# EVAPORATIVE COOLING CAPACITY AND HEAT TOLERANCE IN KALAHARI DESERT BIRDS: EFFECTS OF BODY MASS AND PHYLOGENY

By

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# PREFACE

The experimental work described in this thesis was carried out in Wildsgenot and Leeupan Ranches, Northern Cape, South Africa, between January 2012 and March 2013. The study was conducted under the supervision of Professors Andrew E. McKechnie and Blair O. Wolf.

This thesis contains original work by the author and none of its contents have been submitted in any other form for any other degree/diploma to any other institution. Where data collected by others is described, the authors have been duly acknowledged in the text.

All procedures related to the use of animals in these studies were approved by the Animal Ethics Screening Committee of the University of Pretoria (EC071-11).

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Maxine Whitfield

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# SUMMARY

The roles of phylogeny and body size in avian heat stress physiology, and how they interact to set the upper limits to heat dissipation capacity, are largely unexplored. Determining thermal end points and maximum capacity for evaporative heat dissipation in species from diverse ecological guilds and evolutionary clades is vital for understanding species-specific vulnerability to future climatic scenarios. I measured evaporative water loss (EWL), resting metabolic rate (RMR) and body temperature ($T_b$) in three arid-zone passerines and three columbids of varying mass, namely the scaly-feathered weaver (*Sporopipes squamifrons*, ~11 g, SFW), sociable weaver (*Philetairus socius*, ~26 g, SW), white-browed sparrow weaver (*Plocepasser mahali*, ~40 g, WBW), Namaqua dove (*Oena capensis*, ~37 g, ND), laughing dove (*Spilopelia senegalensis*, ~89 g, LD) and Cape turtle dove (*Streptopelia capicola*, ~148 g, CTD) at maximum air temperatures ($T_a$) of 48–60°C. I found that evaporative water loss increased approximately linearly in all six species above a $T_a$ of ~ 40 °C, which resulted in SFW, SW, WBW, ND, LD and CTD dissipating a maximum of 140, 220, 190, 498, 218 and 231 % of metabolic heat loads at the highest $T_a$s respectively. All six species used facultative hyperthermia at high $T_a$s and were able to regulate $T_b$ up to and just beyond $T_b = 45$ °C. At the highest $T_a$s experienced, passerines exhibited uncontrolled increases in $T_b$ above 45 °C, resulting in 57, 100 and 100 % of SFW, SW and WBW respectively, reaching thermal limits at $T_a = 48$, 52 and 54 °C. Very few doves exhibited uncontrolled hyperthermia or reached thermal limits at their highest respective test $T_a$s ($T_a = 56$, 68 and 60 °C in CTD, LD and ND respectively), suggesting that these birds could potentially survive higher $T_a$s, and that lethal $T_b$ was marginally higher than my conservative estimations. A conventional analysis found significant differences between doves and passerines in the slopes of EWL as well as the magnitude of the change in RMR, EWL and $T_b$ between $T_a$ = 35 and 48 °C. However, once phylogeny was controlled for, these differences were shown to be a result of phylogenetic inertia. Both a conventional analysis and a phylogenetic independent contrast (PIC) found a significant effect of body mass on slope of EWL, change in EWL (PIC only) and change in $T_b$ between $T_a$ = 35 and 48 °C. From the results of this study, I argue that by utilizing high ratios of cutaneous EWL to respiratory EWL, doves generate much less metabolic heat at high $T_a$s than passerines. I suggest that larger passerines are better able to tolerate heat than smaller passerines, whereas the opposite is the case in doves. The lack of data from small doves obscured this finding in the conventional and PIC analyses. Further studies on the upper limits to the avian capacity for evaporative cooling and heat tolerance are critical for larger-scale mechanistic modeling of vulnerability to extreme heat events under current and future climate scenarios.

# CHAPTER 1: GENERAL INTRODUCTION

The intense solar radiation, low primary productivity, scarcity of drinking water and extreme temperature that characterize deserts (Lovegrove 1993; Williams and Tieleman 2005) present significant thermal and energetic challenges to their inhabitants, yet many species of invertebrates, reptiles, amphibians, mammals and birds thrive in these environments (Schmidt-Nielsen 1979; Randall et al 2002). Some of the most long-standing questions in the fields of ecological and evolutionary physiology relate to how desert animals thermoregulate and maintain energy balance in such challenging habitats.

## *Heat balance at high air temperatures*

Animals gain heat from the environment via convection, radiation and conduction, and through the heat generated by metabolism (Porter and Gates 1969). Physical factors that affect the heat load imposed by the environment include air temperature, wind speed, humidity (which influences vapour pressure deficit), thermal radiation and direct and reflected solar radiation (Porter and Gates 1969; Walsberg 1985; Wolf and Walsberg 1996b). Heat is lost to the environment via the same passive mechanisms of convection, conduction and radiation down a temperature gradient (Mitchell 1977), but heat loss is greatly increased by the evaporation of water from the skin and respiratory tract (Bartholomew and Cade 1963; Taylor 1977; Weathers 1981; McKechnie and Wolf 2010).

In terrestrial animals, evaporative water loss (EWL) is the only means of heat dissipation when air temperature ($T_a$) exceeds body temperature ($T_b$) (Dawson and Whittow 2000). Evaporation occurs cutaneously (cutaneous evaporative water loss, CEWL) or via the respiratory passages (respiratory evaporative water loss, REWL) (Dawson 1982) and a rapid, approximately linear increase is observed when $T_a$ exceeds $T_b$ (Wolf and Walsberg 1996a).

### *Birds in desert environments*

Birds, at first glance, do not seem well-suited to desert environments. Most species are diurnal and do not utilize thermal refugia such as burrows (but see Williams et al. 1999), and therefore show a limited ability to avoid the heat of the day compared to many small desert mammals (Bartholomew and Cade 1963). In addition, birds have high rates of mass-specific metabolism, which translate into proportionately higher metabolic heat loads (Dawson 1982). This in turn leads to increased rates of mass-specific evaporative water loss, which is exacerbated by their limited capacity for water storage, high surface area to volume ratios and low thermal inertia imposed by small body size (Dawson 1976). Despite these apparent disadvantages, birds are well represented in desert habitats, which make them fascinating subjects for research on thermoregulatory patterns. What allows these animals to cope with the challenges of desert living?

Birds possess a number of physiological characteristics that are suited to hot, arid conditions. They excrete nitrogenous waste in the form of uric acid- a process which minimizes the loss of water in a water-scarce environment (Bartholomew and Cade 1963). In addition, their small body size and high mobility translate into modest resource requirements and an ability to use widely scattered resources (Wolf 2000). Elevated body temperatures (~41 °C), also confer an advantage to birds in desert environments, and are 3–4 °C higher than those of mammals. This results in reduced heat gain from the environment when $T_a$ exceeds $T_b$ (Calder and King 1974). Birds also use facultative hyperthermia by allowing their $T_b$ to rise by 2–4 °C during periods of heat stress (Tieleman and Williams 1999; Boyles et al 2011). Under conditions of acute heat stress, birds ranging in size from 10-1000 g may reduce rates of total evaporative water loss by as much as 50% through this process (Lasiewski et al. 1966; Tieleman and Williams 1999;). Facultative, regulated hyperthermia differs from pathological hyperthermia in that it involves the maintenance of a stable, sub-lethal body temperature rather than the uncontrolled escalation of body temperature towards lethal limits (Lasiewski et al 1966) [as observed in brown and Abert's towhees (Dawson 1954)].

### *Effects of evolutionary history on the energetic efficiency of evaporative heat loss*

Survival during an extreme heat event requires the avoidance of lethal $T_b$ [~ 46-47 °C (Schmidt-Nielsen 1964; Portner and Farrell 2008; Williams et al 2012)] by offloading exogenous and endogenous heat loads through evaporation of water from the body surfaces. However, conserving body water through both behavioural and physiological means to delay the onset of fatal dehydration [estimated ranges vary from 11 to 20 % of body mass (Arad et al 1989; Wolf 2000)], is equally important (Dawson 1954; McKechnie and Wolf 2010). During very hot weather, therefore, birds face a fundamental trade-off between the risks of lethal hyperthermia and acute dehydration.

