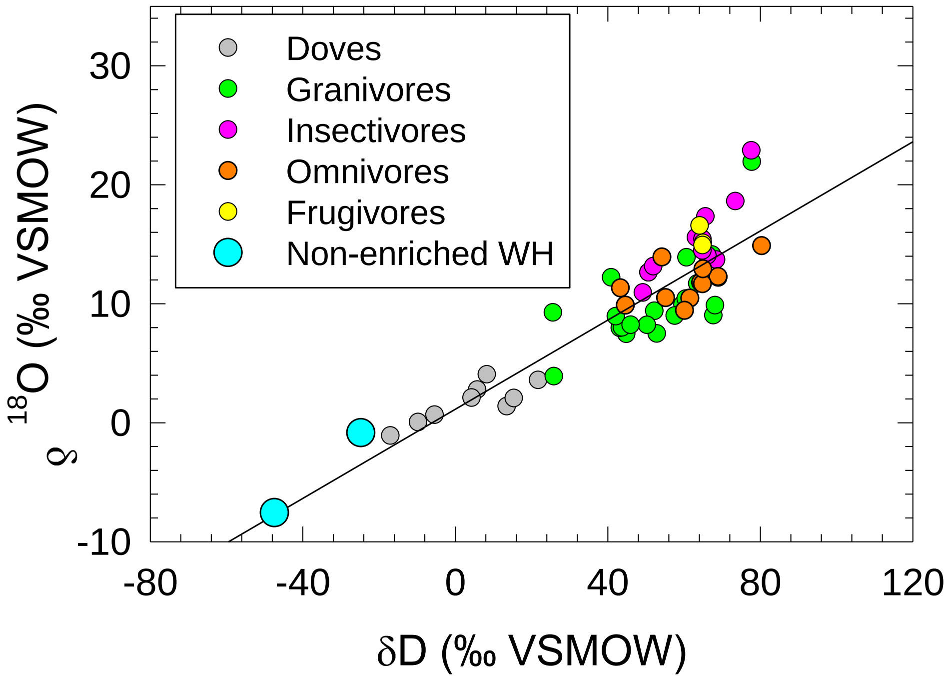

Figure 5: $\delta^{18}O$ and δD values of birds sampled around two non-enriched water sources in Tswalu Kalahari Reserve (October 2011). The trendline represents the linear relationship ($y = 0.19x - 0.77$) between $\delta^{18}O$ and δD values.

I established baseline regression lines for the TKR avian community by plotting $\delta^{18}O$ as a function of δD for both seasons (wet summer and dry summer) including resident species that were never observed to drink from waterholes at TKR, and fitting linear regression models. The intercepts of the baseline regression for the wet summer season ($y = 0.23x - 1.68$, $r^2 = 0.81$, $F_{1,44} = 187.73$, $p < 0.001$) and dry summer season ($y = 0.24x - 0.13$, $r^2 = 0.64$, $F_{1,46} = 81.13$, $p < 0.001$) were significantly different ($F_{1,91} = 70.48$, $p < 0.001$). I subsequently compared samples from potential drinkers to their respective baseline regression lines; I considered δD values falling to the right of the 95 % prediction interval as evidence that individuals obtained water from the enriched waterhole. I used deviations of δD and $\delta^{18}O$ values from the respective baseline regression for the two seasons, to establish P% in the mixing model.

During February 2011 (wet summer season) I enriched the δD levels in Donderkamp waterhole from -41.7 ‰ VSMOW to 264 ‰ VSMOW (average of values obtained over 14 days after enrichment, range = 243–286 ‰ VSMOW). During October 2011 (dry summer season) I enriched the δD levels in Donderkamp waterhole from -31.7 ‰ VSMOW to 238 ‰ VSMOW (average of values obtained over 14 days after enrichment, range = 227–247 ‰ VSMOW).

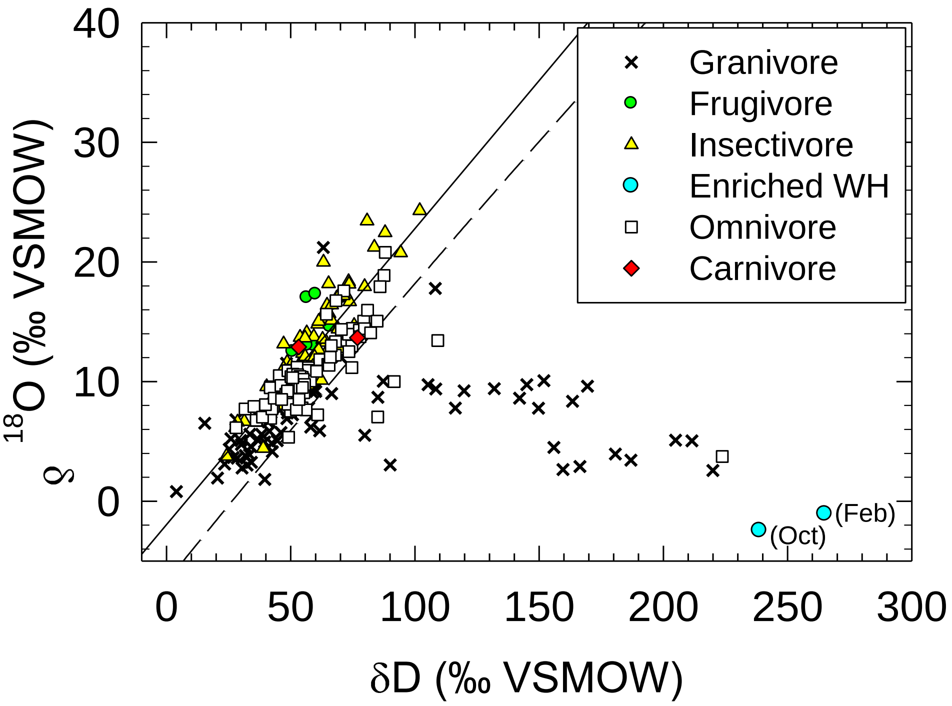

Figure 6: δ^{18}O and δD values of the avian community as a function of dietary guild sampled around an enriched waterhole in Tswalu Kalahari Reserve (during February and October 2011). The trendline represents regression line and lower 95% prediction intervals (y = 0.19x - 0.77) between δ^{18}O and δD values for non-users (see text for explanation). Wet and dry season data were pooled for sake of clarity in this figure. Data points falling to the right of the 95 % prediction interval indicates that individuals used the enriched water hole. The blue circles represent mean δ^{18}O and δD values for the enriched waterhole during the wet and dry seasons.

Only 11 of 42 species trapped during the two seasons used the enriched waterholes. The δD and δ^{18}O ratios for all insectivores, frugivores (White-backed Mousebird and Acacia Pied Barbet) and raptors (Pearl-spotted Owlet and Pygmy

Falcon) fell within the 95 % predicted intervals of the physiological line, indicating that these species did not use the labelled water source (Fig. 6). Granivores and, to a lesser extent omnivores, were the only groups where δD and δ^{18}O ratios fell to the right of the 95 % prediction intervals, indicating use of the enriched water source (Fig. 6). The majority of omnivore samples were represented by three small- to medium-sized ploceid weavers—Southern Masked Weaver, Sociable Weaver and White-browed Sparrow-Weaver (Fig. 7A), and only 11.1 %, 19.4 %, and 8.0 % of individuals for these species, respectively, showed any use of the enriched waterhole. Namaqua Doves made extensive use of the enriched waterhole and 11 of 13 individuals (85 %) showed evidence of drinking (δD levels enriched by up to 225 ‰ VSMOW, Fig. 7B). The two individuals that did not drink from the enriched waterhole had depleted δD and δ^{18}O values, similar to values for non-enriched water holes (Fig. 5). Only a single Cape Turtle Dove and Laughing Dove was trapped around the enriched waterhole; whereas the Cape Turtle Dove had an enriched δD value (166.4 ‰ VSMOW), the Laughing Dove fell within the 95 % prediction interval but showed a depleted δD value (4.0 ‰ VSMOW). Violet-eared Waxbills and Scaly-feathered Finch represented the majority of small granivorous passerines I trapped during the study. Violet-eared Waxbills made extensive use of the enriched waterhole (75 % of individuals) and showed δD values up to 150 ‰ VSMOW (Fig. 7C). Scaly-feathered Finches, in contrast, made less use of the enriched water hole (16.7 %) and only showed δD values up to ~ 60 ‰ VSMOW in drinking birds (Fig. 7C).

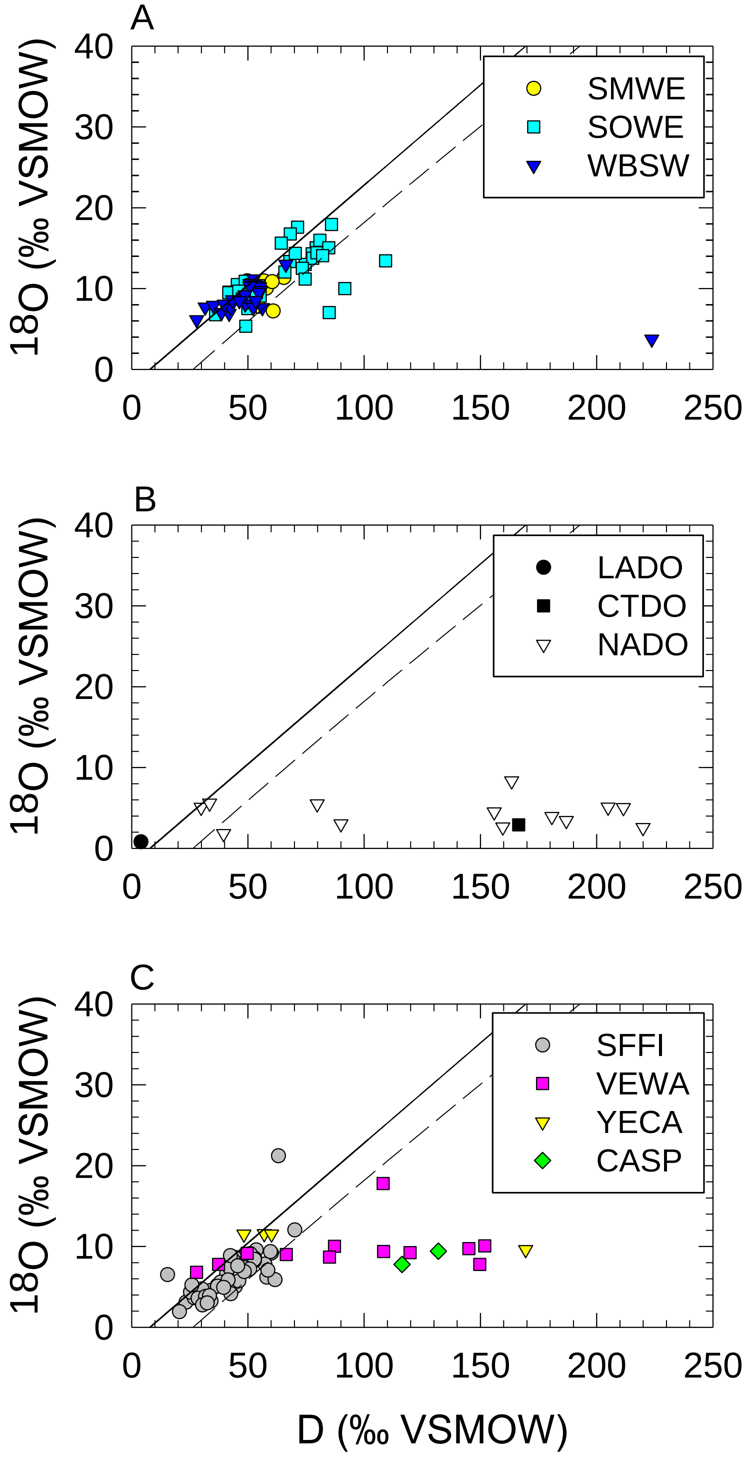

Figure 7: δ^{18}O and δD values in A) three species of weaver, B) three species of dove and C) four small granivorous species, sampled around an enriched water hole in Tswalu Kalahari Reserve (during February and October 2011). The trendline represents regression line and lower 95% prediction intervals (y = 0.19x - 0.77) between δ^{18}O and δD values for non-users (see text for explanation). Wet and dry season data were pooled for sake of clarity in this figure. Data points falling to the right of the 95 % prediction interval indicates that birds used the enriched water hole. Abbreviations: SOWE = Sociable Weaver, SMWE = Southern Masked Weaver, WBSW = White-browed Sparrow-Weaver, CTDO = Cape Turtle Dove, LADO = Laughing Dove, NADO = Namaqua Dove, SFFI = Scaly-feathered Finch, YECA = Yellow Canary, CASP = Cape Sparrow.

Individuals that used the enriched water source had 2.2–93 % of their body water derived from the enriched source. Scaly-feathered Finches had the lowest body water pool derived from the enriched source (generally < 10 %). Namaqua Doves and Violet-eared Waxbills, on the other hand, had the highest body water pool derived from the enriched water source. However, the percentage of body water pool derived from the enriched sourced varied between seasons (Table 1). During the wet season six species utilized the enriched waterhole, compared to nine during the dry season (Table 1). Namaqua Doves obtained a significantly ($t = -4.55$, d.f. = 9, $p = 0.004$) greater proportion (2.5-fold higher) of their total body water from the enriched waterhole during the dry summer season (Table 1). Similarly, although Scaly-feathered Finches showed low overall P% values (with the majority of trapped individuals not drinking), they also obtained a significantly ($t = -2.56$, d.f. = 4, $p = 0.043$) greater proportion of their body water pool (2-fold increase) from the enriched waterhole during the dry season (Table 1). During the dry season a greater proportion (6 of 17) Sociable Weavers utilized the enriched waterhole, and P% was greater (~ 4 fold) than in the single individual (one out of 19 individuals) that utilized the waterhole during the wet season. Violet-eared Waxbills were trapped around the enriched waterhole during the dry season only, and 9 out of 12 individuals obtained an average of 32.8 % of their body water pool from the latter resource.

Table 1. Percentage of the body water pool (P%) derived from the enriched waterhole in bird species during a wet- (February 2011) and dry (October 2011) period in summer at Tswalu Kalahari Reserve. Values in bold text indicate significant differences in P% between seasons (see text for statistics).

	Mean P% ± SD (# enriched/total):	
Species	Wet season (Feb 2011)	Dry season (Oct 2011)
Black-faced Waxbill *Estrilda erythronotos*		29.2 (1/1)
Cape Sparrow *Passer melanurus*		40.5 (2)
Cape Turtle-Dove *Streptopelia capicola*	57.7 (1/1)	
Golden-breasted Bunting *Emberiza flaviventris*		49.8 (1/1)
Southern Masked-Weaver *Ploceus velatus*	7.72 (1/6)	NA (0/3)
Namaqua Dove *Oena capensis*	**30.6±21.7 (5/7)**	**78.7±10.5 (6/6)**
Scaly-feathered Finch *Sporopipes squamifrons*	**3.95±2.47 (4/29)**	**8.60±2.69 (4/19)**
Sociable Weaver *Philetairus socius*	4.59 (1/19)	16.7±7.57 (6/17)
Violet-eared Waxbill *Granatina granatina*		32.8±17.0 (9/12)
White-browed Sparrow-Weaver *Plocepasser mahali*	5.15 (1/11)	92.9 (1/14)
Yellow Canary *Crithagra flaviventris*		63.4 (1/4)

Spatial water use

I summarized the number of individuals trapped and P% of those that drank for each species (most common drinkers and non-drinkers) as a function of distance from the enriched waterhole (Appendix E, Table E1). Namaqua Doves and Violet-eared Waxbills showed enriched P% values at most trapping sites, up to 2 km away from the enriched waterhole (Fig. 8). Small proportions of Scaly-feathered Finches, Sociable Weavers and White-browed Sparrow-Weavers individuals drank, and those trapped within 100 m of the enriched waterhole obtained on average a slightly greater proportion of their body water pool from the source (Fig. 8). For example, Sociable

Weavers trapped near the water hole obtained 17 % of their total body water from the source, compared to 9 % at 1.5 km and < 2 % at 2 km (Fig. 8). Scaly-feathered Finches showed a similar pattern, although a single individual trapped 2.4 km from the water hole obtained 7.6 % of its total body pool from the source, compared to 8.9 and 12.3 % in two individuals < 100 m from the waterhole (Appendix E, Table E1). Although a number of samples were obtained from insectivores within 100 m of the waterhole, none of these individuals used the waterhole (Appendix E, Table E1). I found a weak correlation between drinking frequency and P% in species ($r^2 = 0.35$, $F_{1,7} = 3.84$, $p = 0.091$); species that drank infrequently tended to have low P% but species that drank frequently showed more variable P% (Fig. 9).

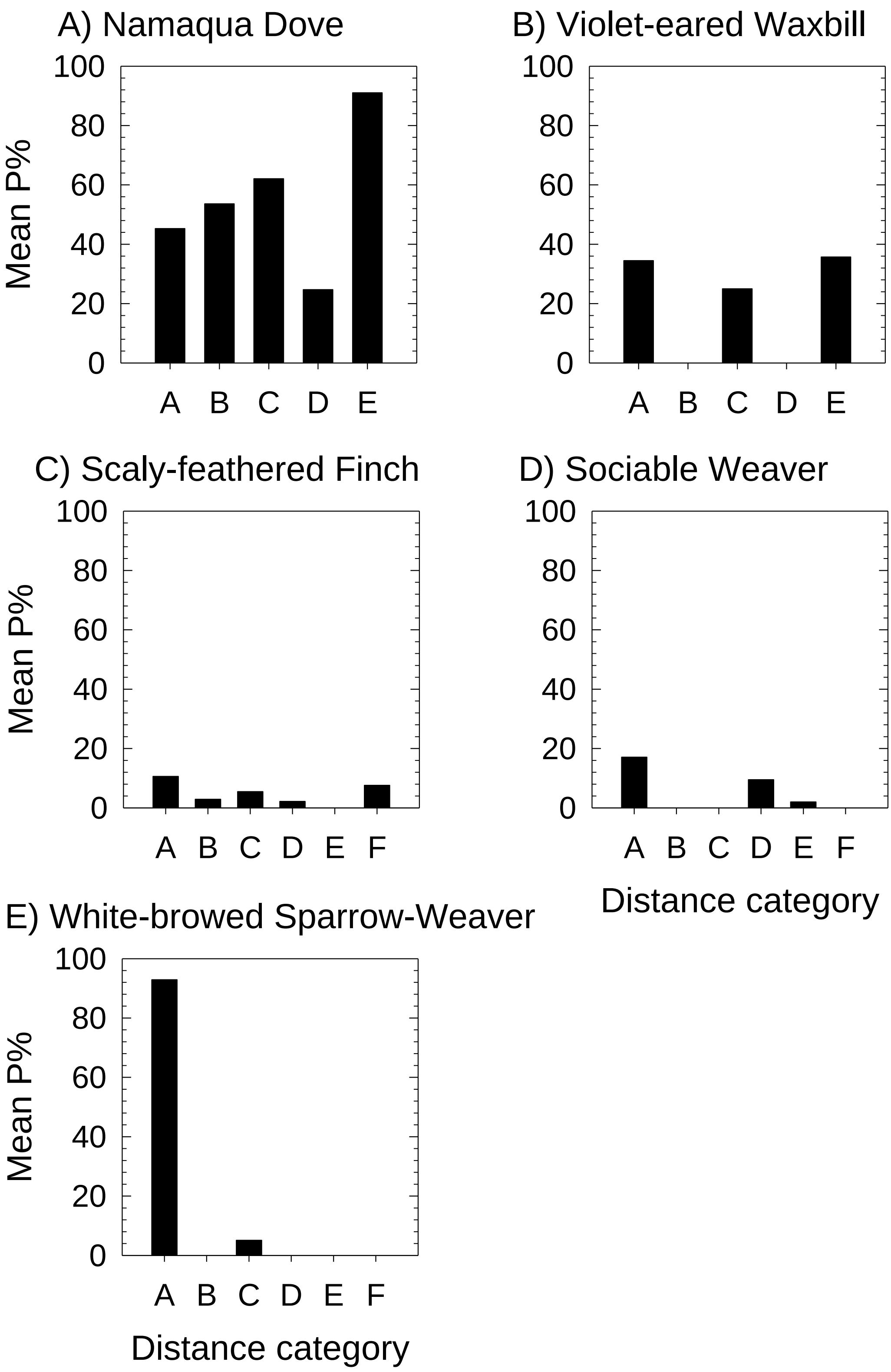

Figure 8: Mean proportion of body water pool derived from the enriched water source as a function of approximate distance (categories A-F) away from the water hole in six species at Tswalu Kalahari Reserve (A < 100m, B <500m, C < 1000m, D < 1500m, E < 2000m, F < 2500m).

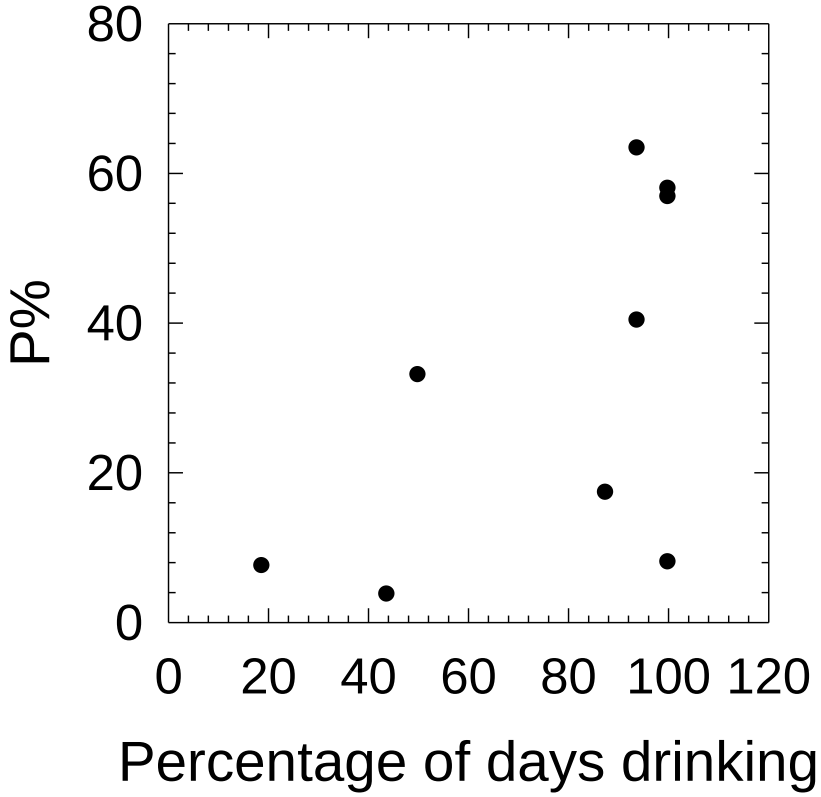

Figure 9: Mean proportion of body water pool derived (P%) from the enriched waterhole as a function drinking frequency (i.e. % of days observed drinking) in species observed drinking during summer at Tswalu Kalahari Reserve ($r^2 = 0.35$, $F_{1,7} = 3.84$, $p = 0.091$).