The energetic efficiency and overall effectiveness of evaporative heat dissipation is greatly affected by the avenues of evaporation employed, which are largely determined by evolutionary history. Many Columbiformes (pigeons and doves), are able to dissipate the majority of their heat load through cutaneous evaporation (Smith and Suthers 1969; Marder and Ben-Asher 1983; Marder and

Arieli 1988; Withers and Williams 1990a). It has been shown that this avenue of heat loss entails lower metabolic costs than respiratory evaporation and could, thus, be more efficient in terms of total water loss (Withers and Williams 1990a; McKechnie and Wolf 2004a). Some nonpasserine taxa such as Caprimulgiformes, Strigiformes, Galliformes, Pelecaniformes, Cuculiformes, Columbiformes and Gruiformes are able to use a form of enhanced REWL known as gular fluttering, which, due to the large vascular nature of the gular surface, requires little metabolic effort (Bartholomew et al 1962; Bartholomew et al 1968; Dawson and Whittow 2000). In passerines REWL prevails, and the relative contribution of CEWL typically decreases as $T_a$ increases (Dawson 1958; Dawson 1982; Wolf and Walsberg 1996b; Williams and Tieleman 2001). Panting requires an increase in ventilatory rate, which results in increased metabolic heat production and could place passerines at a disadvantage relative to taxa that rely predominantly on cutaneous evaporation under conditions of extreme heat stress (Dawson 1958).

### *Effects of body size on thermoregulation at high air temperatures*

Body size plays an integral role in the dynamics of thermoregulation at high $T_a$. Although total EWL increases with body mass (Williams 1996), small birds have higher mass-specific metabolic rates, which leads to increased rates of ventilation and therefore higher mass-specific rates of EWL (Bartholomew and Cade 1963). The higher surface area to volume ratios of small birds results in reduced thermal inertia, and heat is therefore gained and lost at much higher rates compared to larger birds (Wolf and Walsberg 1996b). Theoretically, because small birds may be able to dissipate relatively larger heat loads, maintaining $T_b$ below lethal limits should be possible even in extreme heat, given that enough water is available. However, rates of water loss increase rapidly in small birds, and death by dehydration through the exhaustion of their body water pool, especially over prolonged periods of heat stress, may be the major physiological constraint faced by smaller species (McKechnie and Wolf 2010). In contrast, larger species appear to be more at risk from uncontrolled hyperthermia and heat stroke at high air temperatures, due to their high thermal inertia and lower mass-specific rates of EWL (Weathers 1981).

### *Relevance of mechanism-based, heat tolerance research with respect to Earth's changing climate*

The accelerated rate at which the planet's climate is changing is currently the greatest threat to the diversity of fauna and flora on the planet. We are already observing significant changes in productivity, physiology and growth of plants, and in changes in the phenology and distribution of animals (Hughes 2000; Parmesan and Yohe 2003; Parmesan 2006), and it is likely that the longer-term effects will be of much larger, and of more dire consequences (McLaughlin et al 2002; Williams et al 2003; Thomas et al 2004; McKechnie and Wolf 2010).

Mean annual global temperature is predicted to rise by 2–5 °C by 2080 (IPCC 2011). While this increase in mean temperature is important, an increase in extreme climatic events, during which the physiological tolerance levels of many species are surpassed, may be of greater consequence (Jentsch et al 2007). For birds, heat waves, which are predicted to increase in frequency, intensity and duration in the coming decades (IPCC 2011), are bottlenecks for survival and reproduction (McKechnie et al. 2012). Birds are important members of animal communities, providing critical ecosystem services such as pollination and seed dispersal, and influencing food-webs through their occupation of a range of trophic levels (Whelan et al 2008). Extreme weather events have the potential to change the abundance, diversity and distribution of birds through frequent mass mortality events (Parmesan et al 2000; Albright et al 2010; Mckechnie and Wolf 2010). Mass die-offs of birds as a result of heat waves have already occurred on several occasions during the last century (Finlayson 1932; Keast 1960; Miller 1963; Towie 2009). McKechnie and Wolf (2010) modelled avian water requirements as a function of body mass during extreme heat waves using current $T_a$ maxima as well as values predicted for the 2080's. They found that water requirements will increase drastically in the future, with the magnitude of this increase being most pronounced in smaller species. This could lead to dramatically reduced survival times for small birds during heat waves.

As we become less able to reverse or even slow the process of climate change (IPCC 2011), understanding how future climates will affect species is of critical importance for biodiversity conservation (Root et al 2003). Frameworks to guide researchers are invaluable (Williams et al. 2008; McKechnie et al. 2012), and allow for small-scale research from disparate parts of the world to be reconciled towards meta-analyses of climate change impacts and strategies for mitigation. Climate envelope models (CEMs) have been used to predict shifts in the distribution of species by assuming that current geographic distribution represents a species' ideal environmental requirements (Peterson 2001; Erasmus et al 2002; Araújo et al 2005). Thomas et al. (2004) compiled studies that used the CEM approach, concluding that many species are going to go extinct due to the loss of large parts of their ranges. However, the limitations of pattern-based approaches are becoming increasingly apparent (Thuiller 2004; Hijmans and Graham 2006; Huntley et al. 2010; Hockey et al. 2011; McKechnie et al. 2012), and the support of mechanistic and bioenergetic models (Woodward and Rochefort 1991; Guisan and Zimmermann 2000; Humphries et al 2002; Kearney and Porter 2009; McKechnie and Wolf 2010), which are based on aspects of a species' physiology and energy balance, are vital in producing reliable predictions of climate change effects (Denny and Helmuth 2009).

Williams et al. (2008) proposed that a species' vulnerability to climate change is determined by both sensitivity (intrinsic aspects of an organism's physiology) and exposure (extrinsic climatic or environmental factors), and species-specific studies, such as this dissertation, that quantify avian thermal tolerance and heat dissipation abilities fall into this "sensitivity" category. McKechnie et al. (2012) outlined a new approach for predicting the effects of climate change on arid-zone birds specifically, suggesting that body mass, phylogenetic history and aspects of physiology and ecology that relate to exposure to heat should be taken into account when choosing species to work with.

The ability of different avian taxa to tolerate heat varies with heat dissipation mechanisms (which are determined mainly by phylogenetic history) and body size, and differential extirpation during future heat events could result in changes in avian community structure, which could, in turn, have considerable effects on whole ecosystems and functional biodiversity. McKechnie et al. (2012) encourages researchers to quantify the temperature dependence of various physiological, reproductive and behavioural traits, as well as measure species-specific ranges of thermal tolerance (McKechnie et al 2012). These data will allow for modelling of survival and reproduction by incorporating possible future climate scenarios (McKechnie et al 2012). My study compares and contrasts the physiological responses of members of the Passerinidae and Columbidae families, over a range of body masses, by measuring RMR, EWL, $T_b$ and thermal limits at extremely high $T_a$s,.

### *Doves and passerines as model avian species in heat dissipation research*

Many species of doves, ranging in mass from approximately 30–350 g, are well represented and often found in high abundance in desert habitats, e.g. the deserts of Africa, Australia and North America (Baptista et al 1997). Doves typically group in large numbers on feeding grounds and around water holes. A number of studies have shown that doves have the ability to dissipate large amounts of heat at extraordinarily low metabolic costs by utilizing high rates of CEWL with only modest increases in REWL; these relative rates of evaporation are highly flexible depending on the bird's thermal acclimation (Marder and Arieli 1988; McKechnie and Wolf 2004a). These physiological and ecological characteristics make doves ideal candidates for investigating heat tolerance mechanisms, as well as the role that phenotypic flexibility may play in surviving extreme heat events (Marder and Gavrieli-Levin 1987).

Passerine species, ranging in mass from 7–700 g, are also well represented in many desert ecosystems (Gochfeld et al 1996). Since many studies have used passerines as model species when investigating heat dissipation at $T_a$s above $T_b$, it is relatively straightforward to compare similarly-sized species from varying habitats. Unlike doves, passerine birds dissipate heat loads primarily through respiratory evaporation with relatively low rates of CEWL at high environmental temperatures, and do not increase this CEWL in response to thermal acclimation (Tieleman and Williams 2002a). Doves and passerines provide interesting model taxa for comparing the effectiveness of differing heat dissipation strategies and the vulnerability of these two avian groups to future climate scenarios.

### *Dissertation structure*

This dissertation contains a general introduction and conclusion chapter, as well as two stand-alone chapters, written in manuscript style and based on empirical data. There is some inevitable overlap in the content of the introduction, materials and methods, and structure of results between chapters, though I tried wherever possible to refer to a previous chapter to avoid repetition.

In Chapter 2, I examined the effects of body mass on resting metabolic rate (RMR), EWL, evaporative capacity (the ratio of evaporative heat lost to metabolic heat produced), and $T_b$ at high $T_a$ in three arid-zone passerines (family Ploceidae) varying in mass from ~10-50 g, namely *Sporopipes squamifrons* (scaly-feathered weaver, ~11 g), *Philetairus socius* (sociable weaver, ~27 g) and *Plocepasser mahali* (white-browed sparrow-weaver, ~47 g) (Hockey et al 2005).

In Chapter 3, I examined the effects of body mass on RMR, EWL, evaporative capacity and $T_b$ at high $T_a$ in three arid-zone columbids varying approximately 4-fold in mass, namely *Oena capensis* (Namaqua dove, ~40 g), *Spilopelia senegalensis* (laughing dove, ~100 g; formerly *Streptopelia senegalensis*) and *Streptopelia capicola* (Cape turtle dove, ~153 g) (Hockey et al 2005). I also compared heat tolerance variables between Passeriformes and Columbiformes using seven passerine and six columbid species (including the six species from the present study and data from other sources).

Chapter 4 provides general conclusions and suggestions for future research.

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# CHAPTER 2: SCALING OF HEAT TOLERANCE AND EVAPORATIVE COOLING CAPACITY IN THREE PASSERINES FROM THE KALAHARI DESERT

## Abstract

During heat stress, when air temperature ($T_a$) exceeds body temperature ($T_b$), the dissipation of heat through evaporative water loss (EWL) becomes the only means of avoiding lethal $T_b$. Animals face a conflict, however, as they must regulate EWL so as to avoid lethal dehydration. I measured evaporative water loss (EWL), resting metabolic rate (RMR) and body temperature ($T_b$) in three arid-zone passerines of varying mass, namely the scaly-feathered weaver (*Sporopipes squamifrons*, ~11 g), sociable weaver (*Philetairus socius*, ~26 g) and white-browed sparrow weaver (*Plocepasser mahali*, ~40 g) at air temperatures ($T_a$) of up to 48, 52 and 54 °C respectively. I found that evaporative water loss increased approximately linearly by 10-, 20- and 16-fold in scaly-feathered weavers, sociable weavers and white-browed sparrow-weavers respectively above a $T_a$ of ~ 40 °C, which resulted in the dissipation of a maximum of ~140, 220 and 190 % of metabolic heat loads at their highest respective $T_a$s. All three species used facultative hyperthermia at $T_a$s below 48 °C, but at higher $T_a$ values $T_b$ increased in a manner suggestive of uncontrolled hyperthermia. Average maximum $T_b$ in birds at their thermal limit was ~45.5 °C in all three species. I found a strong effect of body mass on thermal end points—the $T_a$ at which $T_b$ was very close to lethal limits, birds became frantic and/or locomotory activity became disorganised. However, I did not find a predictable effect of body mass on EWL and RMR. Determining thermal end points and maximum capacity for evaporative heat dissipation in species from diverse ecological guilds and evolutionary clades is vital for exploring species-specific vulnerability to future climatic scenarios.

## Introduction

When faced with extremely high air temperatures ($T_a$s), birds typically seek shaded microsites and cease all activity. Although this decreases the heat load imposed upon the bird by the environment, as well as its own metabolic heat production, it also means that water intake via foraging and/or drinking is curtailed (Wolf and Walsberg 1996b). Birds are therefore presented with a trade-off between hyperthermia and dehydration avoidance: They must avoid lethal $T_b$ [~ 46-47 °C (Schmidt-Nielsen 1964; Portner and Farrell 2008; Williams et al 2012)] by dissipating heat loads, a process achieved predominantly through high rates of EWL. However, conserving body water through both behavioural and physiological means (Tieleman and Williams 1999), thereby delaying the onset of fatal dehydration [approximately 11 % of body mass (Wolf 2000)], is equally important.

The energetic efficiency and overall effectiveness of avian evaporative heat dissipation is greatly affected by the avenues of evaporation, which are largely determined by evolutionary history. In passerines, the fractional contribution of CEWL typically decreases as $T_a$ increases, with REWL in the form of panting becoming dominant (Dawson 1958; Calder and Schmidt-Nielsen 1968; Dawson 1982; Wolf and Walsberg 1996b; Williams and Tieleman 2001). This could potentially place passerines at a disadvantage relative to cutaneous evaporators under conditions of severe heat stress, as panting requires an increase in ventilation rate, which presumably results in increased metabolic heat production (Dawson 1958).

Body size plays an integral role in the dynamics of thermoregulation at high $T_a$s. Total EWL increases with increasing mass (Williams 1996). Small birds, however, have higher mass-specific metabolic rates and therefore higher mass-specific rates of EWL (Bartholomew and Cade 1963). The higher surface area/volume ratios of small birds result in reduced thermal inertia, so heat is therefore gained and lost at much higher rates compared to larger birds (Wolf and Walsberg 1996b). Theoretically, because small birds are able to dissipate heat quickly, it is possible that maintaining $T_b$ below lethal limits is not the major constraint on tolerance of extreme heat. Instead, dehydration through the exhaustion of their body water pool, especially over prolonged periods of heat stress, may be the major physiological constraint they face. McKechnie and Wolf (2010) predict reduced survival times for small birds during heat waves. On the other hand, at high $T_a$s large birds would theoretically be at higher risk of pathological hyperthermia than of dehydration, due to their high thermal inertia and lower rates of mass-specific EWL (Weathers 1981).

The roles of body size and evolutionary history in avian heat stress physiology, and how they interact to set the upper limits of heat dissipation abilities, are largely unexplored. In fact, the upper limits to the avian capacity to avoid lethal hyperthermia are relatively unknown. Numerous studies have shown that EWL increases rapidly at $T_a$s above $T_b$ (Cade et al 1964; Dawson and Fisher 1969; Coulombe 1970; Lasiewski et al 1970; Weathers and Caccamise 1975) but, to my knowledge, very few, if any, have explored evaporative capacity at very high $T_a$s, or thermal end point (defined in this study as the $T_a$ at which birds are no longer able to coordinate locomotory activity and $T_b$ increases to near-lethal levels). Evaporative capacity in this study is defined by the ratio of evaporative heat lost to metabolic heat produced, and gives an indication of the net heat energy dissipated by a bird. Evaporative heat dissipation is most effective when the humidity of the surrounding air is low, and it is therefore important to use high enough flow rates during experiments to keep humidity within chambers to low levels (Dawson 1982). To date, relatively few studies have involved very low chamber humidities (e.g. Wolf and Walsberg 1996b; Tieleman et al. 2002b; Tieleman and Williams 2002; McKechnie and Wolf 2004). This species-specific physiological research is the foundation necessary for larger-scale mechanistic models predicting how species vary in their resilience to the more frequent and extreme heat waves predicted to occur as a result of anthropogenic climate change (IPCC 2011).

In this study, I investigated the scaling of, EWL, evaporative capacity, resting metabolic rate (RMR) and $T_b$ at high $T_a$ in three arid-zone passerines (family Ploceidae) varying in mass from ~10-40 g. I expected to see an increase in RMR as $T_a$ exceeded $T_b$, due to the costs of heat dissipation mechanisms. I expected that the slope of the increase in RMR above the upper critical limit (UCL) of the TNZ would be steeper in smaller passerines (Weathers 1981).