DISCUSSION

My data, based on two complimentary techniques, reveal that most species in the southern Kalahari are currently largely independent of drinking free-standing water. These data corroborate previous findings that relatively few species inhabiting arid regions of Africa and Australia depend on drinking water (Willoughby and Cade 1967, Fisher et al. 1972). I found that most species that visited waterholes to drink were granivorous, with only a few daily drinkers. Daily drinkers did not increase drinking on hot days (up to 37 °C). However, many species, including a few insectivores, drank mostly on the hotter days. Insectivores were greatly underrepresented at waterholes, despite my observations showing that this group dominated the avian community at TKR.

The most frequent drinkers (100 % of days) were Namaqua-, Laughing- and Cape Turtle Doves, Burchell's- and Namaqua Sandgrouse, and Southern Masked Weavers. Doves and sandgrouse are well known for travelling long distances to drinking water, and drinking represents an important component of daily time-activity budgets in these taxa (Cade and Maclean 1967, Lloyd, 2005a, 2005b). These species probably take in a surplus amount of water daily (i.e. more than is required for EWL and excretion) and this could explain why none of these showed higher drinking frequencies on hot days. However, one of the potential problems with observing drinking behaviour in the field is that I do not know how much water is taken in during each drinking event. Previous studies have investigated water intake in the laboratory as function the duration of single drinking event and tried to extrapolate these to individuals in the field (Smyth and Coulombe 1971). However such data will be limited to colour-ringed individuals and detailed laboratory calibrations for each drinking species.

Most of the frequently drinking species drank during the cool early morning hours. The advantage of this is that they are not exposed to high environmental temperatures around the water (which is often in full sun), and/or increased heat loads when flying to these sites. Second, they are better assured of maintaining an adequately hydrated state before the warmest part of the day. A few species do seem to drink throughout the day, with some showing a slight peak at midday, for example Violet-eared Waxbill. Namaqua Doves seem to be the only species in my study to focus drinking primarily around midday. The midday drinking pattern has previously been shown in Namaqua Doves (Rowan 1983), and they might be exposed to higher heat loads than other species when drinking. However, a number of Australian birds show the same pattern, for example, Diamond Dove (*Geopelia cuneata*), Spinifex Pigeon (*Geophaps plumifera*), Zebra Finch (*Poephila gutata*) are more frequently recoded drinking during midday (Fisher et al. 1972). I suggest a number of reasons for this drinking pattern, although they are highly speculative. First these species might be more dependent on surface water and opt to drink when evaporative water loss demands are likely highest; although in this case a stronger temperature-dependency of drinking patterns should have be seen in my study (discussed further below). Second, drinking during midday might be predator avoidance behaviour since predator activity levels might be lower during midday on account of high temperatures. Third, these species might allocate time during the morning and afternoon towards foraging further away from water, and subsequently move to the habitat around water points during midday where they rest in surrounding trees and drink. The habitat surrounding water points are often highly degraded of vegetation, i.e. piosphere effect, and birds might need to travel away from piospheres to forage where plant biomass and species diversity is higher (Tolsma et al. 1987). The latter seems most likely since Namaqua Doves spent most of their time resting in trees around waterholes during midday, and are found far away from water holes during other parts of the day (pers. observation).

Very few insectivorous and omnivorous species were observed drinking, and generally these drank in small numbers on warm days (Fig. 4B and Appendix D, Table D1). The numbers of individuals drinking were often so small that I could not reliably detect temperature-dependency of drinking behaviour. It is noteworthy that many of these occasional drinkers are very common in the Kalahari community (for example, Ant-eating Chat, White-browed Sparrow-Weaver, Common Fiscal) and the low drinking numbers suggest that only individuals, pairs or family groups occupying territories or home ranges around the waterhole drank on hot days. An interesting avenue for further study would be to investigate if individuals of these species occupying territories far from free-standing water, might be under pressure to take in more water rich food, and/or to increase foraging effort, to make up for evaporative water losses on hot days.

The finding that no species showed significant increases in drinking events with increases daily maximum air temperature is surprising, especially for the granivores which rely on food with a low water content and would be expected to supplement high rates of EWL on hot days by drinking. Whereas Fisher et al. (1972), showed that a number of Australian species do drink more on hot days, Williams and Koenig (1980) also found positive but non-significant relationships with increasing temperature. However, they have argued that the presence of a crop might be important in frequency of drinking events per day. For example doves and other seedeaters could potentially fill their crop with water during a single visit to the water. If birds are compensating their water intake on the basis of water demands or hydration state, drinking events will be less likely to correlate with water intake. This would make sense since trips to water might be costly in terms of energy and water expenditure and predation risk. Regular drinkers would therefore be expected to take in more water, rather than drinking more often (Williams and Koenig 1980). On the other hand, the number of hot days were few in my study and could be a major reason why I failed to detect a significant temperature dependency since in most species the inflection point at which EWL starts to increase is generally near 40 °C (~ avian T_b) (McKechnie and Wolf 2010). I also suspect that the fluctuation in abundance of nomadic species (e.g. Namaqua Dove, Violet-eared Waxbill, Larklike Bunting, Grey-backed Sparrow-lark, Red-headed Finch and Wattled Starling) at my study site could greatly confound temperature-dependency of drinking behaviours. For example, most of the above-mentioned species appeared to become more common towards the end of the sample period (pers. observation). To avoid nomadic behaviour confounding quantification of drinking dependency through observations would require longer-term data to take drought cycles into account.

I collected blood samples from 42 species along a 2.4 km transect radiating away from the enriched water hole, and found that only 11 of these species showed evidence of drinking at the waterhole. From the above, Namaqua Doves and Violet-eared Waxbills were the most frequently sampled species and both these obtained a substantial amount of their body water pool from the enriched waterhole (up to 2 km away from waterhole). Other species seemed to obtain larger proportions of their body water pool when they were trapped close to the water sources, and very little, to none far away (for example White-browed Sparrow-Weaver). Many species were commonly trapped both at the enriched waterhole and further away, and showed no evidence of drinking, which confirms my observation records for these species. For example, Fawn-coloured Lark, Marico Flycatcher, Chestnut-vented Titbabbler and Black-chested Prinia are common residents and showed no evidence of drinking (Appendix E, Table E1).

Previously the technique of isotope tracers in an environment has been employed to establish the importance of specific resources at species and community level. For example, this technique has been used before to show dependence of White-winged Doves on saguaro fruit as their water source during summer (Wolf and Martinez del Rio 2000). This method has also been used to show how White-winged Doves can obtain both water and energy from these fruits, whereas Mourning doves obtain mainly energy from the sources (Wolf et al. 2002). To the best of my knowledge the present study is the first to use the technique of artificially enriching a water source to establish drinking dependency in an avian community. This method provided valuable quantitative estimates of drinking dependency. For example direct observational data showed many species appeared to drink frequently, but this method suggested that the water source contributed little to their body water pool. However, this method has a number of limitations. Firstly, it can only be applied in an environment where free-standing water sources are scarce, and available water sources should have relatively low recharging rates (very low rainfall). Second, investigating the temperature-dependency of drinking behaviour is likely to be limited to behavioural observations since the stable isotope methods is conducted over a longer time frame making it difficult to directly link a bird's body water pool to daily weather conditions. However, for species that appear to increase drinking on hot days one could expect a correlation between P% and the maximum daily temperature 24hrs prior to sampling. Lastly, as already discussed above, applying this method to the community where most species are nomadic or on passing through on migration could be problematic since birds could obtain water from sources outside the study area.

Most of the species that showed evidence of drinking in their body water pool showed greater dependence on the enriched water source during the dry summer season, compared to the wet summer season. The enriched source accounted for a significantly greater proportion of the total body water pool in, Namaqua Dove and Scaly-feathered Finch, although these were the only two species in which samples sizes of drinking birds were large enough. Further, the number of individuals drinking (i.e. the proportion of birds with enriched levels) was higher during the dry summer in Namaqua Doves, Scaly-feathered Finches and Sociable Weavers. These patterns suggest that some species rely more on free-standing water during dry periods when the availability of water rich foods are lower. For example, after major rainfall events insect abundance appears to increase greatly and many species, for example, Sociable Weavers and Southern Masked Weavers could obtain most of their water from this source.

My findings from the spatial water use study corroborate my observations that granivores are most dependent on free-standing water. Although I could not obtain sufficient samples sizes from many key granivores, such as doves, sandgrouse and sparrows, all the species that obtained large proportions of their body water pool from the enriched sources are predominantly granivores. In most of these species, 30 % or more of their body water pool was derived from the enriched source. These numbers could in fact be higher since many of the granivores are highly mobile and likely to drink from other waterholes. This could explain the few Namaqua Doves, Laughing Doves and Yellow Canaries which did not show evidence of drinking.

Interestingly, Scaly-feathered Finch showed very limited dependence on free-standing water and did not obtain more than 12 % of their body water pool from the enriched source; most of these individuals showing evidence of drinking were caught close to the waterhole (Appendix E, Table E1). This species was also not observed drinking in the video recordings obtained during the study, although small numbers were observed drinking from the enriched reservoir during the stable isotope study. These patterns are strikingly different to those observed in other similar-sized granivores that showed strong dependency on free-standing water (Violet-eared and Black-faced Waxbills). Scaly-feathered Finches have been shown to survive without drinking water on a diet of dry seed, although it is not clear if these birds will be able to maintain body mass on hot days feeding on seed diet only (Cade 1965). However, Edmonds (1968) has shown that another small arid-zone granivore, the 18-g Cut-throat Finch (captive birds) can survive and maintain body mass on a diet of dry seed over many days when maximum temperature exceeds 40 °C. Scaly-feathered Finches inhabit hotter and drier regions of the Kalahari Desert than the Cut-throat Finch (Hockey et al. 2005), and it seems probable that the former species possesses similar physiological abilities. My data suggest that Scaly-feathered Finches are largely independent of drinking water, supporting previous qualitative observations of the drinking habits of this species (Irwin 1956, Prozesky 1963). Further, the δD and $\delta^{18}O$ ratios in the body water of Scaly-feathered Finches were depleted relative to those of small insectivores, suggesting that they were not obtaining a large proportion of their body water from insects, as the ratios were more depleted than in typical insectivores (ratios will be enriched in insectivores due to higher evaporation rates). Therefore, Scaly-feathered Finches probably obtained their water from a combination of seed and metabolic water.

A number of species were observed drinking surface water frequently, although their body water pools suggested that the waterhole contribute minimally to their daily water intake. For example, Southern Masked Weavers, Sociable Weavers and White-backed Mousebirds were frequently observed drinking at waterholes (observed drinking on 100, 80 and 56 % of days), but showed very low enrichment of deuterium levels in their blood; for example, % of body water pool derived from an enriched source were 7, 17 and 0 % for Southern Masked Weavers, Sociable Weavers and White-backed Mousebirds respectively. The above-mentioned species generally feed on food with high water content, e.g. insects and fruit, and could explain why the waterhole contributes very little to their body water pool. This could potentially explain the weak correlation between drinking frequency obtained through observations and dependence on free-standing water source obtained from blood samples (Fig. 9).

Two frugivores, African Red Eyed Bulbul and White-backed Mousebird, were observed to drink regularly, whereas Red-faced Mousebirds were represented less frequently at the waterhole. These frugivores are generally highly mobile in the Kalahari Desert, responding to local availability of fruit and rainfall (Herremans 2004). Red-eyed Bulbul, in particular, is considered a wet season visitor in the Kalahari and from my observations appears to be most dependent on surface water (although I failed to collect blood samples from this species). It is interesting that this species appears so dependent on surface water since its diet (fruit and insects) is high in water content. Drinking in mousebirds have previously been linked to fruit supply, with birds drinking mainly when fruit availability is low (Cade and Greenwald 1996). Although I observed mousebirds drinking in the video recordings, I did not obtain evidence from the blood samples that mousebirds drank. However, my observations were carried out a year after blood sampling, but in the same season and it are likely that the availability of fruit were different between these periods. Acacia Pied Barbet is the only frugivore that was never observed to drink during the study and sampled individuals also contained no enriched levels of deuterium. This is interesting since previous studies have suggested Acacia Pied Barbets are strongly associated with surface water sources (Nuttall 1997) and the increased availability of surface water in arid regions of southern Africa has been proposed to be a major contributing factor towards this species expanding its range (Macdonald 1985). In contrast, I found no evidence that Acacia Pied Barbet rely on free-standing water during summer and calling birds were often seen in the same localities over 3km from surface water sources (pers. observation).

Williams and Koenig (1980) suggested that free surface water is an important resource for birds resident in temperate oak woodland in California. Similarly, resident birds in the Sonoran Desert also seem to make extensive use of surface water (Lynn et al. 2006). In contrast, in my study the species that were most reliant on water (both in terms of drinking and body water pool) are very nomadic in the Kalahari Desert. With the exception of Namaqua and Burchell's Sandgrouse which are resident granivores, most Kalahari residents are insectivorous or omnivorous and my findings suggest that most of them are independent of drinking even on warm days. A reason for this could be that free-standing water would have been extremely rare in deep sands of the Kalahari Desert before agricultural practices. Species that colonised this region would have been under greater selection to become independent of drinking water, or alternatively fly great distances daily to water like sandgrouse do.

The findings of this study illustrate how two methods can be used to obtain complimentary data on drinking dependency in a desert bird community. Information on the temperature-dependency of drinking behaviour will be important for developing water and energy models and time-activity budget models for specific species. For instance, knowledge of whether species need to obtain their water through their food and by foraging, from metabolic water, or from drinking will be important in understanding how much time and energy an individual needs to invest to avoid dehydration on hot days. In summary, these data highlight that artificial waterholes are vital for only a few avian species, mainly granivores, in the Kalahari Desert. The majority of resident species (especially insectivores) are independent of drinking water, and obtained their water through food. However, many non-drinking species start drinking water on hot days, suggesting that these species might become more dependent on free-standing water when experiencing warmer weather.

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CHAPTER 4

THE EFFECTS OF TEMPERATURE ON HEAT DISSIPATION BEHAVIOUR RESPONSES IN KALAHARI DESERT BIRDS

ABSTRACT

Predicting variation in vulnerability to climate change for avian communities using mechanistic data is complicated, time consuming and expensive to undertake. Endotherms can respond to increases in temperature by complex behavioural and physiological and ecological responses. In this study I present methodology for quick and low cost assessment of heat dissipation responses as a proxy for vulnerability to heat stress in the Kalahari Desert avian community. Using data from 35 Kalahari Desert species, a phylogenetic independent analysis showed that activity levels, foraging ecology and body mass could play important roles in explaining heat-dissipation behaviours. Species that are highly active during the day, especially during hot weather (e.g. Acacia Pied Barbet and Red-eyed Bulbul), tend to show elevated levels of panting and gular fluttering at lower temperatures than species which spend most of the day inactive (e.g. sit-and-wait predators such as Common Fiscal and Lesser Grey Shrike). Larger species showed elevated heat-dissipation responses at lower temperatures compared to smaller birds, although this relationship only approached significance (p = 0.059). This could be likely the reason why larger species showed significantly lower activity levels than smaller species at high temperature. These findings support predictions that larger species need to avoid heat load during high temperatures since they have higher thermal inertia and are therefore less efficient at dissipating heat. The heat dissipation patterns observed in the Kalahari species might represent a trade-off between maintaining high activity levels to forage at high temperatures, and being exposed to an increased heat load and elevated demands for evaporative water loss.

INTRODUCTION

Climate change will lead to large-scale range shifts and increased extinction risk for many organisms worldwide. Understanding which species are most vulnerable to climate change has emerged as a major challenge for conservation biologists (McKechnie et al. 2012, Williams et al. 2008). Increases in temperature are of greatest concern as these could greatly affect fitness and survival rates. Although it has been predicted that species will vary in their sensitivity to increasing temperatures, which could lead to large scale changes in community composition, relatively little is known about what make some species more resilient than others.

Over the last decade vulnerability assessments have been dominated by the use of climate change envelope models (Jiguet et al. 2006, Thomas et al. 2004, Erasmus et al. 2002, Simmons et al. 2005). These models assume that geographical distributions of species are largely defined by climatic regions. Although these variables are often well correlated (Chambers et al. 2005), these analyses lack mechanistic value, i.e. they do not incorporate direct effects of temperature on the ecology of a species. Numerous studies have therefore started incorporating mechanistic links between organisms and their environments directly into these models using biophysical ecology theory (Helmuth et al. 2005, Fuller et al. 2010, Kearney et al. 2010). However, detailed data on behavioural and physiological responses, and the complex interactions between these, are lacking for most organisms, particularly endotherms. One of the major difficulties is that collecting detailed field-based physiological and behavioural data on every species, or population, is difficult and time-consuming.

The vulnerability of bird communities to global change has been a prime focus of many ecological studies, and as a taxon, birds are widely represented in climate envelope models (Sorte and Jetz 2010). With the realisation that the latter models are overly pattern-based, there has been a push towards a more mechanistic approach by incorporating direct physiological, behavioural and ecological responses to increasing temperatures (Boyles et al. 2011, McKechnie et al. 2012). McKechnie and Wolf (2010), for example, reviewed the temperature dependency of evaporative water loss (EWL) in birds and showed that birds will face decreasing survival times under future climate predictions during extremely hot weather due to dramatic increases in demands for evaporative cooling. Although these data are very useful for modelling resting evaporative water loss rates, it becomes expensive and time-consuming to obtain data for entire communities. Assessment of heat stress will be necessary in wild populations to understand the direct trade-offs species face between behavioural and physiological responses under increasing temperatures. Overall climate warming will not only result in an increase in frequency of record extremes, but average temperatures will become 3–5 °C higher (IPCC 2011). Whereas extremely high, record maximum temperatures are likely to cause acute heat stress and compromise short-term survival rates (McKechnie and Wolf 2010), an overall increase in average daily temperatures may result in more moderate but chronic heat stress, which could greatly affect the performances, such as foraging success, body condition and reproductive fitness of species. The increased likelihood of chronic heat stress has often been overlooked as a climate change threat to species. Arguably animals might experience these conditions more often than severe, acute heat stress under future warming scenarios.

Heat dissipation behaviour as a proxy for heat stress

During periods of high T_{air} that approach avian T_b, birds will experience increased heat loads, i.e. T_b will start to rise (Dawson, 1954; Dawson and Whittow, 2000), with heat generated through activity further elevating T_b (Bartholomew and Dawson, 1958; Bartholomew, 1972; Dawson and Hudson, 1970; Heinrich, 1977; Wilson and Grémillet, 1996). To prevent T_b from reaching lethal limits, birds increase EWL rates, through panting or gular fluttering, and/or cutaneously, to facilitate evaporative cooling (Calder and King, 1974; Dawson and Hudson, 1970; Dawson and Whittow, 2000). For example, in Chapter 1 I have shown that White-browed Sparrow-Weavers increase time spent panting significantly on hot days (see Fig. 6, Chapter 1), and this was further related to elevations in T_b above normal levels.

When birds spend more water on evaporative cooling, or on activity-related behaviour than they gain during the day (i.e. gained through preformed water, oxidative water or drinking) they risk dehydration. During hot temperatures when activity levels need to be kept at minimum to avoid heat load, birds will start to experience negative water balance (du Plessis et al. 2012). If birds experience chronic negative water balance, to such an extent that they undergo reductions in total body water, they should either increase water intake or make physiological adjustments to maintain blood plasma volumes. It has been argued that endogenous water production, largely through protein catabolism, can alleviate cellular dehydration and help conserve blood plasma volumes (Carmi et al. 1994, Gerson and Guglielmo 2011). This means that when birds are experiencing mismatches between water acquisition and expenditure, they are likely to lose body condition through the catabolism of stored body protein (see Gerson and Guglielmo 2011). These unfavourable physiological effects may be manifested at mild to warm temperatures that are below avian T_b, i.e. 30—40 °C. For example, a conservative estimate of daily water acquisition and expenditure rates suggested that on days above 35 °C, the majority of White-browed Sparrow-Weavers' (*Plocepasser mahali*) daily water intake (which generally depends on preformed water intake through foraging) might be spent on resting EWL (Chapter 2). On days when maximum T_{air} exceeds 42 °C, the entire daily water intake of these birds would need to be allocated to resting EWL. These mismatches could then result in rapid deterioration of lean mass and body condition if birds maintain foraging efforts at these high temperatures. Pied Babblers (*Turdoides bicolour*), for example, maintain foraging effort at high temperatures, but experience a marked reduction in foraging success, largely attributed to increased time spent panting while attempting to search for food (du Plessis et al. 2012). In Pied Babblers, reduced foraging efficiency has repercussions for the individuals' body condition and their chance of future breeding opportunities (Ridley et al. 2008, Ridley and Raihani 2007). Moreover, failure to maintain body condition during summer periods will significantly reduce the chances of surviving cold dry winter periods when the birds are experiencing their greatest energetic bottlenecks (personal comm. A.R. Ridley).