I predicted that the slope of $T_a$ versus mass-specific EWL at $T_a$s above $T_b$ would increase with decreasing body mass (Bartholomew and Cade 1963). I also expected that, due to their higher mass-specific EWL coupled with limited body water supply, smaller birds would become dehydrated quickly, and consequently reach near-lethal $T_b$ levels at lower $T_a$s than larger birds. Therefore, larger birds were expected to have higher thermal end points. It is important to note that these predictions may be specific to the artificial situation of a ramped $T_a$ profile, where birds are exposed to stable $T_a$s for a relatively short time, after which $T_a$ is increased to a higher setpoint. Under natural conditions, which would involve chronic heat stress at a certain $T_a$ for comparatively long time periods, body mass and thermal limit could interact differently.

Because the species being tested are arid-adapted, I also expected facultative hyperthermia to play a significant role at high $T_a$s, with $T_b$ increasing in accordance with increasing $T_a$ to aid in water savings (Tieleman and Williams 1999). Facultative hyperthermia differs from pathological hyperthermia in that it involves the maintenance of a stable, sub-lethal body temperature rather than the uncontrolled escalation of body temperature towards lethal levels (Tieleman and Williams 1999).

## Materials and methods

### *Study sites*

The study was conducted at two sites in the southern Kalahari Desert of South Africa, over two consecutive summer seasons. During the first summer, from 26 January to 1 April 2012, I collected data at Wildsgenot Game Ranch (890m a.s.l., 27°04′ S, 21°23′ E). The following summer, from 27 December 2012 to 3 March 2013, I worked at Leeupan Ranch (26°58′S, 21°50′E). These sites are both situated along the dry Kuruman River, ~50 km apart from each other. Mean annual rainfall is similar at both sites (190-210 mm/year). Habitat and vegetation are also similar, consisting of *Acacia erioloba*-dominated woodland, and sparse grassland on red sand dunes. Maximum $T_a$ during the study periods (including two weeks preceding my first measurements) ranged from 20–43 °C at both Wildsgenot Game Ranch and Leeupan.

### *Study species*

Rates of EWL, RMR and $T_b$ were measured at a range of $T_a$ in three species, namely *Sporopipes squamifrons* (scaly-feathered weaver, ~11 g), *Philetairus socius* (sociable weaver, ~27 g) and *Plocepasser mahali* (white-browed sparrow-weaver, ~47 g) (Hockey et al 2005). All three species are arid-zone passerines of the family Ploceidae, with *S. squamifrons* and *P. socius* endemic to the arid savannah regions of southern Africa, whereas *P. mahali* also occurs in the arid savannahs of East Africa.

All three species are resident year-round within the Kalahari desert region, with the two larger species exhibiting a high degree of site variability and *S. squamifrons* being locally nomadic (Hockey *et al.* 2005). *Philetairus socius* and *P. mahali* are omnivorous, consuming both seeds and insects, and *S. squamifrons* is predominantly granivorous.

Birds were captured using mist nets at various times of the day, and initially held in cloth bags. All birds used in the study were adults and appeared to be healthy. The mean body masses of *S. squamifrons P. socius*, *P. mahali* were 10.4 ± 0.7 g (mean ± SD; n = 16), 24.9 ± 1.0 g (n = 25) and 39.4 ± 2.9 g (n = 30) respectively. Birds were either used for measurements immediately following capture, or held for 1–24 h in cages constructed of shade cloth, with millet seed and/or meal worm larvaeas well as water available *ad libitum*. Birds were always offered water before the experiment, but if they were unwilling to drink freely, a feeding tube attached to a syringe was used to place water directly into the crop. An individual was subjected to a maximum of three $T_a$ values per day, and time in captivity did not exceed 24 h. After an experiment, the bird was cooled down in front of an air conditioner, and offered water after its $T_b$ had stabilised at normothermic levels. The bird was then released at the site of capture after a short rest in a cloth bag.

### *Air and body temperature measurements*

Air temperature within the chambers used for gas exchange measurements was measured using a thermistor probe (model TC-100, Sable Sytems, Las Vegas NV, USA) inserted into the lid of the chamber through a small sealable hole. Temperature-sensitive passive integrated transponder (PIT) tags (Destron Fearing, St. Paul MN, USA) were implanted into each bird's body cavity in the abdominal region. Birds were restrained by one person, while another person created a clear area of skin by parting the feathers just below the ribcage and cleaning the area with ethanol. Using padded surgical forceps, the skin and abdominal wall of the bird were pulled away from the visceral organs and held taut. The sterilised PIT tag was then injected using a sterilised needle under the abdominal wall through the taut skin, paying close attention to keep the needle approximately parallel to the skin, and not to immerse it more than 0.5 cm. Once the PIT tag had been inserted, the small wound was dabbed with a minute amount of cyanoacrylate adhesive to close up the skin and prevent infection. The feathers were then straightened and allowed to dry before the bird was placed in a chamber. During injections, the bird's head was covered to aid in calming it. While the bird was in the chamber, $T_b$ was measured using a pit tag reader and portable tranceiver system (Destron Fearing, St. Paul MN, USA). A representative sample of seventy PIT tags were calibrated using a digital thermocouple reader (model RDXL12SD, Omega, Stamford CT, USA) with Cu–Cn thermocouples (Physitemp, Clifton NJ, USA) in a circulating water bath over temperatures from 39 to 46 °C (representative of the range of bird $T_b$ expected within the thermal neutral zone and above). $T_b$ values measured with the PIT tags deviated from actual values by 0.02 ± 0.09 °C (mean ± SD, n = 70), and it was hence decided that corrections were unnecessary.

### *Gas exchange measurements*

Gas exchange [carbon dioxide production $\dot{V}_{CO_2}$ (ml $g^{-1}$ $hr^{-1}$) and evaporative water loss $\dot{V}_{H_2O}$ (ml $g^{-1}$ $hr^{-1}$)] were measured at a range of $T_a$s between 25 and 54 °C using an open flow-through respirometry system. Birds were placed individually in sealable plastic metabolic chambers with volumes of 1.9 L (*P. socius* and *S. squamifrons*) or 4 L (*P. mahali*). A 1-cm layer of mineral oil was placed in the bottom of each chamber to prevent evaporation from urine and faeces, with a plastic mesh platform (large enough mesh to allow faeces to fall through) positioned approximately 10 cm above the oil layer. The chambers were placed in a controlled-environment box which controlled air temperature via a Peltier device (model AC-162, TE Technology Inc, Traverse City MI, USA) and a custom-built controller. During the first season, atmospheric air was supplied by a pump with a maximum capacity of 10 L min$^{-1}$ (model DOA-P13- BN, Gast Air Pumps, Benton Harbour MI, USA) before being dried by two columns of silica gel and drierite connected in series. During the second season, compressed air was pushed through a membrane dryer (Champion® CMD3 air dryer and filter). During both seasons, the airstream was then split into two channels, namely the baseline and chamber, with baseline flow rates regulated by a needle valve (Swagelok, Solon OH, USA), and chamber flow rates by mass flow controllers (Alicat Scientific Inc., Tuscon AZ, USA). Flow rates for the chamber channel were recorded manually from the screen of the mass flow controller, whereas flow rates for the baseline channel were maintained at approximately 1.5 L/min, checked using the mass flow meter of an subsampling unit (SS-3, Sable Systems, Las Vegas NV, USA). Appropriate flow rates were chosen with the aim of keeping absolute humidity levels within the chamber as low as possible (water vapour pressure below 1 kPa at all times), while still maintaining an accurately measurable difference in [$CO_2$] and water vapour pressure between the baseline and chamber. Depending on $T_a$ and the body mass of the bird, flow rates ranging 2 - 40 L min$^{-1}$ were used. Birds tended to remain calmer when flow rates were higher, and chamber humidity lower (personal observation). Due to the high flow rates used, fractional depletion of oxygen within the chamber was too small for accurate measurements of oxygen consumption (FC-10A, Sable Systems, Las Vegas NV, USA). Birds were held at least one hour before the start of experimental runs and we thus assumed a respiratory exchange ratios (RER) to be 0.71, representative of lipid metabolism in post-absorptive birds (Walsberg and Wolf 1995). To enhance mixing of air within the chambers, the air inlet was positioned near the top of the chamber and the outlet near the bottom. Excurrent air from the chamber and a baseline channel of incurrent air were sequentially subsampled using a flow multiplexer (model MUX3-1101-18M, Sable Systems, Las Vegas NV, USA) in manual mode. At the start of each run, baseline air was subsampled for five minutes, or for as long as it took for the gas readings to stabilise. Subsequently, air from the chamber was subsampled when $T_a$ had stabilised at the target value, and $CO_2$ and $H_2O$ traces were stable for at least five minutes. This was followed by another short baseline period. Subsampled air was pulled through a $CO_2$ /$H_2O$ water vapour analyser (model LI-840A, LI-COR, Lincoln NE, USA) to determine fractional $CO_2$ and $H_2O$ concentrations. The $CO_2$/$H_2O$ analyser was regularly zeroed using nitrogen, and spanned for $CO_2$ against an analytically certified gas with a known $CO_2$ concentration of 2,002 ppm (AFROX, Johannesburg, South Africa) and for $H_2O$ by calculating the water vapour pressure of saturated air at a known temperature, generated by bubbling atmospheric air through water at room temperature and then through water 3–4 °C cooler than room temperature. All tubing used in the system was Bev-A-Line tubing (Thermoplastic Processes Inc., Warren, NJ, USA). Voltage outputs from the analysers and thermistor probes were digitised using a Universal Interface (model UI2-1101-33, Sable Systems, Las Vegas NV, USA) and recorded with a sampling interval of 5 s using a personal computer with Expedata software (Sable Systems, Las Vegas NV, USA).