The cost of behavioural activity, such as foraging under warm conditions and heat dissipation, is central to the demands of regulating a relatively constant body temperature (T_b) over a narrow range. A great deal of these costs could be alleviated if birds relax thermoregulatory demands (Chapter 1), i.e. express temporal heterothermy (Boyles et al. 2011). All endotherms should express some form of variation in T_b regulation, depending on the various energetic and ecological costs associated with maintaining a relatively stable T_b (Angilletta et al. 2010). This variation is often quantified along a thermal generalist-specialist continuum [see Boyles et al. (2011)]. When considering the magnitude of T_b variation above normal set-point levels, thermal specialists can be defined as showing limited deviations in T_b above normal levels, whereas thermal generalists are more likely express a more labile T_b with greater deviations from normal levels (Fig. 1). These respective ends of the continuum could present very different challenges in terms of water requirements and the costs of behavioural decisions in endotherms. Whereas thermal specialists would arguably experience higher evaporative water loss costs and be more at risk of dehydration, regulating a T_b closer to normal levels will optimize performance and a reduce the risk of reaching a lethal body temperature (Fig. 1). Birds can therefore maintain high levels of activity under warm conditions at the costs of elevated water demands. In contrast, thermal generalists would cut down on evaporative water losses if they relax thermoregulation (Fig. 1), but this can result in reduced performance, constrained activity levels and a greater risk of reaching lethal T_b limits at high temperatures.

Body mass should, theoretically, also play an important role in interspecific variation in heat stress sensitivity (McKechnie and Wolf 2010). Large birds generally initiate heat dissipation responses at lower temperatures (i.e. these birds have a lower upper critical limit of thermoneutrality for heat dissipation behaviours) than smaller birds (Weathers 1981). Small birds have high mass-specific metabolic rates (resulting in high rates of heat production and increased rates of respiratory water loss), low thermal inertia and a limited capacity for water storage (Dawson 1982, Dawson 1976, Wolf and Walsberg

1996). Together, these factors suggest that small birds should minimize evaporative water loss when temperatures are high (Wolf 2000). Small birds thus appear to rely more on a large T_b – T_e gradients to dissipate heat via non-evaporative pathways (Weathers 1981). Larger birds, on the other hand, have a higher thermal inertia due to a smaller surface area to volume ratio and would consequently need to devote more time and resources towards heat dissipation to prevent excessive heat load (Weathers 1981). Very little is known about the effects of temperature on behavioural responses in free-ranging birds and how these vary with drinking dependency and body mass (Tieleman and Williams 2002b). Because large birds initiate heat dissipation behaviours at lower temperatures than small birds, the time they allocate to foraging and maintenance behaviours might more constrained by temperature (Weathers 1981).

In this chapter I tested the predictions that heat dissipation behaviours expressed by free-living birds in the Kalahari Desert could be indicative of thermal trade-offs between activity-related demands for foraging and costs of evaporative cooling. I expected that birds which have to allocate greater fractions of their time budgets to foraging will be have elevated heat dissipation costs during hot weather, manifested as more frequent expression of heat dissipation behaviours. In this study I aim to show how assessments of variation in heat dissipation patterns at a community level could provide a framework for assessing vulnerability to heat stress and identifying which species are most sensitive to heat stress.

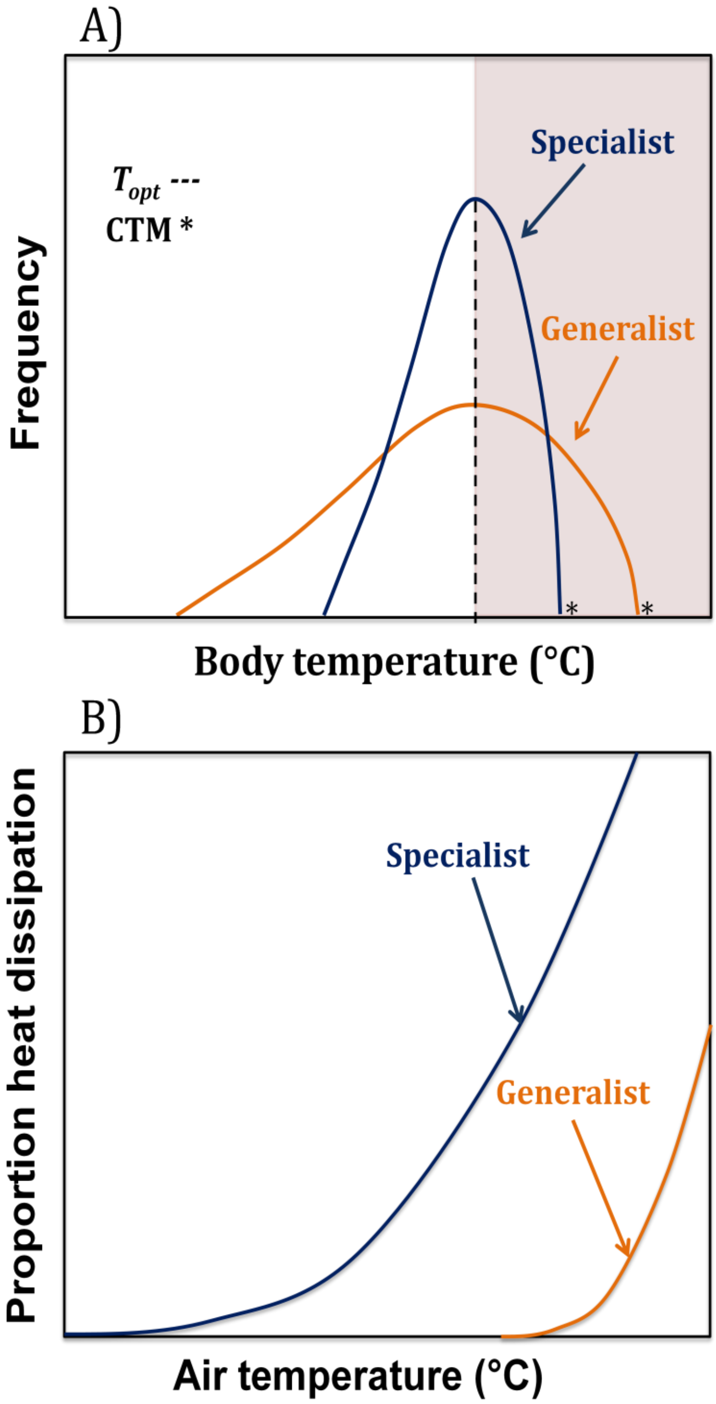

Figure 1: A) Thermal specialist and generalist thermoregulatory patterns adopted from Boyles et al. (2011). The shaded area represent T_b above modal or optimal T_b. Thermal specialist differ from thermal generalist in that T_b shows greater elevation above normal levels, i.e. facultative hyperthermia. B) These alternative thermoregulatory patterns differ primarily in their demands for evaporative cooling. Regulating a T_b within a narrow range, and avoiding large bouts of hyperthermia will elevate evaporative water loss in thermal specialist when they experience increased heat load, either through elevated activity of exposure to high temperatures. Thermal specialist will therefore elevate heat dissipation behaviour at lower temperatures than thermal generalists.

METHODS AND MATERIALS

Study sites

I obtained 5268 behavioural observations of the bird community at Tswalu Kalahari Reserve (TKR), Northern Cape Province, South Africa, during the austral summer, from November 2009 till March 2010 (~1100 m a.s.l. S2719', E2225'). TKR covers approximately 100 000 ha of semi-arid Kalahari savanna on vegetated red sand dunes. Mean annual rainfall over a 30-year period at TKR was 295 ± 172 mm (coefficient of variation, CV = 58.3%) (unpublished data, Tswalu Kalahari Reserve). Weather data were obtained during the study using a portable weather station (Vantage Pro2, Davis Instruments, Hayward, CA), set 2 m above the ground at a central location in the study site (see previous chapters). In the analyses I included behavioural observations (heat dissipation data only) obtained in a similar manner at TKR during the summer of 2010/2011 by R.O. Martin and S.J. Cunningham (n = 6814, total of 3 observers, collected between 11:00 and 16:00). I also included heat dissipation data (n = 2211) obtained from a drier site, Dreghorn Game Ranch (Louw 2011). A small number of observations (n = 65) collected by T. Flower at Kuruman River Reserve were also included for a few target species (e.g. Crimson-breasted Shrike). These data were pooled to obtain estimate of heat-dissipation responses from species (although observations linked to high humdities were excluded; see below). I also investigated variation in heat dissipation between sites and years at intraspecific levels, comparing subsets of the data across similar periods (see below).

Behavioural observations were conducted during the warmer part of the day (approximately from 10h00 to 18h00, with the exception of 2010/2011 data at TKR which were collected between 10h00 and 16h00) where bird behaviour is most likely to be affected by temperature. Sites for observations were selected at random within the landscape at TKR and within each site birds were searched for over a period of 30 minutes to one hour. Sites were separated by approximately 500 m, and were a minimum of 500 m from the nearest surface water source. All sites were in *Acacia*-dominated savanna or woodlands (either red dunes substrate or fossil river bed) and the Korannaberg mountain range at TKR was not sampled, since this habitat supports a different bird community (personal observation).

During observation periods each bird seen was identified to species level, and activity state (mobile/stationary), general behaviour (foraging, resting/scanning, preening, calling, nest maintenance or breeding related activity) recorded for approximately 30 seconds; this allowed adequate time to assess the above behaviour (Louw 2011). Foraging behaviour included 1) running on the ground with intermittent stops to inspect grass-tufts, bushes or plant litter for insects or seeds, pecking at insects, and digging in the ground or plant litter for food, for the terrestrial gleaners; 2) hopping/climbing within a tree or shrub among leaves or crawling along branches while searching for insects or fruit, for arboreal gleaners; and 3) under-taking short flights from a perch to either grab prey in the air (sally) or ground (pounce). Resting or scanning behaviour included perching on the ground, vegetation or an elevated post: individuals often scanned their surroundings (probably vigilance behaviour), preened, or communicated vocally with group members at this time.

I recorded whether each individual was engaged in heat dissipation behaviour (HDB) during any of the above-mentioned activities, i.e. panting (defined as gaping when breathing), or gular fluttering. The latter two behaviours are important and well-documented respiratory heat dissipation behaviours (Dawson and Hudson 1970, Bartholomew and Dawson 1979) and were easily observable in the field. I also recorded whether the birds were wing-spreading (a.k.a. wing drooping), which is defined as lifting the shoulder away from body. Although the precise function of this behaviour is not fully understood it appears to facilitate air-flow over the under-wing, which could increase passive heat loss by exposing thermal windows. However, because of the uncertainty of the potential benefits and costs of wing-spreading behaviour I focussed statistical analyses on respiratory heat-dissipation behaviours—which I expected to be tightly linked to EWL.

With the exception of ambush flights (sallying or pouncing), birds in flight were not recorded, and aerial foragers, such as swifts and swallows, were excluded from the study. Birds were not recorded if their behaviour appeared to have been altered by the presence of the observer, or if the bird was observable for too short a time for behaviours to be determined with certainty. If more than one individual of the same species was encountered and it was considered that the behaviour of each individual was not independent of the other birds in the group (e.g. they are foraging together as a flock) then a judgement of the predominant behaviour of the group was made. In the majority of cases this was not possible (e.g. if there was a pair and each individual was in a different microsite), and in such cases an individual was selected at random.

Statistical analyses

Dreghorn Game Ranch is in close proximity to Wildsgenot Game Ranch (referred to as desert site in Chapter 1 and 2), and provided me with the opportunity to test if HDB showed intraspecific differences between semi-desert and desert sites—similar to the behavioural and physiological differences I observed in White-browed Sparrow-Weavers between the desert and semi-desert site (Chapter 1 and 2). I compared data collected from November to December 2009 at TKR to data collected over the same period at DGR (Louw 2011). Over these two periods TKR and DGR showed similar weather data (Max T_{air} was 34.5 ± 3.4 and 34.6 ± 3.6 °C, mean dew-point was 4.5 ± 6.3 and 3.7 ±7.4 °C, and rainfall was 83.8 and 21.3 mm, respectively for TKR and DGR). I tested for a difference in HDB patterns between these sites only for species that had similar sample sizes over a range of T_{air} recorded. Many species showed comparable sample sizes, but the frequency of HDB was too low at DGR for statistical analyses. Statistical analyses comparing heat dissipation patterns between sites were therefore performed only for White-browed Sparrow-Weavers. Similarly, I compared heat dissipation patterns in White-browed Sparrow-Weavers between the 2009 and the 2010 seasons (November to December) at TKR. During the 2010 season, TKR experienced less rain (24.6 mm; most of which fell towards late December), slightly cooler Max T_{air} (33.0 ± 3.9 °C) and lower dew-point temperatures (1.1 ± 3.6 °C).

I performed logistic regression analyses in R to investigate the effects of T_{air} on heat dissipation (i.e. presence or absence of heat dissipation) in each species separately, using family quasibinomial since most models showed over-dispersion. Although I expected humidity to play an important role in heat stress it could not it be investigated fully since there was not enough variation in ambient humidity across the T_{air} range (see Chapter 1). From visual inspection it seemed likely that incidences of HDB recorded at low T_{air} (< 30 °C) were explained by low vapour pressure deficits (dew-point temperature above 15 °C). To prevent humidity from over estimating HDB responses, that i.e. lower HD_{start} temperatures, I excluded all data collected on days when ambient humidity levels exceeded dew-point temperatures of 15°C; only 7681 observations were therefore considered for statistical analyses.

Logistic regression analyses were generally performed on species for which I obtained more than 30 observations. However, I did perform analyses on species for which I obtained fewer observations if they were observed over a wide range in T_{air}. If a species did not show at least three incidences of heat dissipation I did not perform logistic regressions. In total I could obtain logistic regression estimates from 35 species. I obtained coefficients from each logistic regression models and these were used to estimate for each species 1) the T_{air} where HD was initiated (i.e. HD_{start}), 2) the temperature at which the probability of HD reached 50% (i.e. HD_{50}), and 3) the rate of change between HD_{start} and HD_{50} (see Fig. 2). HD_{start} was estimated as the T_{air} at which the probability of HD exceeds 5%. HD_{50} values were calculated as the intercept value (absolute) divided by beta value (absolute); the HD_{50} value also represents the maximum rate at which HD increases with temperature.

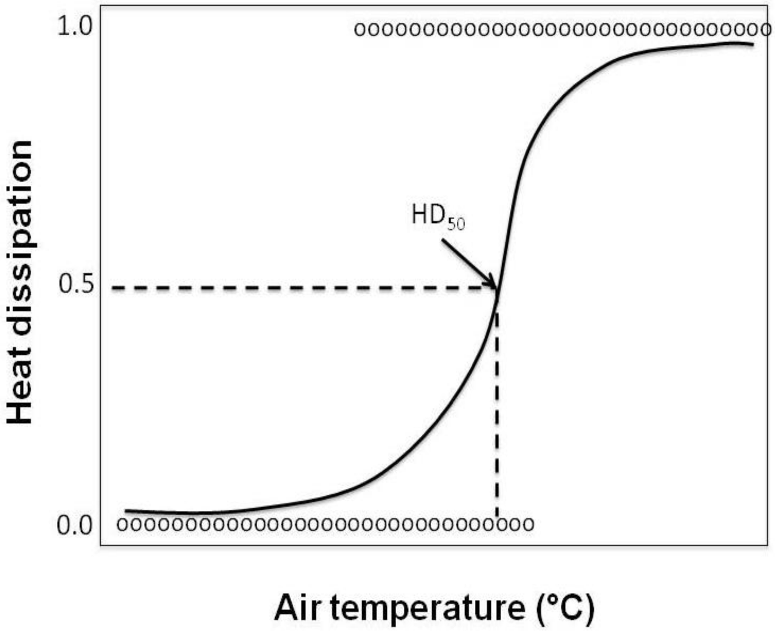

Figure 2: A representation the heat dissipation behaviour (present = 1, or absent = 0) as a function of air temperature. The trendline represents the logistic prediction of the proportion time engaged in heat dissipation behaviour. HD_{start} refers the temperature at which a species is likely to start heat dissipation, i.e. showing heat dissipation more than 5% of time. HD_{50} is the temperature at which the probability of heat dissipation behaviour is 50%.

I obtained predictions of the proportion of time the above-mentioned 30 species will be active at 29 °C and 39 °C using the coefficients of the proportion activity vs. T_{air} models. I then performed a phylogenetic regression analyses (PGLS) in R, using *ape* (Paradis et al. 2013) and *caper* (Orme et al. 2013) packages, to test the relationship between activity levels and body mass, and whether the latter two variables could explain HD_{50}. I sampled 100 phylogenies for the 35 species in my data set from http://www.birdtree.org (Jetz et al. 2012) using the Hackett et al., (2008) phylogeny as back-bone. I used the majority consensus tree identified using the programme Mesquite (Maddison and Maddison 2011).

Both lambda and kappa branch length transformations were carried out and the one with the lowest AIC score was used for subsequent analyses. In general, lambda branch length transformation gave confidence interval bounds around the lambda (λ) value that were too large to infer the phylogenetic signal. AIC values were also generally similar (< 2) and kappa branch length transformations and therefore kappa models are presented. I used the null-models of each trait to establish phylogenetic signal. Whereas strong phylogenetic signals were detected for temperature-dependent activity levels (Proportion active at 39 °C: $K = 0.785$, $p < 0.001$; proportion active at 29 °C: $K = 0.928$, $p < 0.001$) and log body mass ($K = 0.668$, $p < 0.13$), HD_{50} showed no phylogenetic signal ($K = 0.203$, $p = 0.545$). I also established the main foraging guild and dominant diet of each species following Hockey et al (2005), and the main source of water intake (i.e. pre-formed water or drinking) following data obtained in Chapter 3. All these factors could not be included in a full model and each factor was therefore analysed separately.

RESULTS

General patterns of heat dissipation

The majority of birds started showing increased levels of heat dissipation at T_{air} between 30 and 40°C (see Appendix F, Table F1 for summary of all species observed). The initiation of HDB and the rate of increasing HDB as a function of temperature varied widely among species (see examples in Fig. 3). Although heat dissipation behaviour increased with increasing air temperature, these relationships were only significant in 78% of the species (Appendix Table F2). Both Acacia Pied Barbets and White-browed Sparrow-Weavers are examples of species that commenced HDB at T_{air} below 30 °C, but varied in the rate at which HDB increased with increasing T_{air}; the latter species showed a much slower increase (Fig. 3A,E). Similarly, Scaly-feathered Finch and Ant-eating Chat are examples of species that had very different rates in their HDB responses to increasing T_{air}, despite both species only starting to increase HDB levels at T_{air} above 35 °C (Fig. 3C,F). In contrast, White-backed Mousebirds showed one of the most rapid increases in HDB on hot days despite starting HDB at low T_{air} (Fig. 3B). Many species showed very low levels of HDB (e.g. Namaqua Dove, Fig. 3D), and a number of species (e.g. Red-crested Korhaan and Pririt Batis) showed HDB so seldom (heat dissipation $n < 2$), despite being encountered frequently during the study ($N > 50$) (Appendix F, Table F1). The initiation of panting (i.e. > 5% of observations heat dissipating, HD_{start}) varied from 25.4–37.7 °C in 35 species. These were often slightly higher than the coolest incidence of heat dissipation (Appendix F, Table F1). HD_{50} values ranged from 34.3–55.6 °C.

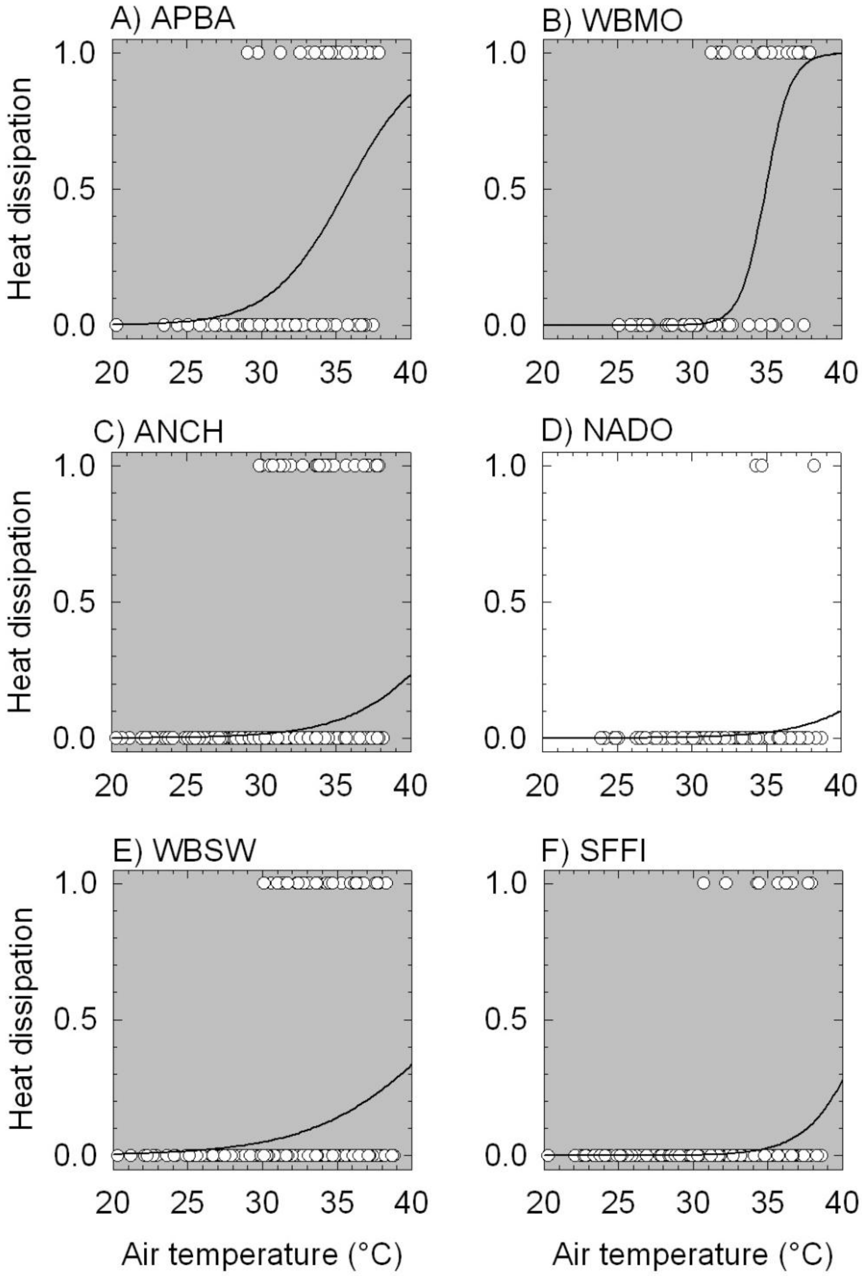

Figure 3: Heat dissipation (presence = 1, absence = 0) as a function of air temperature in six species in the Kalahari Desert; A) Acacia Pied Barbet (APBA), B) White-backed Mousebird (WBMO), C) Ant-eating Chat (ANCH), D) Namaqua Dove (NADO), E) White-browed Sparrow-Weaver (WBSW), F) Scaly-feathered Finch (SFFI). The logistic regressions represent predicted proportion of heat dissipation behaviour. The coefficient for the logistic regression of each species (35 in total) was used to estimate HD_{start} and HD_{50} values. Significant ($p < 0.05$) relationships are indicated by grey panels.

General activity patterns

The temperature dependency of activity patterns varied widely among species (Fig. 4). Very few species showed significant reductions in activity levels at hot temperatures—most showed only slight reductions (Appendix F, Table F2). For example, predicted changes in activity levels from 29 °C to 39 °C ranged from ~ 67 % to ~ 41 % of time in Acacia Pied Barbet (not significant), ~ 13 % to ~ 6% of time in Ant-eating Chat (not significant), and 48 % to ~ 16 % of time in White-browed Sparrow-Weavers (significant) (Fig. 4). For the majority of species activity was dedicated to foraging behaviour and on average 80% of activity behaviour was allocated to foraging (Appendix F, Table F2). There was a strong correlation between activity levels at mild temperatures (29 °C) and activity levels at hot temperatures (39 °C) (Pearson's Correlation Coefficient = 0.830). Species showing high levels of activity at mild temperature also showed high levels of activity at hot temperatures, although the proportion of activity was on average reduced by 10–20% at hot temperatures (Fig. 5). Because of this high degree of correlation in behaviour between mild (T_{air} = 29 °C) and hot (39 °C) temperatures I present analyses for hot temperatures only.

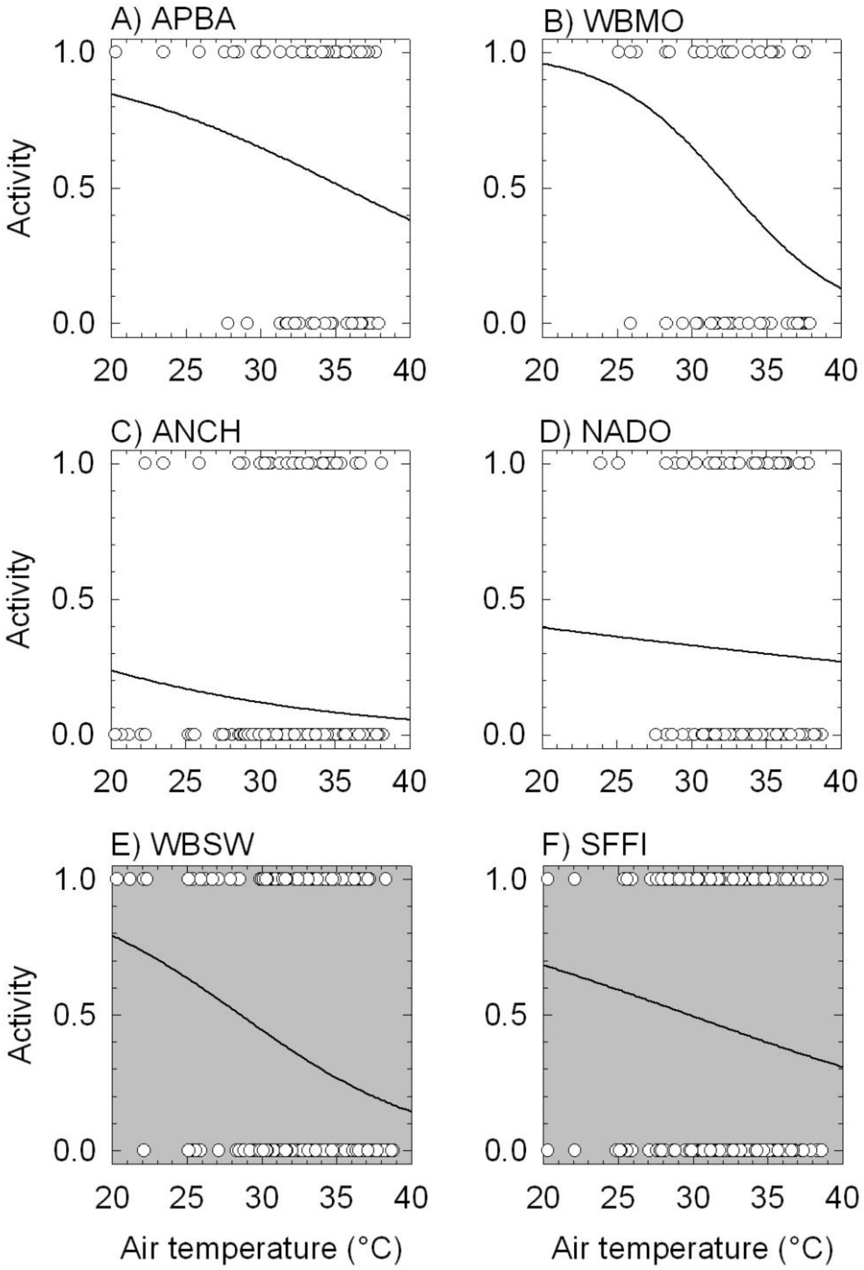

Figure 4: Activity levels (mobile = 1, stationary = 0) as a function of air temperature in six species in the Kalahari Desert; A) Acacia Pied Barbet (APBA), B) White-backed Mousebird (WBMO), C) Ant-eating Chat (ANCH), D) Namaqua Dove (NADO), E) White-browed Sparrow-Weaver (WBSW), F) Scaly-feathered Finch (SFFI). The logistic regressions represent predicted proportion of heat dissipation behaviour. The coefficient for the logistic regression of each species (35 in total) was used to estimate the proportion time spent active at a mild (T_{air} = 29 °C) and hot (39 °C) temperature. Significant ($p < 0.05$) relationships are indicated by grey panels.

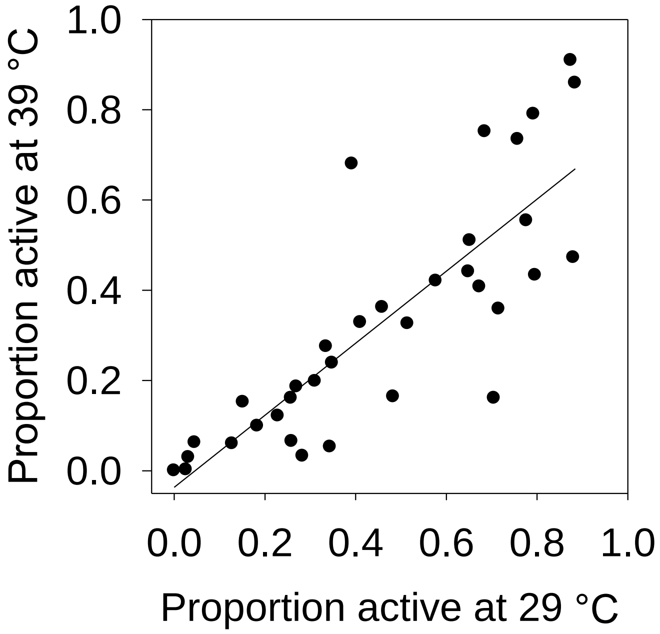

Figure 5: The relationship between proportion time spent active at mild (T_{air} = 29 °C) and hot (39 °C) temperatures. The trendline represents a significant correlation (Pearson's Correlation Coefficient = 0.83).

Body mass ($LogM_b$) was significantly related to activity levels at hot temperatures (39 °C) (Fig. 6A), and larger species showed the lowest activity levels (PGLS: activity at 39 °C, $t_{2,32}$ = -3.833, p < 0.001). Activity levels did not vary significantly as a function of the dominant water source of species (PGLS: $F_{2,32}$ = 0.046, p = 0.955), and non-drinkers showed large variation in activity levels (Fig. 6B). Similarly, activity levels did not vary significantly with diet (PGLS: $F_{5,29}$ = 0.7565, p = 0.588) (Fig. 6C). However, activity levels varied significantly with foraging guild (PGLS: $F_{3,31}$ = 12.97, p < 0.001); sit and wait predators showed the lowest activity levels at high temperatures whereas arboreal gleaners maintained high activity levels (Fig. 6D).

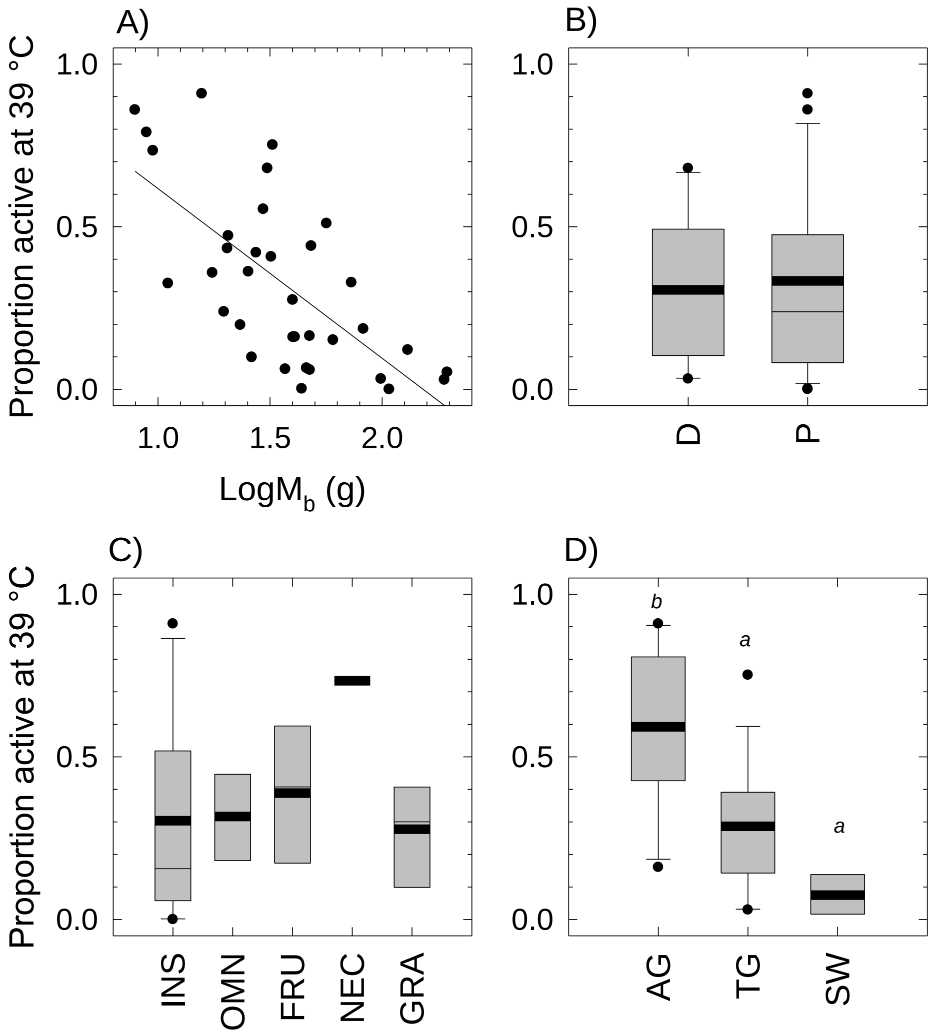

Figure 6: Predicted activity levels for 35 species in the Kalahari Desert at hot temperatures (39 °C) as a function of A) body mass (M_b), B) water source (D = drinking, P = pre-formed water), C) diet (OMN = omnivore, GRA = granivore, INS = insectivore, FRU = frugivore, NEC = nectarivore) and foraging location (TG = terrestrial gleaner, AG = arboreal gleaner, SW = sit and wait predator). Symbols indicate significance at 0.05 level using a Tukey HSD significance test. Mean is indicated by bold line, median by thin line, lower and upper bounds of box represent 25 and 75% percentiles, and upper and lower caps of whiskers represent 10 and 90% percentiles (outliers are indicated by black dots).

Interspecific variation in HD_{50}

HD_{50} values were significantly, negatively related to activity levels at 39 °C (PGLS: $t_{3,31}$ = -3.026, $p < 0.01$) (Fig. 7). Species with high activity levels therefore showed low HD_{50} values, and vice versa (Fig. 7). HD_{50} values were also lower for larger birds (Fig. 8A), although the relationship between HD_{50} and

$\log M_b$ only approached significance (PGLS: $t_{3,31} = -1.961$, $p = 0.059$). Mean HD_{50} values were 38.3 ± 3.7 °C in drinking birds compared to 41.9 ± 5.7 °C in non-drinking birds (Fig. 8B), although this was not highly significant (PGLS: $F_{2,32} = 3.373$, $p = 0.047$). HD_{50} values did not vary significantly with diet (PGLS: $F_{5,29} = 2.296$, $p = 0.071$); however, five frugivores all had consistently lower HD_{50} values (35.3 ± 1.1 °C), compared to other dietary groups (Fig. 8C). Insectivores had the highest HD_{50} values (43.1 ± 5.8 °C) (Fig. 8C). HD_{50} values varied significantly with foraging guild (PGLS: $F_{3,31} = 5.849$, $p < 0.01$). HD_{50} values were 45.8 ± 5.4 °C in sit-and-wait predators, compared to 40.6 ± 5.1 °C for terrestrial gleaners, and 37.4 ± 2.6 °C for arboreal gleaners (Fig. 8D).

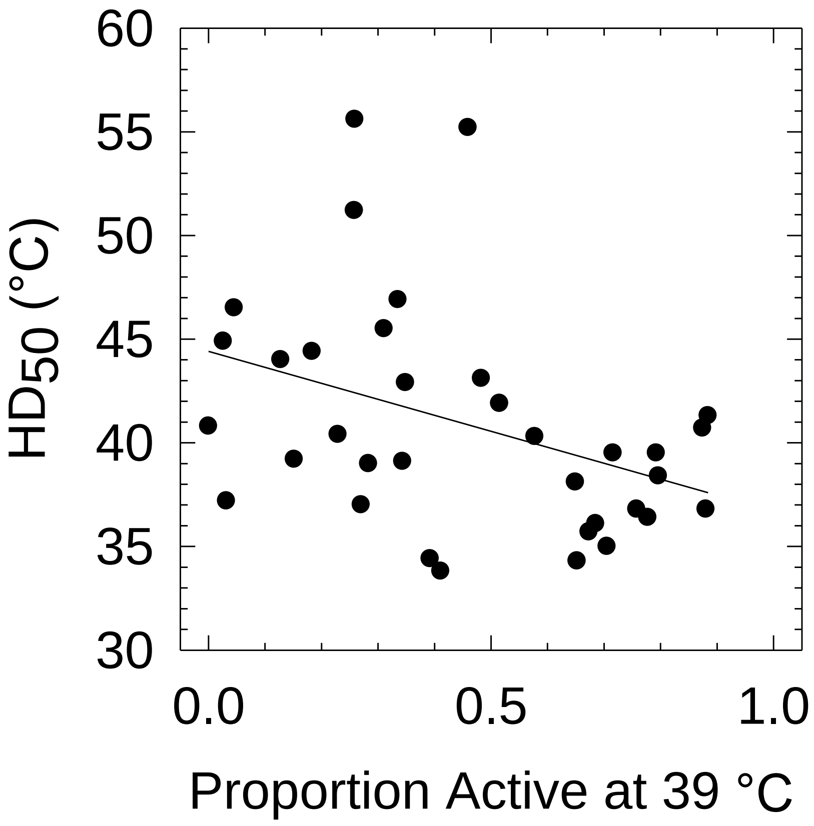

Figure 7: HD_{50} values of 35 species in the Kalahari Desert as a function of predicted proportion of activity at hot temperatures (39 °C). The trendline indicates a significant relationship ($p < 0.05$).

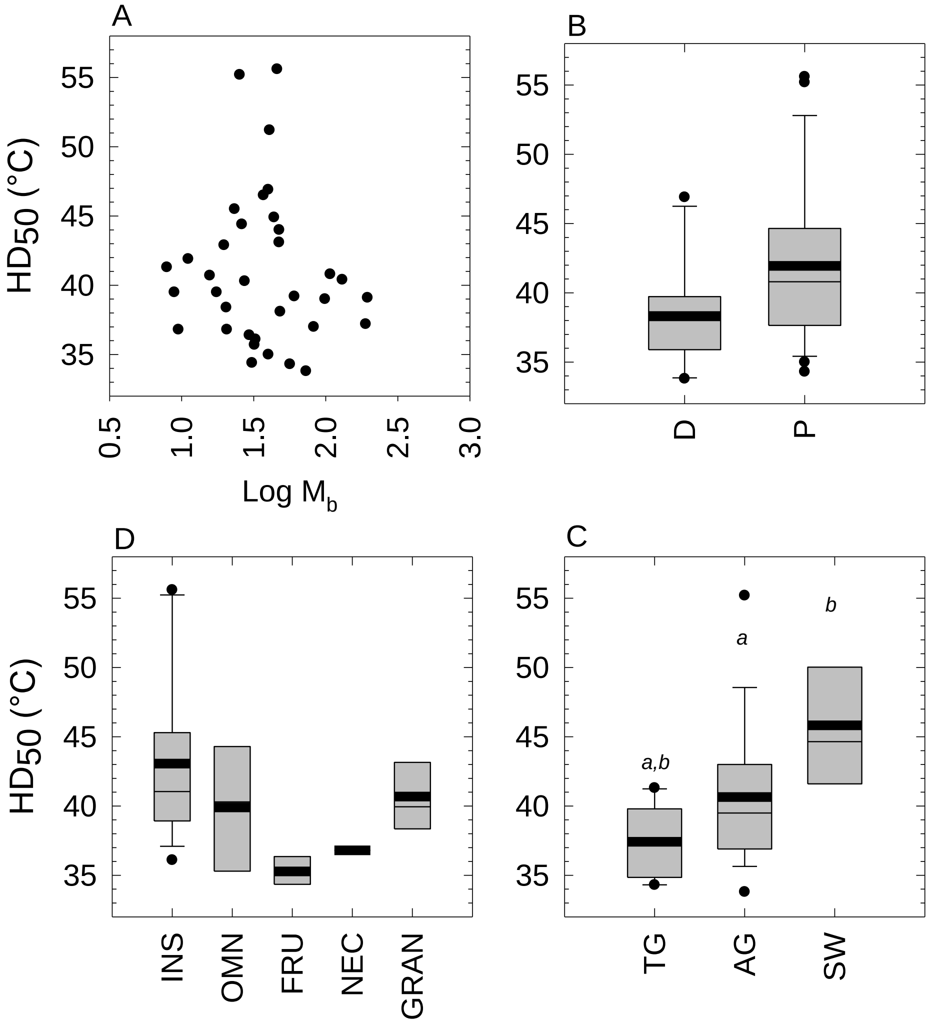

Figure 8: HD$_{50}$ values of 35 species as a function of A) body mass (M$_b$), B) water source (D = drinking, P = pre-formed), C) diet (OMN = omnivore, GRA = granivore, INS = insectivore, FRU = frugivore, NEC = nectarivore), and D) foraging location (AG$_a$ = arboreal gleaner, TG$_{a,b}$ = terrestrial gleaner, SW$_b$ = sit & wait predator. Symbols indicate significance at $p< 0.05$, using a Tukey HSD significance test. Mean is indicated by bold line, median by thin line, lower and upper bounds of box represent 25 and 75% percentiles, and upper and lower caps of whiskers represent 10 and 90% percentiles (outliers are indicated by black dots).

Intraspecific variation in heat dissipation

White-browed Sparrow-Weavers in during the wet summer in TKR (semi-desert site, n = 174) showed lower HD$_{50}$ values than sparrow-weavers in DGR (desert site, n = 99) (Fig. 9A,C). HD$_{50}$ was 38.6 °C at the semi-desert site compared to 42.9°C at the desert site. However, panting responses also varied between summers at TKR (Fig. 9A,B). White-browed Sparrow-Weavers panted often at

T_{air} above 30 °C at TKR during November to December 2009, but were never observed to pant the following year (n = 133) over a similar temperature range.