### *Experimental Protocol*

Experiments took place during the day, during the active phase of the birds' circadian cycle. Birds were exposed to $T_a$s of 25–54 °C in 5 °C increments, except above 40 °C, where $T_a$ was increased in increments of 2 °C. Each individual was exposed to one or two low $T_a$s (25-35 °C) and three high (> 40 °C) $T_a$ values, selected randomly on the day, for a minimum of ten minutes per $T_a$ value. A full experimental run rarely lasted more than three hours. The chamber wherein the bird was placed was completely dark in order to keep the birds calm, but by using infrared light I was able to monitor the birds through a live video stream. During all measurements, $T_b$ and activity were continuously monitored, and the run was terminated if the bird displayed prolonged escape behaviour such as agitated jumping, pecking and wing flapping; signs of extreme heat stress such as loss of coordination or balance; a sudden drop in EWL or metabolic rate and/or uncontrolled increase in $T_b$ above 45 °C. The bird was then recorded as having reached its thermal end point. A bird that had reached its thermal end point was removed immediately from the chamber and held in front of an air conditioner (set at 20 °C), and a cotton pad soaked in ethanol was rubbed on the bird's body to aid in lowering $T_b$. Once $T_b$ stabilised at normothermic levels (40-42 °C), the bird was offered water and placed in a cloth bag at room temperature to rest. The bird was then released soon afterwards at the site of capture. I aimed for a sample size of at least six individuals at each $T_a$.

### *Data extraction and analyses*

Voltage outputs from the analysers, thermistor probe and pit tags were digitised using a Universal Interface (model UI2-1101-33, Sable Systems, Las Vegas NV, USA) and recorded with a sampling interval of 5 s using a personal computer with Expedata software (Sable Systems, Las Vegas NV, USA). $\dot{V}_{CO_2}$ and $\dot{V}_{H_2O}$ were calculated using equations 10.5 and 10.9 respectively (Lighton 2008), assuming 0.803 mg $H_2O$ per ml of water vapour. Metabolic heat gain (mW) was calculated as in (Walsberg and Wolf 1995) assuming an RER of 0.71. Evaporative heat loss (mW) was calculated using 2.26 J $mg^{-1}$. Evaporative capacity is the ratio of metabolic heat produced to evaporative heat lost. Resting metabolic rates and rates of EWL were calculated from steady-state traces of $\dot{V}_{CO_2}$ (combined with assumed RERs) and $\dot{V}_{H_2O}$ in ExpeData, with the lowest 1-min mean values considered to be representative of resting values. Rate of $T_b$ increase (°C $min^{-1}$) was calculated as the difference between the first and last $T_b$ measurement during the final ten minutes of a test $T_a$, divided by the amount of time between the first and last measurement (~ 10 mins).

Broken stick analyses were performed in R3.0 (R Development Core Team 2011b) using the package *segmented* (Muggeo 2008) to estimate inflection points for $\dot{V}_{H_2O}$, $\dot{V}_{CO_2}$, evaporative capacity, mean $T_b$ and rate of $T_b$ increase. All data points associated with agitation or activity in the metabolic chambers were excluded from statistical analyses. I did not test for the effect of activity on response parameters since I seldom had enough active data to conduct conclusive statistics for this factor, and because of the difficulty in interpreting and standardising the manner of activity observed between individuals. Data above the inflection point were used to obtain slopes for the relationships of $\dot{V}_{H_2O}$, $\dot{V}_{CO_2}$, evaporative capacity, mean $T_b$ and rate of $T_b$ increase as function of increasing $T_a$. For these subsets of the data I performed generalised mixed-effect models, with packages nlme (Pinheiro et al 2009) to test for an effect of $T_a$ on the above parameters. I used individual as a random factor. In addition to the linear regression, a polynomial relationship between $T_a$ and EWL was fitted using a generalised linear regression, and the coefficients for this polynomial regression, along with the Akaike Information Criterion (AIC) for both the segmented and polynomial regressions are shown in Table 2. For comparative purposes, however, only the linear regressions are presented in the results.

All results are mass-specific, and expressed as mean ± SD for inactive birds, unless otherwise stated.

## Results

### *Scaly-feathered weavers*

There was a decrease in RMR from 24 ± 1.1 at $T_a = 25$ °C to 15.4 ± 4.2 mW $g^{-1}$ at $T_a = 30$ °C (Fig. 1). Above $T_a = 35$ °C, RMR increased linearly with increasing $T_a$ up to 19.9 ± 3.5 mW $g^{-1}$ at $T_a = 48$ °C (Fig. 1, Table 1). This increase in RMR at a rate of 0.47 mW $g^{-1}$ °$C^{-1}$ (Figs. 1 and 6), was statistically significant ($t_{1,24} = 6.95$, $p < 0.001$).

When $25 < T_a < 39$ °C, EWL was consistently low, averaging 4.0 ± 2.9 mg $g^{-1}$ $h^{-1}$ (Fig. 2). Above $T_a = 40$ °C, EWL increased linearly with increasing $T_a$ to 43.2 ± 6.2 mg $g^{-1}$ $h^{-1}$ at $T_a = 48$ °C (Fig. 2, Table 1). This nearly 11-fold increase in EWL, at a rate of 4.52 mg $g^{-1}$ °$C^{-1}$, was statistically significant ($t_{1,18} = 16.14$, $p < 0.001$).

Above $T_a = 40$ °C, evaporative capacity increased linearly and significantly from 15 ± 13 % to 141 ± 39 % at $T_a = 48$ °C, at a rate of 12 % °$C^{-1}$ ($t_{1,18} = 9.95$, $p < 0.001$, Fig. 3, Table 1). Evaporative capacity in inactive scaly-feathered weavers appeared to reach a maximum at high $T_a$s, increasing by 34 % between $T_a = 44$ and 46 °C, but by only 14 % between $T_a = 46$ and 48 °C.

**Table 1.** Mean (± SD) maximum body temperature ($T_{b,max}$), rate of $T_b$ increase (~ 10 minute period), evaporative water loss (EWL), resting metabolic rate (RMR) and evaporative capacity in scaly-feathered weavers (n = 6), sociable weavers (n = 6) and white-browed sparrow-weavers (n = 8) at firstly, the highest shared air temperature ($T_a$)* at which all species were tested (~ 48 °C), and secondly, scaly-feathered weavers (n = 4), sociable weavers (n = 8) and white-browed sparrow-weavers (n = 6) that had reached their thermal end point** at the highest air temperature ($T_a$) at which each species was tested (~ 48, ~ 52 and ~ 54 °C for scaly-feathered weavers, sociable weavers and white-browed sparrow-weavers, respectively).

| | **White-browed sparrow-weaver** | **Sociable weaver** | **Scaly-feathered weaver** |
|---|---|---|---|
| **Birds at $T_a$ = 48°C** | | | |
| mean $T_b$ ± SD (°C) | 43.0 ± 0.5 | 44.1 ± 0.4 | 44.7 ± 0.6 |
| mean $T_{b,\ max}$ ± SD (°C) | 43.2 ± 0.5 | 44.3 ± 0.3 | 44.9 ± 0.8 |
| mean rate of $T_b$ increase ± SD (°C $min^{-1}$) | 0.034 ± 0.024 | 0.030 ± 0.022 | 0.056 ± 0.047 |
| mean EWL ± SD (mg $g^{-1}$ $h^{-1}$) | 38.51 ± 4.80 | 37.47 ± 3.76 | 43.22 ± 6.24 |
| mean RMR ± SD (mW $g^{-1}$) | 16.78 ± 2.14 | 15.24 ± 2.84 | 19.93 ± 3.50 |
| mean evaporative capacity ± SD | 1.46 ± 0.23 | 1.61 ± 0.44 | 1.41 ± 0.39 |
| birds at thermal limit (%) | 0 | 0 | 43 |
| **Birds at thermal end point** | | | |
| mean $T_b$ ± SD (°C) | 44.4 ± 0.9 | 44.5 ± 0.5 | 44.6 ± 0.6 |
| mean $T_{b,\ max}$ ± SD (°C) | 45.5 ± 0.1 | 45.3 ± 0.4 | 45.5 ± 0.6 |
| mean rate of $T_b$ increase ± SD (°C $min^{-1}$) | 0.173 ± 0.055 | 0.137 ± 0.040 | 0.075 ± 0.042 |
| mean EWL ± SD (mg $g^{-1}$ $h^{-1}$) | 68.2 ± 7.9 | 64.0 ± 13.4 | 44.7 ± 7.5 |
| mean RMR ± SD (mW $g^{-1}$) | 24.5 ± 5.6 | 19.5 ± 4.5 | 21.8 ± 2.7 |
| mean evaporative capacity ± SD | 1.79 ± 0.3 | 2.09 ± 0.30 | 1.32 ± 0.36 |
| birds at thermal end point (% of total birds tested) | 100 | 100 | 57 |

* Only inactive birds were included.

** Active and inactive birds were included, as extreme escape behavior was considered as a behavioural signal of thermal limits being reached.

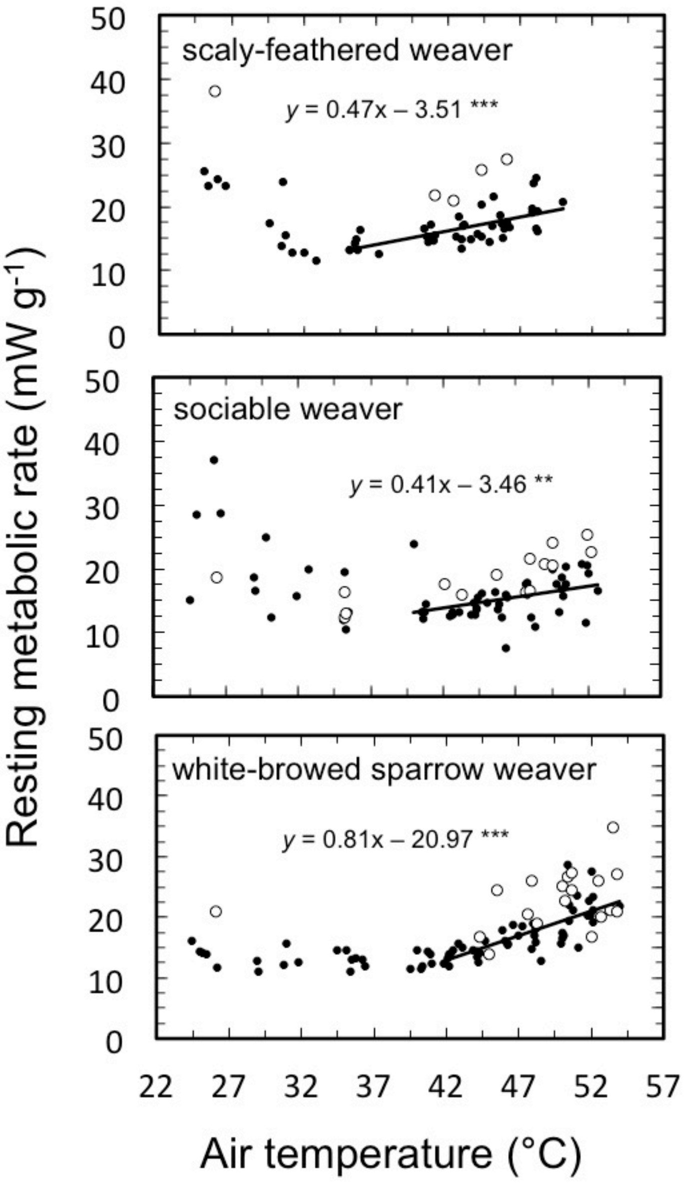

**Figure 1.** Resting metabolic rate (RMR) in scaly-feathered weavers (n=15), sociable weavers (n=25) and white-browed sparrow-weavers (n=31) over a range of air temperatures ($T_a$). Data from calm and active birds are shown by solid and unfilled circles respectively. Segmented regressions were used to estimate the inflection point in the relationship between RMR and $T_a$ for calm birds only. Statistical analyses were performed on data from calm birds to determine coefficients for the linear relationships above inflection points. Significant relationships are represented by asterisks.
Significance levels: * = < 0.05, ** = < 0.01, *** = < 0.001