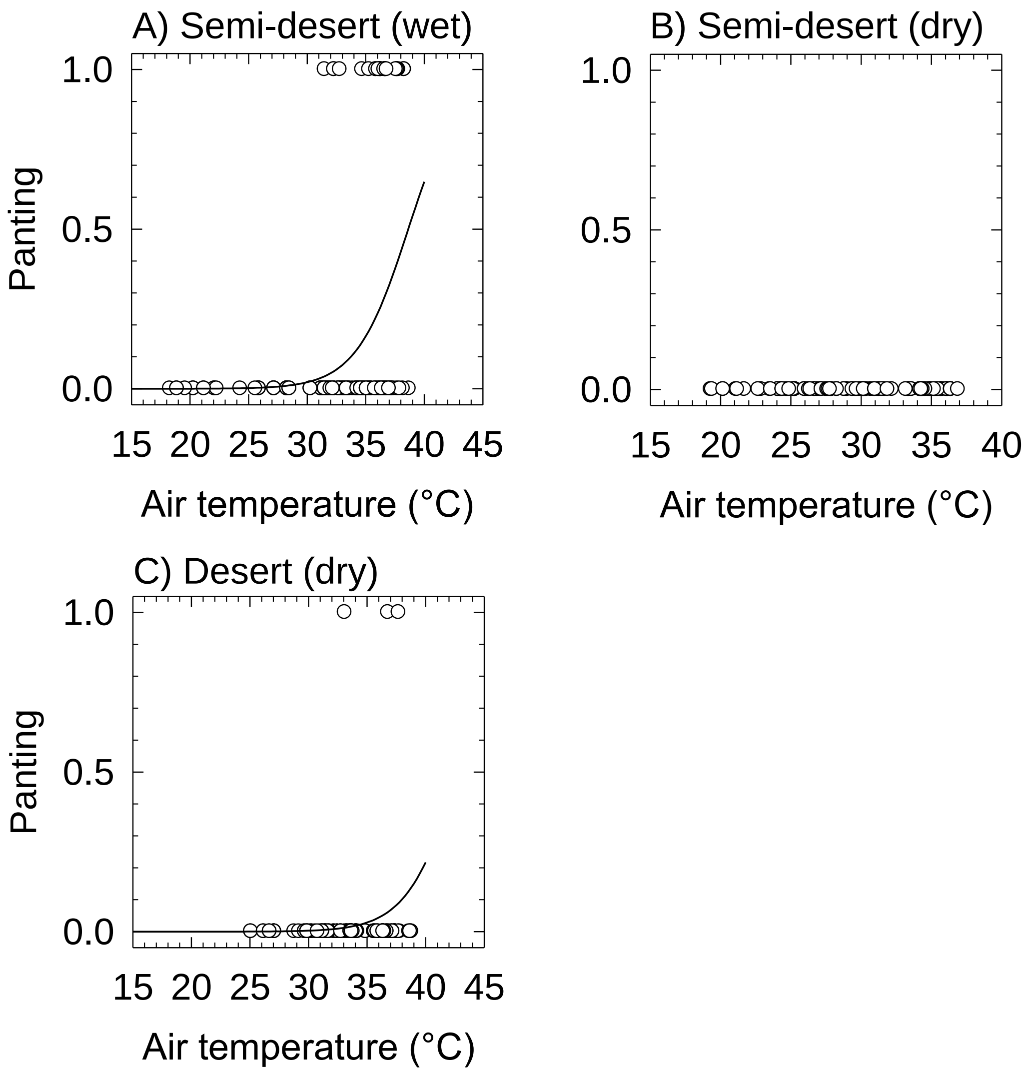

Figure 9: Heat dissipation (panting: presence = 1, absence = 0) as a function of air temperature in White-browed Sparrow-Weavers (Plocepasser mahali) at A) during a wet (November to December 2009), B) a dry early-summer (Nov to Dec 2010) at Tswalu Kalahari Reserve (semi-desert site), and C) normal early-summer (Nov to Dec 2010) at Dreghorn Game Ranch (desert site). The trendlines represent predicted proportion of heat dissipation behaviour.

DISCUSSION

My findings reveal considerable variation in heat dissipation responses to T_{air} between species. This variation was manifested by HD_{50} values ranging over a

20 °C range of T_{air}, and this diversity in pattern could be indicative of variation in sensitivity to heat stress. Although elucidating the ecological drivers of variation in heat dissipation patterns is complicated, my data suggests that general activity levels (i.e. time spent active), body size and foraging ecology (diet, mode and location) could play an important role in heat dissipation behaviour under natural conditions. However, it is noteworthy that the role of humidity in HDB could not be assessed fully in this chapter, but in part explains HDB observed at low T_{air}. Overall these data suggest that avian sensitivity to heat stress might represent complex interactions between a species' ecological and physiological characteristics.

In Chapter 1, I have demonstrated that heat dissipation effort was related to elevations in T_b above normal levels (i.e. modal T_b) in White-browed Sparrow-Weavers (Chapter 1). These patterns suggest that panting is indicative of regulation of T_b closer to normal levels. To prevent hyperthermia, i.e. elevations in T_b above set-point levels, birds will spend more water on evaporative cooling. Increased levels of activity during warm weather, such as increased foraging effort, are likely to elevate T_b and trigger a trade-off between thermoregulation and elevated water demands (du Plessis et al. 2012). The variation in heat dissipation patterns observed in this chapter in White-browed Sparrow-Weavers between TKR (semi-desert) and DGR (desert), as well as between summers at TKR, could represent such a trade-off.

The data presented in this chapter, show that under similar weather conditions sparrow-weavers at the desert site are predicted to spend ~ 15 % of time panting under warm conditions (39 °C) compared to 54 % for birds in the semi desert site (Fig. 9A,C). These patterns corroborate my findings that the higher set-point T_b of sparrow-weavers during summer at the desert site would reduce their demands for evaporative water loss. Desert birds therefore rely more on passive heat loss by having an elevated T_b, before they needed to initiate panting levels (Chapter 1). However, these responses also varied between summer seasons at the semi-desert site; during a dry summer season at TKR, sparrow-weavers were not observed panting (Fig. 9B). In support of these findings, I observed that during a severely dry summer with consistently high maximum temperatures in the Kalahari Desert, near Van Zylsrus, South Africa (<10 mm of rain, and mean Max T_{air} for January = 38.7 °C compared to normal mean of ~ 35 °C), White-browed Sparrow-Weavers were often observed foraging at T_{air} as high as 42.3 °C without panting (pers. observation). These observations provide further support that heat dissipation behaviour represents a flexible trait in some species, and that heat dissipation effort is potentially linked to demand and supply of water.

I therefore propose that the interspecific variation in heat dissipation patterns could represent a trade-off between thermoregulation (i.e. investment in evaporative cooling) and activity levels (e.g. foraging effort). In hot environments, high levels of activity could quickly lead to excessive heat loads, and most water gained through foraging might be spent on evaporative cooling (see Chapter 1 and 2). Birds that minimize activity levels, without compromising foraging opportunities, and/or birds that tolerate fluctuations in T_b (or express adaptive shifts in T_b such as reported in White-browed Sparrow-Weavers at the desert site), would spend less water on thermoregulation (Angilletta et al. 2010, Boyles et al. 2011). In contrast, birds that spend a large proportion of time defending T_b will likely be more at risk of dehydration and/or suffer reduced performance (Boyles et al. 2011). It could be argued that birds with low HD_{50} values, i.e. have higher heat dissipation effort at lower temperatures, are likely thermal specialist and are undergoing stronger trade-offs between thermoregulation and daily activities. Birds that commence heat dissipation at comparatively higher T_a during warm weather could 1) be largely inactive and therefore not likely to experience excessive heat load, 2) experience heat load but be more tolerant of elevations in T_b, or 3) incorporate other avenues of heat dissipation not manifested as panting or gular fluttering (i.e. cutaneous evaporative cooling).

Interestingly, the species with the lowest HD_{50} values in this study were all predominantly frugivores, including White-backed Mousebird, Red-faced Mousebird, Acacia Pied Barbet and Red-eyed Bulbul (Fig. 8D). Wattled Starlings also had low HD_{50} values, and fruit represents a significant component of their diet (Craig 2005). One likely explanation for the low HD_{50} in these species is that they experience high heat loads if their foraging effort is linked to higher energetic cost. Dusky Sunbird, the only nectarivore in my study, also appeared to have a low HD_{50} (36.8 °C) compared to other small passerines of similar size; for example, Black-chested Prinia, Scaly-feathered Finch and Yellow-bellied Eremomela showed HD_{50} values of 39.5, 41.9 and 41.3 °C, respectively. In the Kalahari Desert, frugivores and nectarivores might need to forage over larger areas, and switch between foraging sites more frequently since fruit and flowering plants are generally widely scattered in this region (Dean et al. 1999), and these species potentially experience activity-related heat load. Although the frugivores did not show significantly elevated activity levels compared to other groups, my data did not directly assess activity type and intensity, and distances travelled at species level. This presents an interesting avenue for future research; species that are constantly on the move (i.e. nomadic), forage over large home ranges, or frequently cover large distances to specific resources such as water daily, are likely to experience greater heat loads and higher EWL costs. Frugivores and nectarivores consume a diet that is high in preformed water content and can potentially afford high EWL costs.

Sit-and-wait hunters, in contrast, which generally sit on an elevated perch while scanning for prey items and only periodically take short flights, such as Common Fiscal, Lesser Grey Shrike, and Lilac-breasted Rollers, show higher HD_{50} values. My analyses of HD_{50} as a function of predicted activity levels provided stronger support that heat load produced through activity might be driving heat dissipation demands. For most species, activity levels are likely to be a reliable proxy of foraging effort. For example Scaly-feathered Finches were active for 57.7 % of time, of which 77.9 % was spent foraging. However, for sit-and-wait hunters these activity levels are likely an underestimate of total foraging opportunities.

The role of body mass in my data set is difficult to interpret. Overall, larger birds showed lower activity levels, and also showed lower HD_{50} values. However, larger birds (over 200 g) are underrepresented in my data set, and in general in the Kalahari Desert; especially compared to the Australian deserts that have many parrots, and larger passerines above 400 g (Blakers et al. 1984). Raptors represent most of the larger species in the Kalahari Desert, e.g. goshawks, eagles, vultures and falcons, but also a few bustard species. Raptors were rare in TKR (see species reporting rates, Chapter 3, Table 1). Interestingly, the two bustard species (Red-crested Korhaan and Northern Black Korhaan) and one larger raptor (Southern Pale-chanting Goshawk) that were often observed in TKR showed heat dissipation too infrequently to be included in analyses (Table 1). The two bustard species were largely inactive during the day, generally standing still and performing territorial calls (however these data are probably biased towards detecting males since females do not call), and heat dissipation was detected very seldom (Table 1). For example, the only Red-crested Korhaan observed showing heat dissipation behaviour (gular-fluttering) was an individual foraging in the sun early during the day (30 °C). These observations suggest that the larger species in my study are able to limit activity levels during warm parts of the day and therefore experience a lower heat load. This raises the question whether these species have been under stronger selective pressure to reduce activity levels. Arguably larger birds would experience a more stringent trade-off between activity-related heat load, and activity related foraging demands under hot conditions. Most notably, the benefits of an elevated T_b (i.e. facultative hyperthermia) will likely be lower in larger birds (Tieleman and Williams 1999). Tieleman and Williams (1999) have shown that whereas small birds benefit from bouts of hyperthermia, in terms of total water savings, larger birds will tend to expend more water on long bouts of hyperthermia than they would have expended if they remained normothermic. The smaller surface area to volume ratio of large birds (i.e. greater thermal inertia), means that larger birds should avoid elevation in T_b as they might be more at risk of reaching lethal T_b if they cannot dissipate heat efficiently.

It is noteworthy that respiratory heat-dissipation behaviours (easily observed here) provide a conservative estimate of the demands for heat dissipation through evaporative cooling. Many species make use of cutaneous evaporative water loss. In fact, for taxa such as the Columbiformes cutaneous evaporative water loss could represent the dominant avenue of water loss (Marder et al. 2003, McKechnie and Wolf 2004). It is not possible to observe cutaneous evaporative cooling in the field, and respiratory heat dissipation might be a poor proxy for the demands of heat dissipation in these taxa. However, relience on cutaneous evaporative cooling is not likely to be indicative of the same degree heat stress as relying respiratory evaporative cooling, since the former has been correlated with lower T_b and lower metabolic rate during exposure to high T_{air} (McKechnie and Wolf 2004). Many birds in my study were observed wing-spreading more regularly than panting. Namaqua Doves, for example, showed wing-spreading more frequently than gular-fluttering (Fig. 10). The traditional explanation for wing-spreading is that it facilitates passive heat loss by exposing thermal windows underneath wings to cooler air. An interesting avenue of further study would be to investigate if wing-spreading could play a role in facilitating cutaneous evaporative cooling under the wings. Interestingly, I did not observe behaviours such as elevation of scapulars or ptilo-erection [often described elsewhere; see Bartholomew and Dawson (1979)] frequently enough to incorporate into analyses. These behaviours were seen on a few occasions in sangrouse species, but I did not collect more than 20 observations on these species.

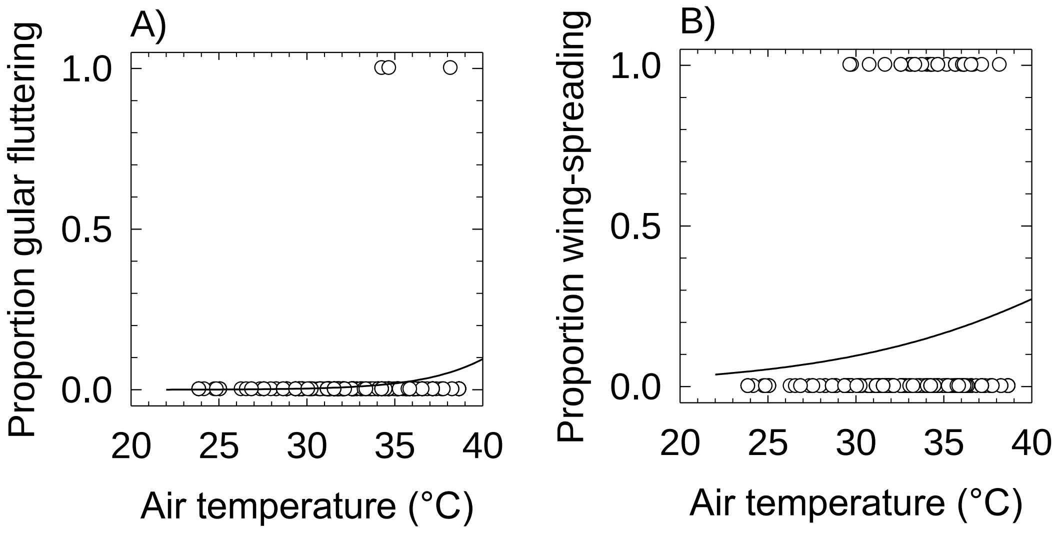

Figure 10: Heat dissipation (presence = 1, absence = 0) representative of A) gular-fluttering (i.e. respiratory heat dissipation) and B) wing-spreading as a function of air temperature in Namaqua Dove (*Oena capensis*) at Tswalu Kalahari reserve. The trendlines represent predicted proportion of heat dissipation behaviour.

Limitations to the method

The methodology used in this chapter could potentially allow for rapid assessment of sensitivity to heat stress in avian communities. However, there are a number of shortcomings in this approach that should to be treated with caution: first, data collection could be biased towards only observing certain types of behaviour, second, heat dissipation responses are likely an effect of behaviour prior to the observation (which is not known), and third, variation in environmental temperature experienced by different species need to be accounted for.

Some species will be easier to observe performing specific behaviour than others. For example, the instantaneous data collection could be more biased towards observing species foraging or perching in open elevated sites. In contrast, terrestrial foragers could be difficult to detect without disturbing them when ground cover (grass or shrubs) is dense. Complications may thus arise when comparing taxa that spend a large part of the day in dense vegetation. For example, many of the smaller granivores, e.g. finches, sparrows, canaries and waxbills, are difficult to observe when foraging in tall grass tufts or underneath dense shrubs. Observations might, therefore, be biased towards individuals scanning (for vigilance) or resting, and in many instances these behaviours coincided with heat dissipation when individuals moved into sites that were more exposed to wind. In my study, for example, arboreal gleaners and sit-and-wait hunters would have been less likely to spend time in sites where they would go undetected, compared to terrestrial foragers. I argue these problems are largely a function of vegetation structure. Most of the trees in my study site were less than 5m in height and canopies were generally sparsely vegetated, whereas ground cover varied from open with scattered grass tufts during dry periods, to dense grass cover during wet periods. The greatest challenge in my study was therefore detecting birds foraging on ground, rather than detecting birds resting in the vegetation shaded canopies of trees. The current methodology might be limited to relatively open habitats where birds can easily be detected in the dominant cover. Collecting similar data in densely wooded habitats could be challenging if birds cannot be observed easily for extended periods of time.

Another major limitation of the data protocol was that I could not assess the type and intensity of activities of birds prior to being observed. Prior activity could be a strong confounding factor in heat load. Birds that were foraging in hot microsites, or undertaking long flights prior to an observation are more likely to express heat dissipation behaviour. This could be a problem for highly mobile species (discussed above). In particular, Red-eyed Bulbul, Wattled Starling and Dusky Sunbird, often took-off during observations and flew beyond the visual boundaries of the site. Many of the HDB data for these birds could represent observations shortly after long flights.

One solution would be to obtain more detailed focal observation data whereby an individual is tracked for a period of time, e.g. 30min (see Chapter 1). The benefits to this approach are that behaviour can be linked directly to heat dissipation behaviour. However, this would require more intensive behavioural studies on individual species, and in many cases it would be essential to visually mark individuals, e.g. colour banding, for continuous assessment. One further drawback to this approach—which will limit larger scale community-based studies, is that obtaining longer focal observations on individuals could disturb them or cause them to alter their behaviour. The focal approach tends to work best where study birds are habituated to the presence of the observer [see du Plessis et al., (2012)].

The results obtained from detailed focal observations and instantaneous observations could also be different. In White-browed Sparrow-Weavers, for example, logistic regressions obtained through instantaneous observations showed initiation of HDB at higher T_{air}, compared to focal observations (Chapter 1). This discrepancy is probably a result of an increased likelihood of detecting heat dissipation when individuals are observed for longer. These findings suggest that obtaining meaningful predictions of heat dissipation for any particular temperature could be limited when using instantaneous observations. For example, many species in this study showed HD_{50} values over 40 °C, in some as high as 56 °C. These models extrapolate to HD_{50} values above actual T_{air} values observed in my study. If observations could be obtained at T_{air} exceeding 40 °C, it seems likely that HD_{50} values will be lower in these species than predicted.

However, I suspect that the only significant change heat dissipation responses of these species will be the slope of the response rather than the intercept; i.e. the species will initiate panting at a similar temperature, but HD effort might increase more at higher T_{air}.

Lastly, all the behaviours in my study were linked to T_{air} recorded at a set height by a weather station, but in reality species could vary greatly in the thermal environments they experience. The majority of variation in HDB observed between species is most likely therefore a combined effect of microsite use (thermal heat load) and activity levels (metabolic heat load). It would thus be important to charaterise variation in microclimates and how these correlate with standard measures of T_{air}.

Predictions and future research

The diversity of HD_{50} values reported in this study and the correlations with ecological factors (such as foraging mode and activity levels) strongly suggest that HD_{50} could be an important indicator of vulnerability to heat stress. To validate the implication of these findings and the usefulness of the HD_{50} method, we need be to establish how well HD_{50} is explained by physiological traits indicative of heat stress, e.g. the probability of a species approaching dehydration or lethal body temperature limits. Species with low HD_{50}, are categorized by initiating HDB at low temperatures, and often, elevated HDB at a high rate when temperatures increased (Fig. 11A). HD_{50} values could therefore give an indication a species thermal sensitivity. Species with low HD_{50} values fall in the start-low respond-quick catergory and therefore appears to be more sensitive to increasing temperatures. One potential outcome is that species with low HD_{50}

values could experience a higher probability of reaching dehydration limits during hot weather. In Chapter 5, I provide more support for this idea and show that species with low HD_{50} values are significantly more dependent on drinking free-standing water daily, compared to species with high HD_{50} values. I therefore predict that these species will show higher EWL rates (as a % of total body water) on a hot day, compared to species with high HD_{50} values.

The higher effort attributed to HDB in some of these species, might also be indicative of a limited scope to express facultative elevations in T_b above normal levels; i.e. species that cannot tolerate large elevations above normal T_b need to increase their reliance on evaporative cooling (therefore a low HD_{50}) to prevent lethal T_b. As a corollary, I expect that species with high HD_{50} values are more likely to express adaptive thermoregulatory responses, such as facultative hyperthermia or an elevated set-point T_b to cut down on evaporative water losses (Chapter 1). The above predictions can also be relevant at an intraspecific scale. Future research could investigate if variation in HD_{50} values between seasons, in separate climates, represents differences in behavioural and physiological traits.

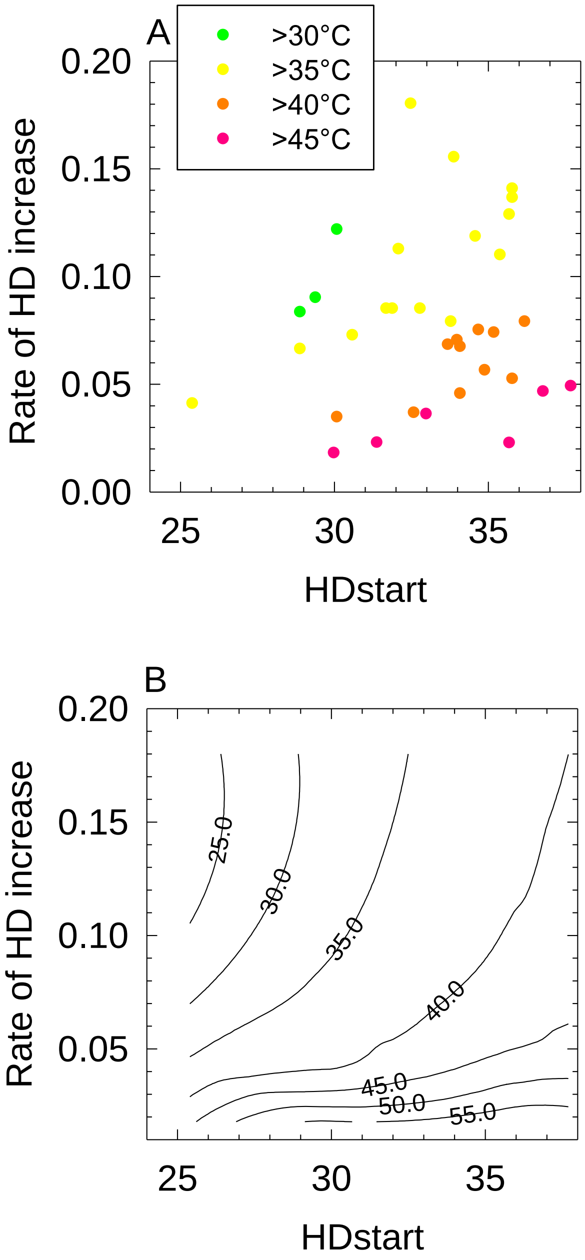

Figure 11: Heat dissipation behaviour slope (rate of change from HD_{start} to HD_{50}; see Fig. 2 for definitions) as a function of HD_{start} in 35 species in the Kalahari Desert; ranges in HD_{50} values are colour coded. Birds which start heat dissipation behaviours at low temperatures, and show a high degree of sensitivity to heat (steep slope) might be more at risk of chronic heat stress than species that start heat dissipating at higher temperatures. Species with low HD_{50} values tend to fall in the start-low respond-quick category.