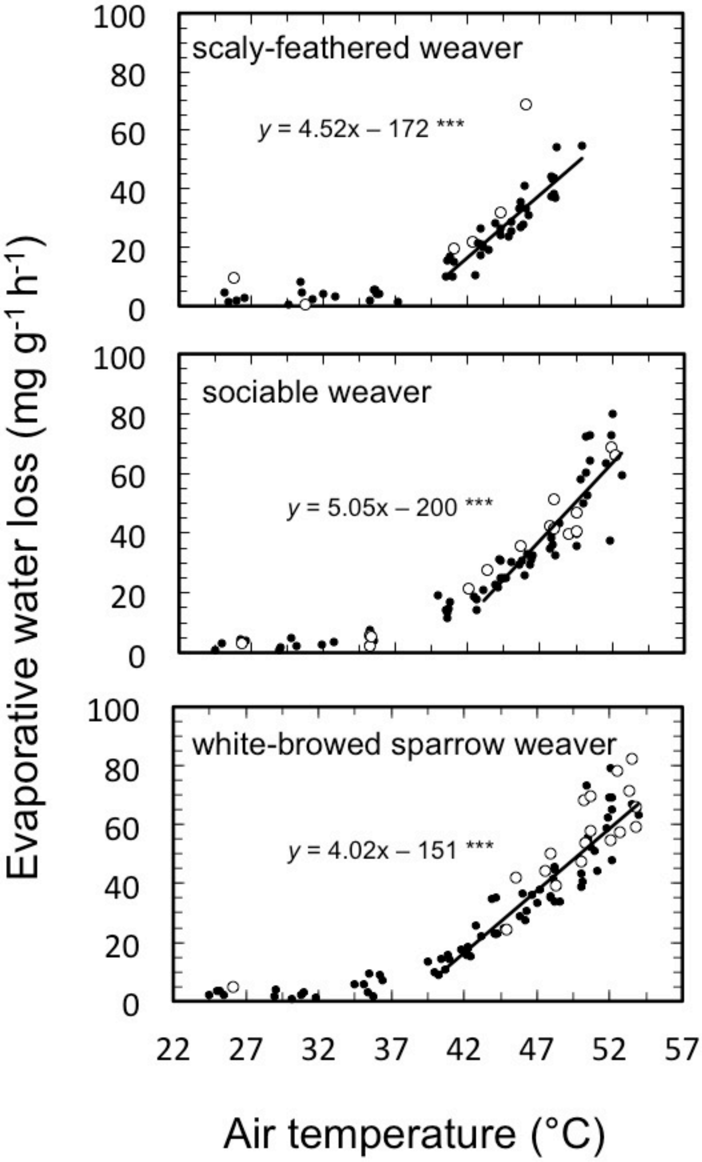

**Figure 2.** Evaporative water loss (EWL) in scaly-feathered weavers (n=15), sociable weavers (n=25) and white-browed sparrow-weavers (n=31) over a range of air temperatures ($T_a$). Data from calm and active birds are shown by solid and unfilled circles respectively. Segmented regressions were used to estimate the inflection point in the relationship between EWL and $T_a$ for calm birds only. Statistical analyses were performed on calm birds to determine coefficients for the linear relationships above inflection points. Significant relationships are represented by asterisks.
Significance levels: * = < 0.05, ** = < 0.01, *** = < 0.001

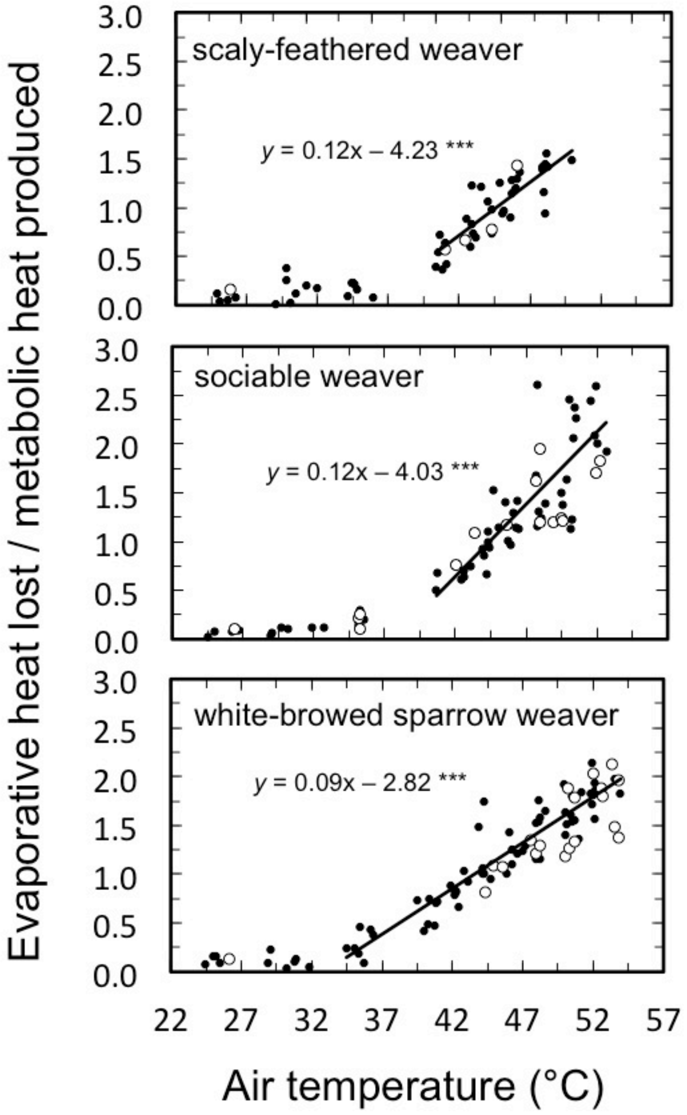

**Figure 3.** Evaporative capacity (the ratio of evaporative heat lost to metabolic heat produced) for scaly-feathered weavers (n=15), sociable weavers (n=25) and white-browed sparrow-weavers (n=31) over a range of air temperatures ($T_a$). Data from calm and active birds are shown by solid and unfilled circles respectively. Segmented regressions were used to estimate the inflection point in the relationship between evaporative capacity and $T_a$ for calm birds only. Statistical analyses were performed on calm birds to determine coefficients for the linear relationships above inflection points. Significant relationships are represented by asterisks.
Significance levels: * = < 0.05, ** = < 0.01, *** = < 0.001

Mean $T_b$ averaged 40.1 ± 0.74°C at $T_a < 35$ °C, but began to increase significantly ($t_{1,17} = 9.9$, $p < 0.001$) at a rate of 0.37 °C °C$^{-1}$ at $T_a = 35$ °C (Fig. 4). At $T_a = 48$ °C, mean $T_b$ was 44.7 ± 0.6 °C (Fig. 4, Table 1).

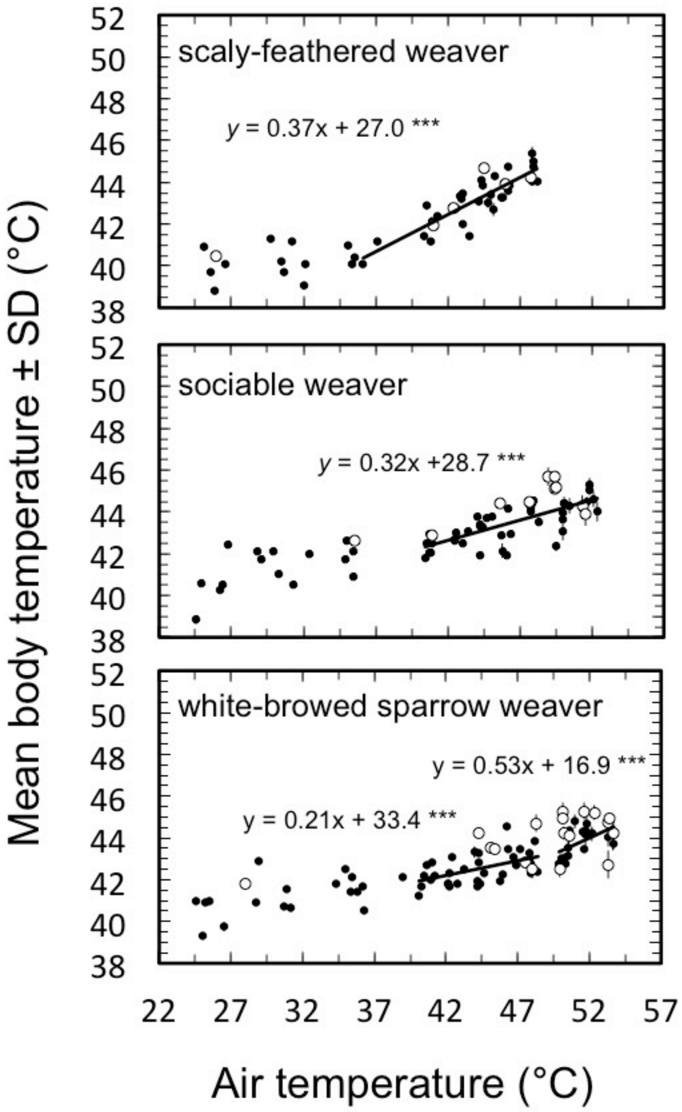

**Figure 4.** Mean (± SD) body temperature ($T_b$) for scaly-feathered weavers (n=15), sociable weavers (n=25) and white-browed sparrow-weavers (n=31) over a range of air temperatures ($T_a$). Data from calm and active birds are shown by solid and unfilled circles respectively. Segmented regressions were used to estimate the inflection point in the relationship between mean $T_b$ and $T_a$ for calm birds only. In the case of white-browed sparrow-weavers, two inflection points were found. Statistical analyses were performed on calm birds to determine coefficients for the linear relationships above inflection points. Significant relationships are represented by asterisks.
Significance levels: * = < 0.05, ** = < 0.01, *** = < 0.001

The relationship between $T_a$ and the rate of $T_b$ increase was not significant ($t_{1,5}$ = 0.97, p = 0.38), with the majority of $T_b$ traces remaining constant, increasing slightly and sometimes decreasing over the ~10 min period, but averaging a rate of 0.007 ± 0.037 °C $min^{-1}$ (Fig. 5). Between $T_a$ = 44 and 48 °C, however, six birds displayed a greater rate of $T_b$ increase, up to 0.12 °C $min^{-1}$, than that seen at the lower

$T_a$s (Fig. 5). At $T_a$ = 48 °C, rate of $T_b$ increase averaged 0.06 ± 0.05 °C $min^{-1}$ (Fig. 5, Table 1).