Finally, my data showed that activity levels are an important predictor of HD_{50} and future studies need to establish whether this represents a trade-off between water acquisition and expenditure. For instance, do species with low

HD_{50} values simply express HDB more often since they can afford it? For example, in the frugivores and nectarivores elevated costs of foraging have a diet with high preformed water content. Or, alternatively, do these species show lower heat tolerance? These questions can be addressed if foraging effort can be manipulated, possibly through water and food supplementation experiments.

In conclusion, this study presents a method for quick and low-cost assessment of variation in behavioural patterns of heat stress in bird communities. My study showed that species that minimised activity levels showed the lowest levels of heat dissipation, and species that expressed high levels of foraging effort at high temperatures started HDB at the lowest air temperatures. This method could potentially be used to identify species that are more at risk of lethal dehydration or species that show low heat tolerance. In addition, when employed at an intraspecific level, this method could also be indicative of trade-offs between energy and water demands, foraging effort and thermoregulation.

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CHAPTER 5

CONCLUDING REMARKS: LINKING PHYSIOLOGY AND BEHAVIOUR IN CLIMATE CHANGE PREDICTIONS

Although many studies have predicted that climate change will result in species losses in desert regions, few of these models are based on the direct effects of increases in air temperature on daily water use, energy expenditure, and body temperature in birds (McKechnie et al. 2012). Data based on physiological responses to high temperatures (e.g. evaporative water loss demands) consist almost entirely of data collected under laboratory conditions (Wolf 2000, Tieleman et al. 2002a, 2002b, McKechnie and Wolf 2010), and physiological data from free-living endotherms are relatively limited.

Many predictions of the effects of climate change on endotherms assume that species' physiological responses to temperature are relatively fixed compared to behavioural responses (Williams et al. 2008), and that these constraints are directly related to the current distributions of species (Chambers et al. 2005). These assumptions often implicitly form the basis for correlative models. Once air temperature exceeds normal avian body temperatures (T_b), birds increase evaporative water loss rates greatly to maintain body temperature below lethal limits (Wolf 2000). However, birds experience additional physiological costs, for example a high metabolic rate, that may require continous foraging during the heat of the day to meet energetic requirements when food availability is low (Tieleman and Williams 2002, du Plessis et al. 2012). These conditions could induce trade-offs between physiology and behaviour; for example, increased foraging effort to meet water and energy demands, at the costs of elevated heat load and heat dissipation demands (du Plessis et al. 2012, Smit et al. 2013), especially if foraging gains during cooler parts of the day are not sufficient. Data on how physiological responses such as water flux, energy expenditure and body temperature (which play an important role in determining daily time-activity budgets) are directly affected by changes in air temperature below avian body temperature, are extremely limited for free-living birds (McKechnie et al. 2012).

CURRENT AND FUTURE CLIMATE IN THE KALAHARI DESERT

In this chapter I present frequency distributions of maximum air temperatures (T_{air}) Kalahari Desert birds experience currently and those they are likely to experience under future warming scenarios. I obtained daily maximum T_{air} over nine consecutive summer seasons (1 November to 31 March, 2004–2012) for Twee Rivieren and Kathu weather stations, respectively (refer to Fig. 1, General Introduction) from Weather Underground (www.wunderground.com). I generated frequency distributions of the 2010s (i.e. 2004–2012) temperatures for both sites to represent present conditions, and frequency distributions for the 2080s assuming an overall increase in maximum temperatures of 3.5 °C; this is the midpoint of the predicted 2–5 °C increase IPCC SREX report (2011).

Currently the eastern margin of the southern Kalahari Desert region experiences markedly cooler temperatures (Fig. 1), than the western parts. For example, maximum T_{air} values are currently not exceeding 40 °C in the Kathu region (Fig. 1A). Weather data obtained during my study period at Tswalu Kalahari Reserve over three summers corroborate largely with the Kathu climate; summer maximum temperatures never exceeded 40 °C. In contrast, maximum T_{air} at Twee Rivieren frequently exceeds 40 °C during summer. Over the last nine summers (2004 to 2012), maximum T_{air} exceeded 40 °C on about 18% of summer days (Fig. 1B). Weather data obtained at the desert study sites (Wildsgenot Game Ranch, Dreghorn Game Ranch), closely followed the Twee

Rivieren pattern. Taken together with my data on physiological and behavioural variation in White-browed Sparrow-Weavers, these patterns therefore confirm my findings that variation in climate over small spatial scales (100–150km) could be a strong driver of physiological and behavioural responses.

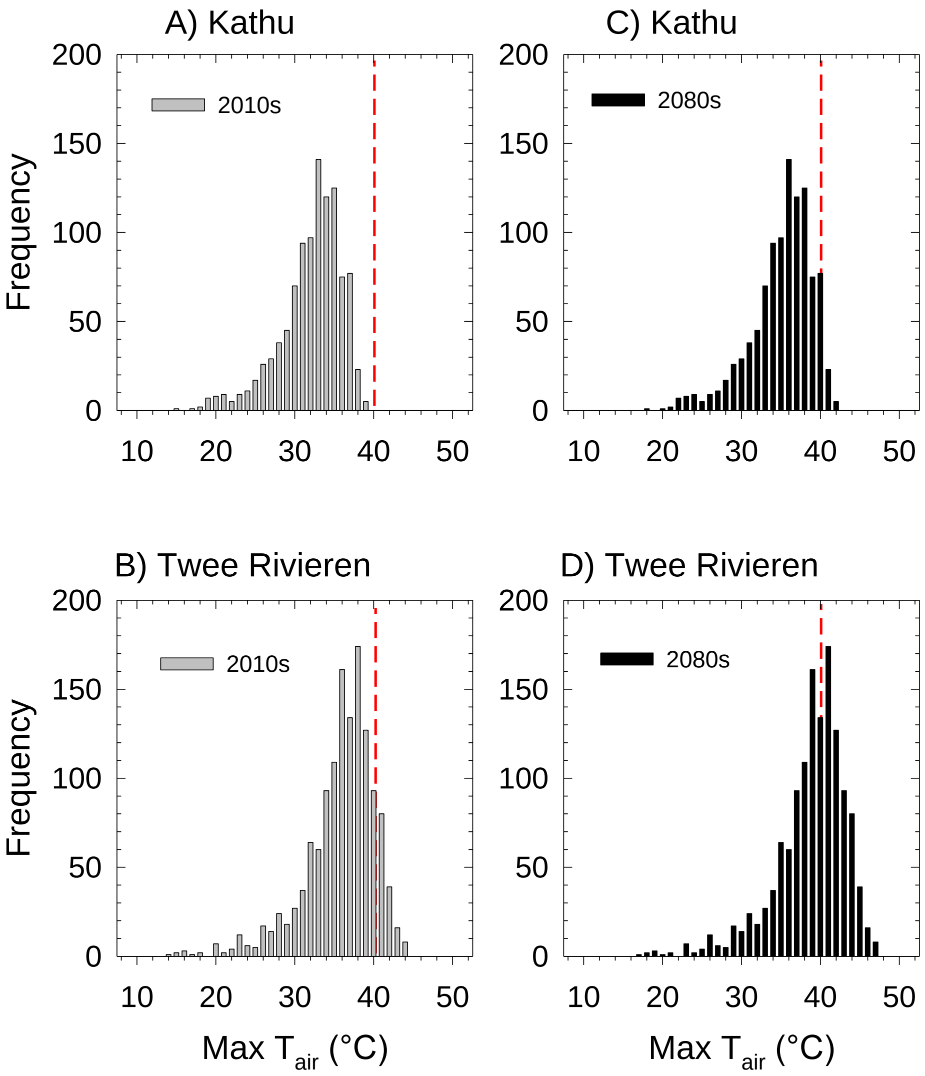

Figure 1: Frequency distribution of maximum daily air temperatures (Max T_{air}) for five summer months (1 November to 31 March), recorded between 2004 and 2012 (i.e. 2010s), for A) Kathu (eastern margin in southern Kalahari) and B) Twee Rivieren (western part of southern Kalahari). Predicted future frequency distributions assume an upward shift in temperatures of 3.5 °C by the 2080s for C) Kathu and D) Twee Rivieren. The red dashed line marks 40 °C.

Predictions of maximum temperatures suggest that the Twee Rivieren region of the Kalahari Desert could experience temperatures over 40 °C on about 50 % of days in summer, compared to 10 % of days in the Kathu region. Average maximum T_{air} in the 2080s will therefore approach or exceed typical avian T_b in the western regions of the Kalahari Desert. In contrast, average summer maximum T_{air} in the eastern margins of the Kalahari Desert might still be about 5 °C lower. Moreover, whereas the average maximum T_{air}s in Twee Rivieren showed a strong warming trend over the last decade, no trend is evident for Kathu region (Fig. 2A). A longer term study, by Kruger and Sekele (2012), confirmed this warming trend for Twee Rivieren, with this area identified as one of the regions showing the fastest warming rate in South Africa over the last five decades. Twee Rivieren has shown a marked and significant increase in the number of days when maximum $T_{air} > 40$ °C; this pattern is very similar to the rapid warming observed in the deserts of central Australia where large-scale die-offs have been observed over the last few decades (McKechnie et al. 2012).

In Chapter 2, I showed that on days when maximum T_{air} exceeded 42 °C, White-browed Sparrow-Weavers are likely to spend most of their daily water budget on resting EWL. Currently, this arid-zone species rarely experiences maximum temperatures above 42 °C (< 5 % of summer days over the last decade). However, by the 2080s, 27 % of the days during summer may exceed this threshold in the Twee Rivieren region. Free-standing water sources might become essential for sparrow-weavers (which generally do not drink) to persist in the western regions of the Kalahari Desert in the near future.

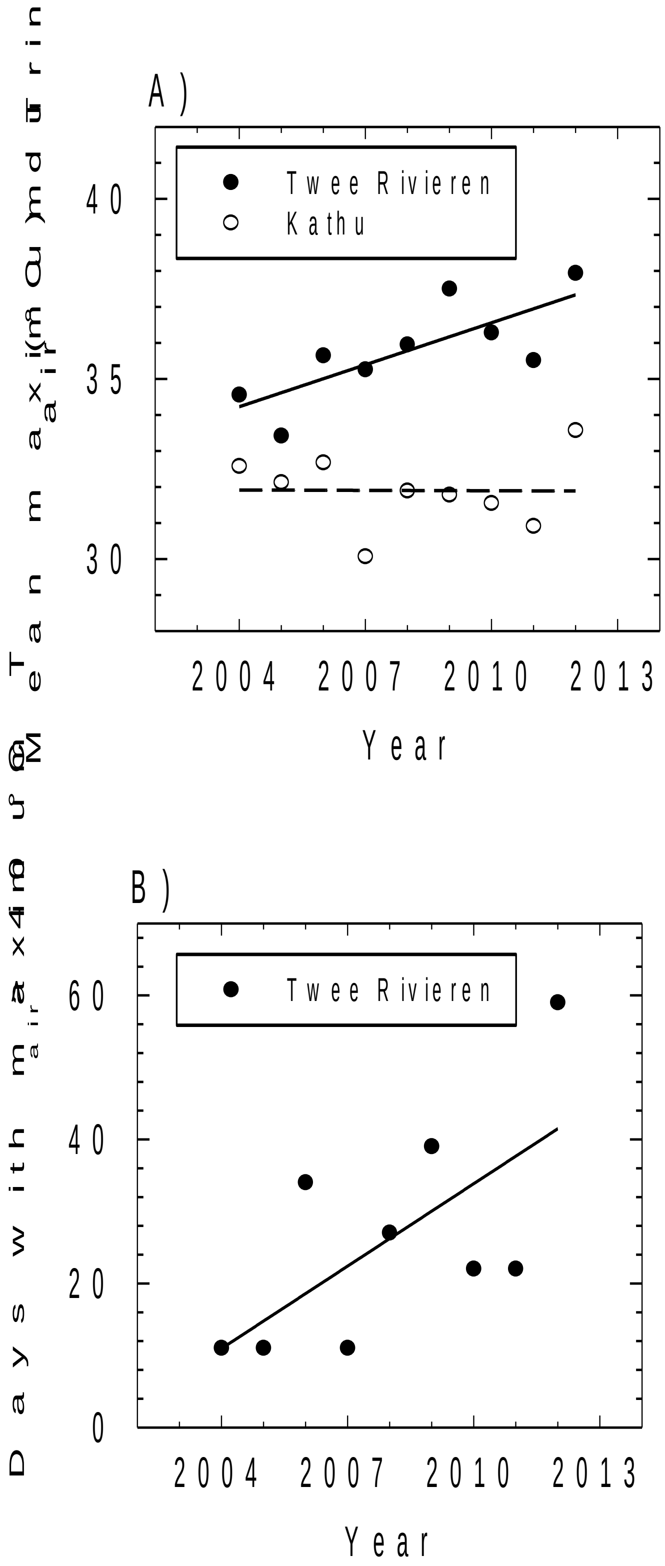

Figure 2: A) Mean maximum air temperature (T_{air}) during summer (pooled from 1 November to 31) over nine consecutive years (2004 to 2012) for Kathu and Twee Rivieren. B) The number of days where maximum temperatures exceed 40 C over nine consecutive summers (2004 to 2012). Solid trendlines indicate a significant correlation ($p < 0.05$).

For most other southern Kalahari Desert species, future warming scenarios could present an even more ominous picture. In Chapter 4, I obtained HD_{50} as a comparative metric for 35 Kalahari species. In this data set, mean and median HD_{50} were 40.9 and 39.5 °C respectively (Fig. 3). The HD_{50} value for White-browed Sparrow-Weavers (43.1 °C) was slightly above the median and mean, suggesting that they are relatively more heat tolerant than the other species. If HD_{50} values are a reliable indicator of vulnerability to heat stress, this could mean that most of the species investigated in this study could have lower temperature thresholds for water balance compared to sparrow-weavers.

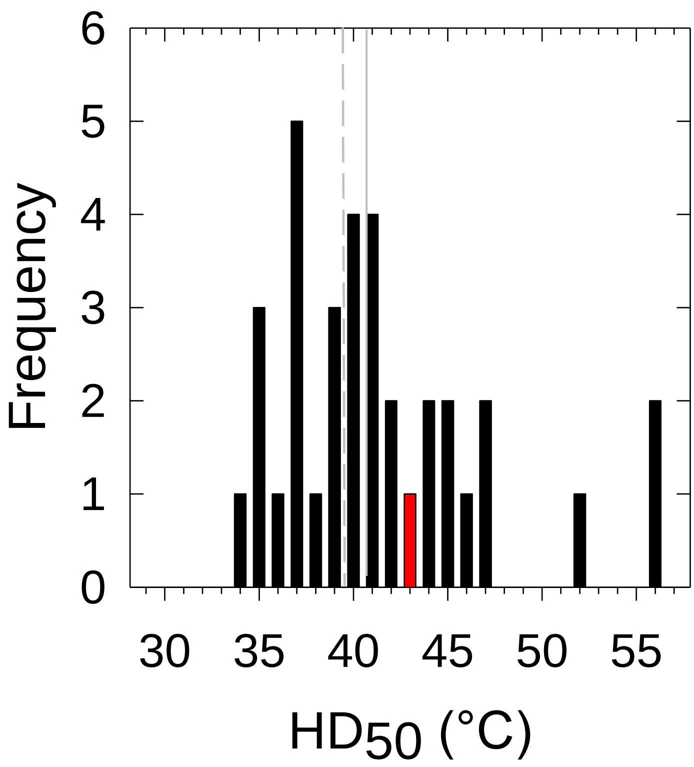

Figure 3: Frequency distribution of HD_{50} values obtained for 35 species (Chapter 4), showing median (dashed grey line) and mean (solid grey line). These patterns indicate that HD_{50} values are positively skewed and that most species have low HD_{50} values. The datum in red represents White-browed Sparrow-Weaver.

I explored the relationship between drinking dependency and heat dissipation effort in the Kalahari species from this thesis, by testing for a correlation between Max T_{drink} (Chapter 3) and HD_{50} values (Chapter 4). Whereas species with low Max T_{drink} values generally drank every day, (irrespective of maximum daily air temperature), species with high Max T_{drink} drank on hotter days. The positive relationship Max T_{drink} and HD_{50} was highly significant ($r^2 = 0.55$, $p < 0.001$, Fig. 4). This further suggests that birds with low HD_{50} are regular drinkers, and could mean that they 1) have a greater water budget available to spend on EWL, 2) rely less on hyperthermia, or 3) are more sensitive to dehydration, than birds with high HD_{50}. Many of the birds with high HD_{50} values were never observed to drink.

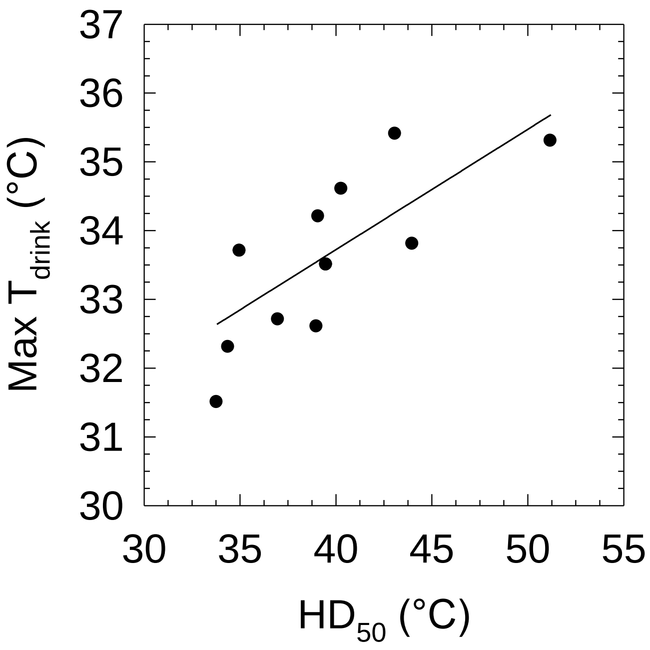

Figure 4: The relationship between the temperature dependency of drinking, measured as mean maximum air temperature (Max T_{drink}) associated with each drinking event, and heat dissipation sensitivity, measured as the air temperature where the probability of heat dissipation is 50% (HD_{50}). These data were obtained from Chapter 3 and 4. Each datum represents the mean value per species. The trendline through the black symbols represent the significant relationship between Max T_{drink} and HD_{50}

The dry western regions of the southern Kalahari Desert (around the Kgalagadi Transfrontier Park) could lose many avian species over the next few decades (Tews et al. 2004a). One of the greatest concerns are the loss of large trees, such as *Acacia erioloba*, which provide keystone structures in terms of microsite, and nesting and roosting sites for many Kalahari bird species (Tews et al. 2004b, Seymore 2006). Studies that investigate the vulnerability of other organisms that bird species depend on for food, habitat and favourable microsites and nesting sites, are therefore urgently needed. As a precautionary measure, habitat conservation should be prioritised along the eastern margin of the southern Kalahari Desert region in South Africa (where current temperatures are milder and droughts are less frequent), as these could serve as future refugia for many Kalahari species. These include the eastern Kalahari bushveld types, stretching roughly from Olifantshoek and Tswalu Kalahari Reserve in the west, to Kimberly and Mahikeng on the extreme eastern limits of the Kalahari Desert (Mucina and Rutherford 2006). However, it is worrying that the eastern margins of Kalahari region is currently under severe pressure from habitat transformation (Mucina and Rutherford 2006), mostly in the form of mining, cultivation, and large scale bush clearing by non-selective poisoning of all dichotomous plants to increase grazing land (Seymore 2006).

SUMMARY

My thesis reports novel field data showing large changes in behaviour and physiology at relatively mild air temperatures (T_{air}) approaching avian body temperatures (T_b). Moreover, I showed that other environmental factors such as humidity, rainfall and aridity could significantly affect how birds respond to

increasing air temperature. The thermoregulatory data I collected in wild birds, in particular, provided important and novel links between behaviour and body temperature regulation, showing that some birds might need to adjust their behavioural patterns by reducing important activities such as foraging, to maintain optimal levels of body temperature.

An important finding in this thesis is the spatial and temporal variation displayed in thermoregulation, behaviour, water and energy demands in White-browed Sparrow-Weavers. Whether these patterns are driven by phenotypic plasticity or genetic variation could not be established, but present a very interesting avenue for further research. Future studies should establish if other resident Kalahari species also show these patterns in behaviour and physiology between the hot western and milder eastern regions of the southern Kalahari Desert. I predict that many of the resident Kalahari species with similar foraging ecology are likely to show similar temporal and spatial variation in physiological and behavioural patterns to the sparrow-weavers. It seems highly probable that populations resident in the hotter and drier regions of the Kalahari Desert, where droughts are more frequent and severe, would experience very different selective pressures on physiological, behavioural and life history traits, compared to populations in more mesic, and milder habitats. The spatial and temporal unpredictability of the southern Kalahari Desert region could select for a high degree of resiliency to climatic extremes, or alternatively, favour nomadic behaviour in species which are ecologically or physiologically more specialized (Boyles et al. 2011). Given the large degree of variation in rainfall patterns and T_{air} across the east-west gradient in the Kalahari Desert, many of the mobile species could move to the eastern margins of the Kalahari Desert during hot dry years where temperatures are likely to be lower and productivity higher (Herremans 2004).

Although this study did not report physiological and weather data at extremely hot temperatures, it nevertheless showed significant effects of temperature on these traits at relatively mild temperatures (below avian T_b). My findings suggest that the possible trade-offs species will experience at this temperature range could greatly affect their fitness and survival in hot environments. This could lead to reduced species diversity in diverse avian desert communities, such as the Kalahari Desert. Heat dissipation behaviour studies could be employed to identify which species would suffer the greater reduction in fitness, although this would rely on future studies quantifying the value of HD_{50} as an indicator of vulnerability to heat stress. Finally, my work suggests that longer term, chronic heat stress resulting from warmer than average temperatures will lead to trade-off between energy, water balance, and thermoregulation which could strongly affect the longer term performance, body condition and reproductive fitness of many species.

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LIST OF APPENDICES

Appendix A

Study species and study site information, including photographs and summary of weather recorded during the study (Chapter 1).

Appendix B

Additional figures on body temperature and behaviour patterns of white-browed sparrow-weavers (*Plocepasser mahali*) (Chapter 1).

Appendix C

Final models describing body temperature and behaviour in white-browed sparrow-weavers (*Plocepasser mahali*) (Chapter 1).

Appendix D

Summary of drinking patterns and water dependency (Chapter 3)

Appendix E

The effect of distance from waterhole on water use (Chapter 3)

Appendix F

Summary of heat dissipation observations (Chapter 4)

APPENDIX A: STUDY SPECIES AND STUDY SITE INFORMATION, INCLUDING PHOTOGRAPHS AND SUMMARY OF WEATHER RECORDED DURING THE STUDY. (CHAPTER 1)

Fig A1. A female white-browed sparrow-weaver (*Plocepasser mahali*) showing heat dissipation behavior (panting and slight wing-spreading). White-browed sparrow-weavers (35-50 g) breed co-operatively, living in family groups of 2-10 individuals, and occur in the arid savanna regions of southern and eastern Africa (du Plessis, 2005). These birds are omnivorous and feed on insects (80% of diet), seeds, and fruit (du Plessis, 2005). Family groups mostly occur far from free-standing water, and only individuals in territories surrounding a free-standing water source drink periodically (Chapter 3). Photo credit: Ben Smit.


A2a


A2b

Figure A2. Photographs taken during summer at A) end of dry season and B) wet season, at the semi-desert site, Tswalu Kalahari Reserve, and C) at desert site, Wildsgenot Game Ranch. Mean annual rainfall is higher at semi-desert site than desert site, mainly because semi-desert site lies closer to the western boundaries of the inter-tropical-temperate troughs that bring predictable summer rain (Reason, Landman, & Tennant, 2006; Usman & Reason, 2004). Mean ± SD annual rainfall at semi-desert site was 295±172 mm (coefficient of variation, CV = 58.3%) over a 30-year period (unpublished data, Tswalu Kalahari Reserve). Mean ± SD annual rainfall at desert site was 190 ± 125 mm (CV = 66%) over a 60-year period (GHD Scholtz, unpublished data). The climate at the desert site is more extreme (both hotter by day and colder at night) and less humid than at the semi-desert site. The semi-desert site is located near the 33°C isotherm for mean daily maximum T_{air} during mid-summer, whereas the desert site lies beyond the 35°C isotherm where in some years mean daily maximum T_{air} can exceed 41°C for over a month at a time (South African Weather Service). Mean water vapor pressure deficit (measured at 14h00 each day in January) is typically 3-4 kPa at the semi-desert site compared to >4 kPa at the desert site (Schulze, 1997). Photo credit: Ben Smit.

Table A1: Weather during the study period at Tswalu Kalahari Reserve (semi-desert) and Wildsgenot Game Ranch (desert). Thermoregulatory data at the semi-desert site were collected during the dry summer (Period 1: Dec 2010) and wet summer (Period 2: Jan to Feb 2011), and at the desert site during the dry summer (Period 3: Nov to Dec 2011). Values represent mean ± standard deviation (range: minimum - maximum). Both 'dry season' data collection periods were at the end of typical annual dry cycles, which last from April to December, and neither site received any significant rainfall for at least seven months prior to the sampling periods.

	Semi-desert (dry)	Semi-desert (wet)	Desert (dry)
	Period 1	Period 2	Period 3
Minimum Temperature (°C)	18.7 ± 2.6 (14.2 - 23.5)	20.1 ± 1.7 (16.7 - 23.7)	15.8 ± 4.4 (6.6 - 23.1)
Maximum Temperature (°C)	34.6 ± 3.0 (25.2 - 38.3)	31.7 ± 2.1 (28.3 - 35.1)	34.2 ± 3.2 (27.6 - 39.2)
Dew Point (°C)*	4.9 ± 6.8 (-12.1 - 16.6)	17.0 ± 2.3 (11.1 - 21.1)	3.4 ± 4.1 (-8.5 - 18.5)
Water Vapour Pressure Deficit (kPa)*	4.3 ± 0.9 (1.3 - 5.4)	2.3 ± 0.8 (0.54 - 3.9)	4.1 ± 1.1 (1.1 - 5.9)
Total rainfall (mm)	20.3	244.1	11.2

* Mean measurements at 14h00

APPENDIX B. ADDITIONAL FIGURES ON BODY TEMPERATURE AND BEHAVIOUR PATTERNS OF WHITE-BROWED SPARROW-WEAVERS (*PLOCEPASSER MAHALI*). (CHAPTER 1)

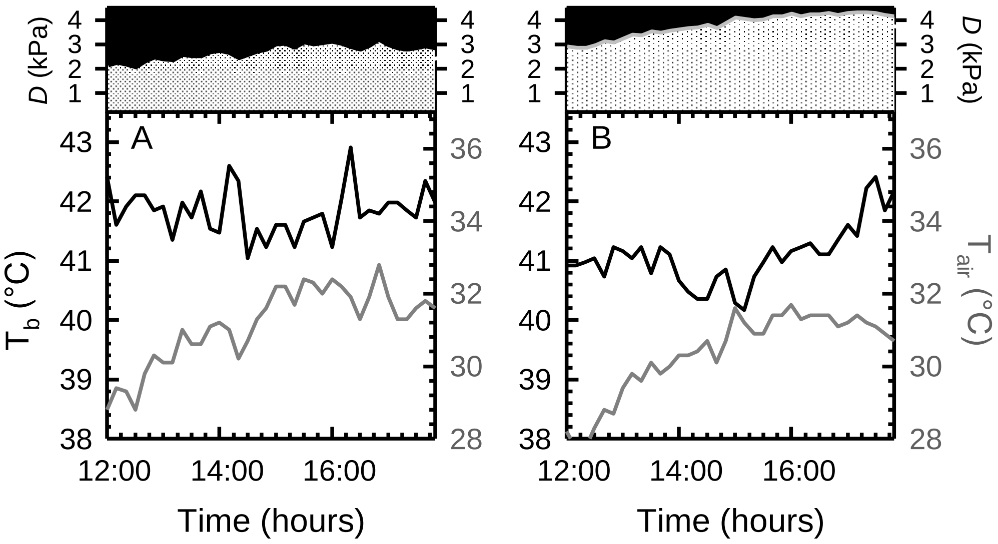

Figure B1: Representative traces of vapor pressure deficit (*D* - top panels), body temperature (T_b, displayed on left y-axes by black line) of a white-browed sparrow-weaver (*Plocepasser mahali*) and air temperature (T_{air}, displayed on right y-axes by grey line), between 12:00 and 18:00 hours on A) a humid day (mean dew point = 16.1°C) and B) a dry day (mean dew point 1.7°C) at Wildsgenot Game Ranch (desert). On humid days, T_b was generally higher. The top panels display water vapor pressures (kPa); the black area is an approximation of the absolute humidity (saturation vapor pressure was between 4.2 and 4.5 kPa), and the hatched area indicates *D*.

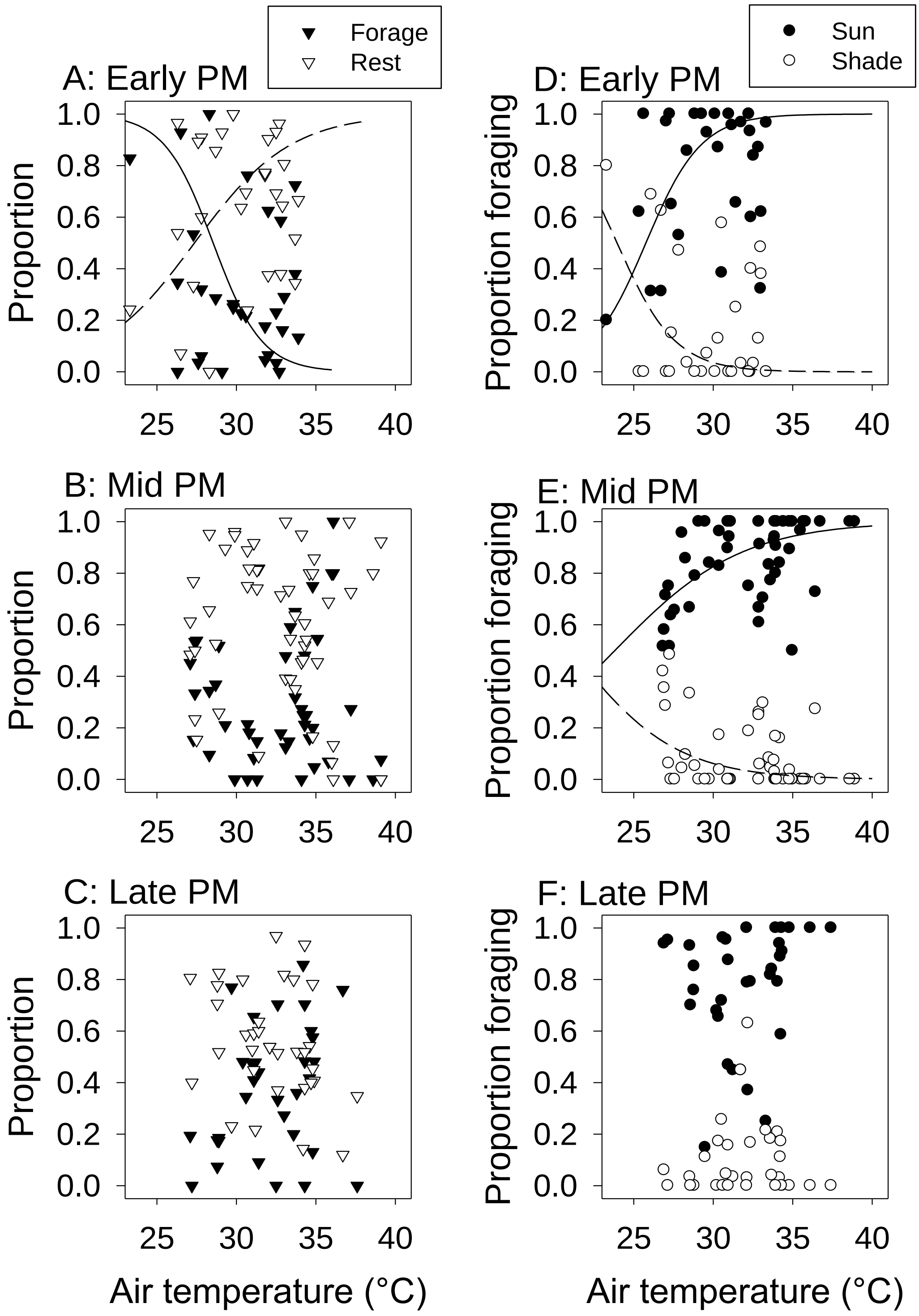

Figure B2: Behavioural responses to air temperature (T_{air}) by white-browed sparrow-weavers (*Plocepasser mahali*) between 12:00 and 18:00. The majority of these observations were recorded during January and February 2011 in Tswalu Kalahari Reserve (semi-desert site, wet season). The proportion of time spent resting or foraging during focal observations varied as a function of air temperature (T_{air}) between A) early(12:00 – 14:00 hours), B) mid (14:00 – 16:00 hours), and C) late (16:00 – 18:00 hours) afternoon (PM). Proportion of time spent foraging in shade or sun also varied as a function of T_{air} between D) midday, E) afternoon and F) evening. A logistic curve indicates a significant trend.

APPENDIX C. FINAL MODELS DESCRIBING BODY TEMPERATURE AND BEHAVIOUR IN WHITE-BROWED SPARROW-WEAVERS (*PLOCEPASSER MAHALI*). (CHAPTER 1)

Table C2: Final models showing the most important predictors of body temperature (mean and a maximum Tb, both absolute and as a function of modal body temperature) and behaviour (foraging, behaviors and heat dissipation) in white-browed sparrow-weavers (*Plocepasser mahali*) during the warmest part of the day (12h00 - 18h00) at Tswalu.Kalahari Reserve (semi-desert) and Wildsgenot Game Ranch (desert). Study period and vapor pressure deficit (*D*) were not included in behavioral models. All of these predictors and interactions were significantly related the respective response variables (see text for details).

Response:	Final model
Body temperature	$T_{air} + D$ + Time + Study period + $T_{air}*D$ + Time* $T_{air}*D$ + Study period* $T_{air}*D$
Foraging/resting behaviour	T_{air} + Time + T_{air}*time
Foraging site (sun/shade)	T_{air} + Time + T_{air}*time
Panting	T_{air} + Time + T_{air}*Time + Activity* T_{air}*Time
Wing-spreading behaviour	T_{air} + Time

APPENDIX D. SUMMARY OF DRINKING PATTERNS AND WATER DEPENDENCY. (CHAPTER 3)

Table D1: Summary of reporting rate (based on surveys), drinking dependency (% of days observed drinking), mean drinking events per day, mean maximum temperature associated with drinking event (Max T_{drink}) and birds for which body water samples were obtained for the avian community at Tswalu Kalahari Reserve. Values are presented as mean±SD. The total number of samples and number of enriched samples are presented for both wet (February 2011) and dry (October 2011) seasons. Species are categorized accoring to dominant dietary guild; i.e. frugivores (FRU), insectivores (INS), granivores (GRA), omnivores (OMN), nectarivores (NEC), carnivores (CAR). Superscript s = summer visitor, n = nomadic visitor, i - irregular visitor

Species	**Diet**	**Reporting rate (%)**	**Days observed drinking (%)**	**Mean drinking events per day**	**Mean Max T_{drink}**	**# Samples Wet/dry**	**# Enriched Wet/dry**
Acacia Pied Barbet *Tricholaema leucomelas*	FRU	16.1				3/2	0/0/
African Red-eyed Bulbul *Pycnonotus nigricans*	FRU	16.1	93.8	6.7±3.6	32.3±3.6		
Anteating Chat *Myrmecocichla formicivora*	INS	56.5	43.8	2.3±1.8	33.8±2.8	1/1	0/0
Ashy Tit *Parus cinerascens*	INS	16.1				2/2	0/0
^{s}Barn Swallow *Hirundo rustica*	INS	12.9					
Black-chested Prinia *Prinia flavicans*	INS	66.1				11/12	0/0
^{i}Black-faced Waxbill *Estrilda erythronotos*	GRA	3.2	12.5	1	34.4±1	0/1	0/1
^{n}Black-throated Canary *Chrithagra atrogularis*	GRA	4.8	43.8	2.7±2.6	32.9±3.6		
Bokmakierie *Telephorus zeylonus*	INS	33.9	12.5	1±0	35.6±2.5	1/0	0/0
Brubru *Nilaus afer*	INS	4.8					

Species	**Diet**	**Reporting rate (%)**	**Days observed drinking (%)**	**Mean drinking events per day**	**Mean Max T_{drink}**	**# Samples Wet/dry**	**# Enriched Wet/dry**
[i]Buffy Pipit *Anthus vaalensis*	INS	1.6					
Burchell's Sandgrouse *Pterocles burchelli*	GRA		100	18.1±16.5	32.8±3.6		
Cape Glossy Starling *Lamprotornis nitens*	OMN	8.1	87.5	2.6±1.6	32.7±3.0		
Cape Penduline Tit *Anthoscopus minutus*	INS	1.6				0/1	0/0
Cape Sparrow *Passer melanurus*	GRA	17.7	93.8	10.9±5.2	32.9±3.4	0/2	0/2
Cape Turtle-Dove *Streptopelia capicola*	GRA	37.1	100	156.2±83.9	32.1±3.6	1/0	1/0
Chat Flycatcher *Bradornis infuscatus*	INS	3.2					
Chestnut-vented Tit-Babbler *Parisoma subcaeruleum*	INS	37.1				4/6	0/0/
Common Fiscal *Lanius collaris subcoronatus*	INS	46.8	25	1	35.3±1.3	4/2	0/0/
Common Ostrich *Struthio camelas*	GRA	14.5	37.5	8.0±9.4	35.1±2.6		
Common Scimitarbill *Rhinopomastus cyanomelas*	INS	6.5				2/0	0/0
[s]Common Swift *Apus apus*	INS	1.6					
[s]Common Whitethroat *Sylvia communis*	INS	1.6					
Crimson-breasted Shrike *Laniarius atrococcineus*	INS	16.1				1/0	0/0

Species	**Diet**	**Reporting rate (%)**	**Days observed drinking (%)**	**Mean drinking events per day**	**Mean Max T_{drink}**	**# Samples Wet/dry**	**# Enriched Wet/dry**
Crowned Lapwing *Vanellus coronatus*	INS	6.5	37.5	1.7±1.2	34.2±3.3		
Desert Cisticola *Cisticola aridulus*	INS	3.2					
[s]Diderick Cuckoo *Chrysococyx cupreas*	INS	6.5				1/0	0/0
[n]Dusky Sunbird *Cinnyris fuscus*	NEC	4.8					
Eastern Clapper Lark *Mirafra fasciolata*	OMN	32.3					
[s]Eurasian Golden Oriole *Oriolus oriolus*	FRU	3.2					
Fawn-coloured Lark *Calendulauda africanoides*	OMN	64.5				6/5	0/0
Golden-breasted Bunting *Emberiza flaviventris*	GRA	1.6	6.3	1	34.9	0/1	0/1
[n]Grey-backed Sparrowlark *Eremopterix verticalis*	GRA	3.2	6.3	3	31.5		
[s]Jacobin Cuckoo *Clamator jacobinus*	INS	4.8					
Kalahari Scrub-Robin *Cercotrichas paena*	INS	54.8				8/8(16)	0/0/(0)
Kori Bustard *Ardeotis kori*	INS	1.6					
Kurrichane Buttonquail *Turnix sylvacticus*	INS	6.5					
Lappet-faced Vulture *Aegypius tracheliotos*	CAR		25.0	3	33.7±1.9		

Species	**Diet**	**Reporting rate (%)**	**Days observed drinking (%)**	**Mean drinking events per day**	**Mean Max T_{drink}**	**# Samples Wet/dry**	**# Enriched Wet/dry**
[n]Lark-like Bunting *Emberiza impetuani*	GRA	19.4	62.5	6.3±4.4	34.2±3.3		
[i]Laughing Dove *Streptopelia senegalensis*	GRA	33.9	100	36.7±37.6	32.6±3.5	1/0	0/0
[s]Lesser Grey Shrike *Lanius minor*	INS	24.2					
Long-billed Crombec *Sylvietta rufescens*	INS	3.2					
Marico Flycatcher *Bradornis mariquensis*	INS	22.6				0/5	0/0
[n]Namaqua Dove *Oena capensis*	GRA	59.7	100	387.3±131.8	32.2±3.6	7/6	5/6
Namaqua Sandgrouse *Pterocles namaqua*	GRA		100	31.6±19.9	31.6±3.5		
[i]Northern Black Korhaan *Afrotis afraoides*	INS	19.4					
Pearl-spotted Owlet *Glaucidium perlatum*	CAR					1/0	0/0
Pririt Batis *Batis pririt*	INS	6.5					
Pygmy Falcon *Polihierax semitorquatus*	CAR	1.6				1/0	0/0
[s]Red-backed Shrike *Lanius collurio*	INS	4.8	18.8	2±1	33.3±2.0		
[i]Red-billed Quelea *Quelea quelea*	GRA	1.6					
Red-crested Korhaan *Lophotis ruficrista*	INS	30.6					

Species	**Diet**	**Reporting rate (%)**	**Days observed drinking (%)**	**Mean drinking events per day**	**Mean Max T_{drink}**	**# Samples Wet/dry**	**# Enriched Wet/dry**
[n]Red-faced Mousebird *Urocolius indicus*	FRU	8.1	18.8	5±5	32.8±1.9		
[i]Red-headed Finch *Amadina erythrocephala*	GRA	17.7	31.3	2.2±1.1	33.3±1.8		
Red-necked Falcon *Falco chicquera*	CAR	1.6					
Cinnamon-breasted Bunting *Emberiza tahapisi*	GRA					0/1	0/0
[s]Rufous-cheecked Nightjar *Caprimulgus rufigena*	INS					1/0	0/0
Rufous-eared Warbler *Malcorus pectoralis*	INS	3.2				1/2	0/0
Scaly-feathered Finch *Sporopipes squamifrons*	GRA	62.9				29/19	4/4
Secretarybird *Sagittarius serpentarius*	CAR	3.2	18.8	1.3±0.6	32.4±4.1		
[i]Shaft-tailed Whydah *Vidua regia*	GRA	3.2	6.3	1	37.4		
Sociable Weaver *Philetairus socius*	OMN	25.8	87.5	69.3±110.7	34.6±2.4	19/17	1/6
Southern Grey-headed Sparrow *Passer diffusus*	GRA	6.5	6.3	1	34.9		
[i]Southern Masked-Weaver *Ploceus velatus*	OMN	29	100	16.6±19.2	31.9±3.3	6/3	1/0
Southern Pale Chanting Goshawk *Melierax canorus*	CAR	1.6	18.8	1	36.6±2.5		
Southern Yellow-billed Hornbill *Tockus leucomelas*	OMN	1.6					

Species	**Diet**	**Reporting rate (%)**	**Days observed drinking (%)**	**Mean drinking events per day**	**Mean Max T_{drink}**	**# Samples Wet/dry**	**# Enriched Wet/dry**
Spike-heeled Lark *Chersomanes albofasciata*	OMN	6.5				1/0	0/0
Tinkling Cisticola *Cisticola rufilatus*	INS					1/0	0/0
[i]Violet-eared Waxbill *Granatina granatina*	GRA	8.1	50	2.5±1.3	34.1±2.6	0/12	0/9
[i]Wattled Starling *Creatophora cinerea*	OMN	6.5	6.3	9	31.5		
White-backed Mousebird *Colius colius*	FRU	14.5	56.3	5.3±4.6	33.7±3.9	4/6	0/0
White-backed Vulture *Gyps africanus*	CAR		6.3	41	34.8		
White-browed Sparrow-Weaver *Plocepasser mahali*	OMN	81	43.8	4.3±3.3	35.4±2.7	11/14	1/1
Yellow Canary *Crithagra flaviventris*	GRA	26.6	93.8	18.2±14.4	33.5±3.4	0/4	0/1
Yellow-bellied Eremomela *Eremomela icteropygialis*	INS	10.8				0/3	0/0

APPENDIX E. THE EFFECT OF DISTANCE FROM WATERHOLE ON WATER USE (CHAPTER 3)

Table E1: Mean % body water pool (P% ±SD) derived from the enriched source at different distances from the sources in species that drank frequently and in a number of species not observed to drink.

	Mean ± SD P% (number enriched/total sampled)					
Species	**100 m**	**500 m**	**1000 m**	**1500 m**	**2000 m**	**2500 m**
Namaqua Dove *Oena capensis*	45.3±34.9 (7/8)	53.6 (1/1)	62.1 (1/1)	24.72 (1/2)	91.04 (1/1)	
[i]Violet-eared Waxbill *Granatina granatina*	34.5±23.0 (4/5)		25.0±8.9 (2/2)		35.7±15.6 (3/5)	
Sociable Weaver *Philetairus socius*	17.1±9.1 (5/9)	N/A (0/4)	N/A (0/5)	9.5 (1/4)	1.99 (1/10)	N/A (0/4)
[i]Southern Masked-Weaver *Ploceus velatus*	N/A (0/4)		7.7 (1/2)			N/A (0/3)
Scaly-feathered Finch *Sporopipes squamifrons*	10.6±2.4 (2/7)	2.9 (1/6)	5.5±2.1 (3/17)	2.2 (1/7)	N/A (0/9)	7.6 (1/2)
White-browed Sparrow-Weaver *Plocepasser mahali*	92.9 (1/3)	N/A (0/4)	5.1 (1/4)		N/A (0/10)	N/A (0/4)
Yellow Canary *Crithagra flaviventris*	63.4 (1/4)					
Fawn-coloured Lark *Calendulauda africanoides*	N/A (0/4)	N/A (0/2)	N/A (0/2)	N/A (0/1)	N/A (0/2)	
Black-chested Prinia *Prinia flavicans*	N/A (0/5)	N/A (0/3)	N/A (0/6)	N/A (0/3)	N/A (0/4)	
Common Fiscal *Lanius collaris subcoronatus*	N/A (0/1)	N/A (0/2)	N/A (0/1)		N/A (0/2)	
Marico Flycatcher *Bradornis mariquensis*	N/A (0/3)		N/A (0/1)			N/A (0/1)

	Mean ± SD P% (number enriched/total sampled)					
Species	**100 m**	**500 m**	**1000 m**	**1500 m**	**2000 m**	**2500 m**
Acacia Pied Barbet *Tricholaema leucomelas*	N/A (0/1)	N/A (0/1)			N/A (0/1)	N/A (0/1)
Chestnut-vented Tit-Babbler *Parisoma subcaeruleum*	N/A (0/2)		N/A (0/1)	N/A (0/2)	N/A (0/1)	
White-backed Mousebird *Colius colius*	N/A (0/5)		N/A (0/1)	N/A (0/1)		

APPENDIX F: SUMMARY OF HEAT DISSIPATION OBSERVATIONS (CHAPTER 4)

Table F1: Summary of heat dissipation observations of all species observed at Tswalu Kalahari Reserve (TKR) and Dreghorn Game Ranch (DGR). Mb represents body mass. Birds were categorized according to their foraging guild, i.e. arboreal gleaners (AG), terrestrial gleaners (TG), aerial foragers (AF) and sit and wait predators (SW); diet, i.e. omnivores, granivores (GRA), frugivores (FRU), insectivores (INS) (*including a few species that feed on vertebrates), and nectarivores (NEC). N represents the total number of observations for each species, and n the number of observations where individuals were engaged in heat-dissipation behaviour (i.e. panting or gular-fluttering). HD_{min} represents the lowest temperature at which heat dissipation was observed, HD_{start} was estimated as the T_{air} at which the probability of HD exceeds 5%, HD_{50} represents the temperature at which the probability of HD is 50%, and NHD_{max} represents the maximum temperature at which a species was observed while not showing heat dissipation.

Species	**Order**	**Mb (g)**	**Forage guild**	**Diet**	**Water source**	**n(N)**	**HD_{min} (°C)**	**HD_{start} (°C)**	**HD_{50} (°C)**	**NHD_{max} (°C)**
Acacia Pied Barbet *Tricholaema leucomelas*	Piciformes	32	AG	FRU	P	29(79)	29.8	28.9	35.7	37.5
African Hoopoe *Upupa africana*	Upupiformes	57	TG	INS	P	2(10)	36.3			36.6
African Red-eyed Bulbul *Pycnonotus nigricans*	Passeriformes	30.8	AG	FRU	D	20(46)	32.3	29.4	34.4	35.9
Anteating Chat *Myrmecocichla formicivora*	Passeriformes	47.6	SW	INS	P	29(546)	29.9	34.1	44	38.2
Ashy Tit *Parus cinerascens*	Passeriformes	20.4	AG	INS	P	10(148)	31.4	34.6	38.4	38.7
Black-chested Prinia *Prinia flavicans*	Passeriformes	8.9	AG	INS	P	21(529)	33.0	35.4	39.5	38.3
Black-faced Waxbill *Estrilda erythronotos*	Passeriformes	8.5	TG	GRA	D	0(5)				35.8

Species	**Order**	**Mb (g)**	**Forage guild**	**Diet**	**Water source**	**n(N)**	**HD$_{min}$ (°C)**	**HD$_{start}$ (°C)**	**HD$_{50}$ (°C)**	**NHD$_{max}$ (°C)**
Black-throated Canary *Crithagra atrogularis*	Passeriformes	12.7	TG	GRA	D	0(9)				35.8
Bokmakierie *Telophorus zeylonus*	Passeriformes	65	TG	INS	P	2(31)	29.7			38.3
Brown-crowned Tchagra *Tchagra australis*	Passeriformes	35	AG	INS	P	2(15)	30.3			37.1
Brubru *Nilaus afer*	Passeriformes	24	AG	INS	P	0(25)				38.7
Burchell's Sandgrouse *Pterocles burchelli*	Pterocliformes	250	TG	GRA	D	0(18)				33.8
Cape Glossy Starling *Lamprotornis nitens*	Passeriformes	82.5	TG	FRU	D	15(72)	34.6	31.7	37	38.8
Cape Penduline-Tit *Anthoscopus minutus*	Passeriformes	7	AG	INS	P	0(2)				33.6
Cape Sparrow *Passer melanurus*	Passeriformes	29.5	TG	GRA	D	8(27)	31.1	25.4	36.4	38.3
Cape Turtle-Dove *Streptopelia capicola*	Columbiformes	130.3	TG	GRA	D	20(307)	31.3	34	40.4	38.7
Capped Wheatear *Oenanthe pileata*	Passeriformes	25	TG	INS	P	0(6)				37.7
Cardinal Woodpecker *Dendropicos fuscescens*	Piciformes	30	AG	INS	P	0(6)				36.5
Chat Flycatcher *Bradornis infuscatus*	Passeriformes	37	SW	INS	P	2(92)	33.0			38.3

Species	**Order**	**Mb (g)**	**Forage guild**	**Diet**	**Water source**	**n(N)**	**HD$_{min}$ (°C)**	**HD$_{start}$ (°C)**	**HD$_{50}$ (°C)**	**NHD$_{max}$ (°C)**
Chestnut-vented Tit-Babbler *Parisoma subcaeruleum*	Passeriformes	15.7	AG	INS	P	16(295)	30.3	34.7	40.7	38.7
Common Fiscal *Lanius collaris subcoronatus*	Passeriformes	40.8	SW	INS	P	12(155)	29.4	31.4	51.2	38.7
Common Ostrich *Struthio camelas*	Struthioniformes	68700	TG	GRA	D	40(66)	27.8			35.7
Common Scimitarbill *Rhinopomastus cyanomelas*	Upupiformes	32.5	TG	INS	P	17(84)	30.6	32.1	36.1	37.7
Crimson-breasted Shrike *Laniarius atrococcineus*	Passeriformes	45	AG	INS	P	12(90)	32.9	32.8	38.1	38.0
Crowned Lapwing *Vanellus coronatus*	Charadriiformes	195	TG	INS	D	4(101)	35.7	35.8	39.1	38.7
Diderick cuckoo *Chrysococyx cupreas*	Cuculiformes	36.6	AG	INS	P	3(9)	35.8			38.4
Dusky Sunbird *Cinnyris fuscus*	Passeriformes	9.5	AG	NEC	P	4(53)	31.1	33.9	36.8	37.3
Eastern Clapper Lark *Mirafra fasciolata*	Passeriformes	30	TG	OMN	P	0(32)				37.4
Familiar Chat *Cercomela familiaris*	Passeriformes	22	SW	INS	P	0(11)				37.4
Fawn-coloured Lark *Calendulauda africanoides*	Passeriformes	23.3	TG	OMN	P	27(489)	29.0	33	45.5	38.2
Fork-tailed Drongo *Dicrurus adsimilis*	Passeriformes	43.8	SW	INS	P	15(207)	29.3	32.6	44.9	38.8

Species	**Order**	**Mb (g)**	**Forage guild**	**Diet**	**Water source**	**n(N)**	**HD$_{min}$ (°C)**	**HD$_{start}$ (°C)**	**HD$_{50}$ (°C)**	**NHD$_{max}$ (°C)**
Green-winged Pytilia *Pytilia melba*	Passeriformes	15	TG	GRA	D	3(7)	35.8			37.3
Grey-backed Sparrowlark *Eremopterix verticalis*	Passeriformes	17	TG	GRA	D	0(18)				38.6
Groundscraper Thrush *Psophocichla litsitsirupa*	Passeriformes	76.1	TG	INS	P	2(15)	36.3			38.7
Jacobin Cuckoo *Clamator jacobinus*	Cuculiformes	83	TG	INS	P	4(11)	32.7			35.6
Kalahari Scrub-Robin *Cercotrichas paena*	Passeriformes	19.7	TG	INS	P	20(541)	30.1	34.9	42.9	38.6
Kori Bustard *Ardeotis kori*	Gruiformes	9050	TG	INS	P	5(18)	31.0			37.0
Lark-like Bunting *Emberiza impetuani*	Passeriformes	15	TG	GRA	D	1(40)	33.8			38.4
Laughing Dove *Streptopelia senegalensis*	Columbiformes	98.8	TG	GRA	D	4(108)	36.1	35.8	39	37.9
Lesser Grey Shrike *Lanius minor*	Passeriformes	46	SW	INS	P	4(119)	31.3	35.7	55.6	38.3
Lilac-breasted Roller *Coracias caudatus*	Coraciiformes	107.5	SW	INS	P	3(36)	34.8	34.1	40.8	38.8
Long-billed Crombec *Sylvietta rufescens*	Passeriformes	11.1	AG	INS	P	1(11)	36.3			38.7
Ludwig's Bustard *Neotis ludwigii*	Gruiformes	4000	TG	INS	P	0(2)				34.5

Species	**Order**	**Mb (g)**	**Forage guild**	**Diet**	**Water source**	**n(N)**	**HD_{min} (°C)**	**HD_{start} (°C)**	**HD_{50} (°C)**	**NHD_{max} (°C)**
Marico Flycatcher *Bradornis mariquensis*	Passeriformes	26.2	SW	INS	P	13(360)	30.3	35.8	44.4	38.8
Namaqua Dove *Oena capensis*	Columbiformes	39.9	TG	GRA	D	3(172)	34.3	37.7	46.9	38.7
Namaqua Sandgrouse *Pterocles namaqua*	Pterocliformes	180.5	TG	GRA	D	0(8)				35.9
Northern Black Korhaan *Afrotis afraoides*	Gruiformes	739	TG	INS	P	2(43)	34.1			38.6
Pearl-spotted Owlet *Glaucidium perlatum*	Strigiformes	75	SW	INS	P	1(5)	37.0			37.0
Pririt Batis *Batis pririt*	Passeriformes	9.3	AG	INS	P	1(64)	35.1			38.7
Pygmy Falcon *Polihierax semitorquatus*	Falconiformes	60.5	SW	INS	P	5(53)	36.0	35.7	39.2	38.6
Red-backed Shrike *Lanius collurio*	Passeriformes	28.9	SW	INS	P	4(35)	32.1			37.4
Red-crested Korhaan *Lophotis ruficrista*	Gruiformes	674.5	TG	INS	P	1(55)	30.4			38.4
Red-faced Mousebird *Urocolius indicus*	Coliiformes	56.5	AG	FRU	P	9(28)	31.8	28.9	34.3	36.9
Red-headed Finch *Amadina erythrocephala*	Passeriformes	11.5	TG	GRA	D	0(8)				34.4
Rufous-eared Warbler *Malcorus pectoralis*	Passeriformes	10.2	AG	INS	P	1(7)	32.7			37.0

Species	**Order**	**Mb (g)**	**Forage guild**	**Diet**	**Water source**	**n(N)**	**HD$_{min}$ (°C)**	**HD$_{start}$ (°C)**	**HD$_{50}$ (°C)**	**NHD$_{max}$ (°C)**
Sabota Lark *Calendulauda sabota*	Passeriformes	25	TG	OMN	P	2(31)	36.8	35.4	40.3	38.6
Scaly-feathered Finch *Sporopipes squamifrons*	Passeriformes	11.1	TG	GRA	P	13(611)	30.7	36.2	41.9	38.6
Sociable Weaver *Philetairus socius*	Passeriformes	27.4	TG	OMN	P	44(538)	26.2	33.7	40.3	38.6
Southern Grey-headed Sparrow *Passer diffusus*	Passeriformes	24.7	TG	GRA	D	3(4)	32.1			31.8
Southern Masked-Weaver *Ploceus velatus*	Passeriformes	20.6	TG	OMN	D	17(74)	33.3	30.6	36.8	38.7
Southern Pale Chanting Goshawk *Melierax canorus*	Accipitiriformes	822	SW	INS*	D	0(26)				38.7
Southern Yellow-billed Hornbill *Tockus leucomelas*	Coraciiformes	189.5	TG	INS	P	19(99)	32.8	31.9	37.2	37.8
Spike-heeled Lark *Chersomanes albofasciata*	Passeriformes	25.3	TG	INS	P	7(50)	31.3	30	55.2	36.9
Spotted Eagle-Owl *Bubu africanus*	Strigiformes	600	SW	INS*	P	0(6)				37.4
Spotted Flycatcher *Muscicapa caerulescens*	Passeriformes	15	SW	OMN	P	0(13)				37.5
Spotted Thick-knee *Burhinus capensis*	Charadriiformes	472.2	TG	INS	D	0(5)				36.4
Swallow-tailed Bee-eater *Merops hirundineus*	Coraciiformes	20	SW	INS	P	2(67)	34.8			38.7

Species	**Order**	**Mb (g)**	**Forage guild**	**Diet**	**Water source**	**n(N)**	**HD_{min} (°C)**	**HD_{start} (°C)**	**HD_{50} (°C)**	**NHD_{max} (°C)**
Verreaux's Eagle-Owl *Bubu lacteus*	Strigiformes	2500	SW	INS*	P	0(3)				37.0
Violet-eared Waxbill *Granatina granatina*	Passeriformes	11.8	TG	GRA	D	1(14)	32.8			37.6
Wattled Starling *Creatophora cinerea*	Passeriformes	73	TG	OMN	D	8(19)	30.1	30.1	33.8	37.5
White-backed Mousebird *Colius colius*	Coliiformes	40	AG	FRU	P	20(50)	31.9	32.5	35.0	37.5
White-browed Sparrow-Weaver *Plocepasser mahali*	Passeriformes	42.7	TG	OMN	P	51(449)	30.1	30.1	43.1	38.8
Yellow Canary *Crithagra flaviventris*	Passeriformes	17.5	TG	GRA	D	6(124)	34.3	33.8	39.5	38.1
Yellow-bellied Eremomela *Eremomela icteropygialis*	Passeriformes	7.9	AG	INS	P	6(159)	34.1	35.2	41.3	38.1

Table F2: Estimates (intercept and slope) and p-values of for the logistic relationships of activity levels and heat dissipation behaviour (panting or gular fluttering) as a function of air temperature for 35 species in the Kalahari Desert. The % of all activity behaviour allocated towards foraging is indicated for each species, even species for which statistical analyses could not be performed.

	Activity levels			**% Activity allocated to foraging**	**Heat dissipation**		
Species	**a**	**b**	**p-value**		**a**	**b**	**p-value**
Acacia Pied Barbet *Tricholaema leucomelas*	3.91	-0.11	0.210	63	-14.24	0.40	< 0.001
African Red-eyed Bulbul *Pycnonotus nigricans*	-3.89	0.12	0.536	73	-20.32	0.59	< 0.01
Anteating Chat *Myrmecocichla formicivora*	0.50	-0.08	0.103	100	-13.13	0.30	< 0.01
Ashy Tit *Parus cinerascens*	6.09	-0.16	0.0121	100	-29.51	0.77	< 0.001
Black-chested Prinia *Prinia flavicans*	1.38	0.00	0.941	61	-27.97	0.71	< 0.001
Cape Glossy Starling *Lamprotornis nitens*	0.40	-0.05	0.367	84	-20.33	0.55	< 0.001
Cape Sparrow *Passer melanurus*	4.24	-0.10	0.43	75	-9.67	0.27	0.083
Cape Turtle-Dove *Streptopelia capicola*	1.01	-0.08	< 0.05	81	-18.45	0.46	< 0.001
Chat Flycatcher *Bradornis infuscatus*	-4.00	0.09	0.379	100			
Chestnut-vented Tit-Babbler *Parisoma subcaeruleum*	0.89	0.04	0.572	80	-19.90	0.49	< 0.01
Common Fiscal *Lanius collaris subcoronatus*	0.67	-0.06	0.345	100	-7.60	0.15	0.08

	Activity levels			% Activity allocated to foraging	Heat dissipation		
Species	**a**	**b**	**p-value**		**a**	**b**	**p-value**
Common Ostrich *Struthio camelas*	-2.28	0.08	0.324	67	-10.59	0.34	< 0.01
Common Scimitarbill *Rhinopomastus cyanomelas*	-0.18	0.03	0.689	100	-26.49	0.74	< 0.01
Crimson-breasted Shrike *Laniarius atrococcineus*	3.09	-0.09	0.246	93	-21.26	0.56	< 0.01
Crowned Lapwing *Vanellus coronatus*	5.87	-0.22	< 0.001	80	-34.79	0.89	< 0.001
Dusky Sunbird *Cinnyris fuscus*	1.50	-0.01	0.932	64	-37.19	1.01	0.064
Fawn-coloured Lark *Calendulauda africanoides*	0.95	-0.06	< 0.05	61	-10.61	0.23	< 0.01
Fork-tailed Drongo *Dicrurus adsimilis*	3.74	-0.25	0.094	100	-10.78	0.24	<0.05
Kalahari Scrub-Robin *Cercotrichas paena*	0.93	-0.05	0.119	64	-15.80	0.37	< 0.001
Lark-like Bunting *Emberiza impetuani*	14.42	-0.50	0.142				
Laughing Dove *Streptopelia senegalensis*	6.24	-0.25	< 0.05	58	-35.47	0.91	< 0.001
Lesser Grey Shrike *Lanius minor*	3.62	-0.16	0.292	100	-8.22	0.15	0.553
Lilac-breasted Roller *Coracias caudatus*	-25.57	0.00	1	100	-18.04	0.44	0.137
Marico Flycatcher *Bradornis mariquensis*	0.59	-0.07	0.105	100	-15.29	0.35	< 0.01

Species	**Activity levels**			**% Activity allocated to foraging**	**Heat dissipation**		
	a	**b**	**p-value**		**a**	**b**	**p-value**
Namaqua Dove *Oena capensis*	0.14	-0.03	0.521	66	-15.02	0.32	0.139
Northern Black Korhaan *Afrotis afraoides*	7.42	-0.24	0.051	38			
Pririt Batis *Batis pririt*	6.66	-0.18	0.162	91			
Pygmy Falcon *Polihierax semitorquatus*	-11.62	0.22	0.555	100	-32.88	0.84	< 0.01
Red-crested Korhaan *Lophotis ruficrista*				17			
Red-faced Mousebird *Urocolius indicus*	2.33	-0.06	0.675	81	-18.57	0.54	0.109
Sabota Lark *Calendulauda sabota*	15.07	-0.39	0.107	100			
Scaly-feathered Finch *Sporopipes squamifrons*	2.35	-0.08	< 0.05	60	-21.47	0.51	< 0.001
Sociable Weaver *Philetairus socius*	2.15	-0.06	< 0.05	82	-17.85	0.44	< 0.001
Southern Masked-Weaver *Ploceus velatus*	8.10	-0.21	0.1003	62	-17.52	0.48	< 0.01
Southern Yellow-billed Hornbill *Tockus leucomelas*	-3.21	-0.01	0.962	100	-20.48	0.55	< 0.001
Spike-heeled Lark *Chersomanes albofasciata*	1.00	-0.04	0.395	62	-4.86	0.09	0.248
Swallow-tailed Bee-eater *Merops hirundineus*	-6.14	-0.11	0.421	100			

Species	Activity levels			% Activity allocated to foraging	Heat dissipation		
	a	**b**	**p-value**		**a**	**b**	**p-value**
Wattled Starling *Creatophora cinerea*	0.67	-0.04	0.87	100	-16.29	0.47	0.124
White-backed Mousebird *Colius colius*	8.20	-0.25	< 0.05	88	-25.75	0.7359	< 0.001
White-browed Sparrow-Weaver *Plocepasser mahali*	4.46	-0.16	< 0.05	82	-9.69	0.23	< 0.001
Yellow Canary *Crithagra flaviventris*	5.29	-0.15	0.507	67	-20.24	0.51	< 0.001
Yellow-bellied Eremomela *Eremomela icteropygialis*	2.68	-0.02	0.81	95	-20.14	0.49	< 0.01

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