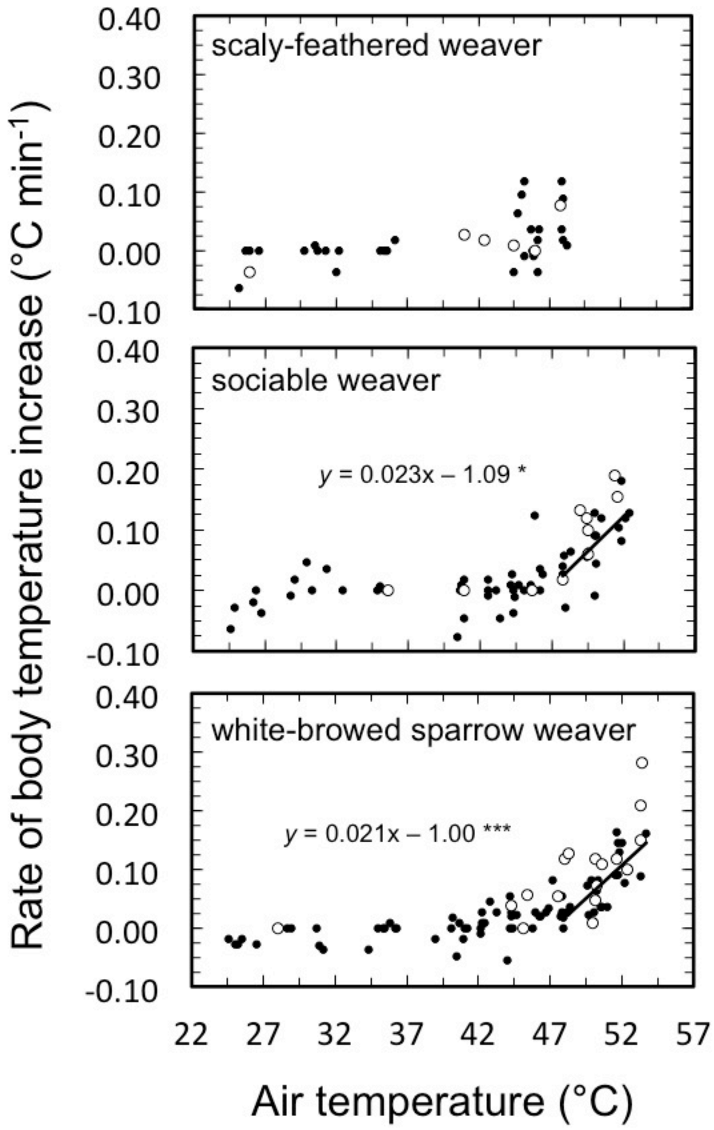

**Figure 5.** Rate of body temperature ($T_b$) increase over ~ 10 mins for scaly-feathered weavers (n=15), sociable weavers (n=25) and white-browed sparrow-weavers (n=31) over a range of air temperatures ($T_a$). Data from calm and active birds are shown by solid and unfilled circles respectively. Segmented regressions were used to estimate the inflection point in the relationship between the rate of $T_b$ increase and $T_a$ for calm birds only. Statistical analyses were performed on calm birds to determine coefficients for the linear relationships above inflection points. Significant relationships are represented by asterisks. In the case of scaly-feathered weavers, the relationship was not statistically significant, and so is not shown.
Significance levels: * = < 0.05, ** = < 0.01, *** = < 0.001

I accounted for individual $T_b$ at a specific $T_a$ to test the effect of the heat gradient between the bird and its environment on evaporative heat loss (EHL) (Fig. 6). For scaly-feathered weavers, when $T_a$ was 3-5 °C lower than $T_b$, EHL was 2.6 ± 0.4 mW $g^{-1}$. As $T_a$ approached $T_b$, EHL increased, averaging 14 ± 1.2 mW $g^{-1}$ when $T_a \approx T_b$ (Fig. 6), and increasing at a rate of 3.78 mW $g^{-1}$ °$C^{-1}$ ($t_{1,15} = 8.49$, $p < 0.001$). Evaporative heat loss averaged 25.3 ± 2.1 mW $g^{-1}$ when $T_a$ exceeded $T_b$ by 3-4 °C (at $T_a \approx 48$ °C) (Fig. 6).

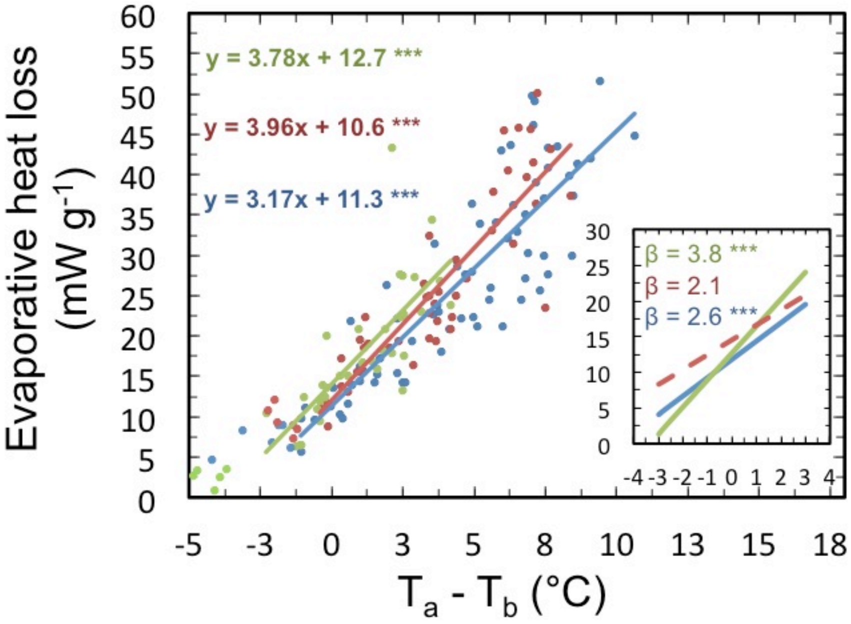

**Figure 6.** Evaporative heat loss (EHL) as a function of the gradient between air and body temperature ($T_a - T_b$) for scaly-feathered weavers (n=15, green), sociable weavers (n=25, red) and white-browed sparrow-weavers (n=31, blue). Inset displays same parameters at $T_a < 48$ °C. Segmented regressions were used to estimate the inflection point in the relationship between EHL and $T_a - T_b$ for calm birds only. Statistical analyses were performed on calm birds to determine coefficients for the linear relationships above inflection points. Significant relationships are represented by asterisks. Significance levels: * = < 0.05, ** = < 0.01, *** = < 0.001

Thermal end points were reached at $T_a = 44$ °C by 11 % of scaly-feathered weavers (Fig. 7). This increased to 14 % at $T_a = 46$ °C, and 57 % at $T_a = 48$ °C (Fig. 7). I was unable to experimentally show the $T_a$ at which 100 % of scaly-feathered weavers had reached their thermal end point, and can therefore only postulate from extrapolation of the data, that it would be at $T_a \approx 50$ °C (Fig. 7). Of the birds that reached their thermal end point at $T_a$ = 48 °C, mean $T_b$ was 44.6 ± 0.6 °C, mean $T_{b,max}$ was 45.5 ± 0.6 °C and mean evaporative capacity was 1.32 ± 0.36 (Table 1).

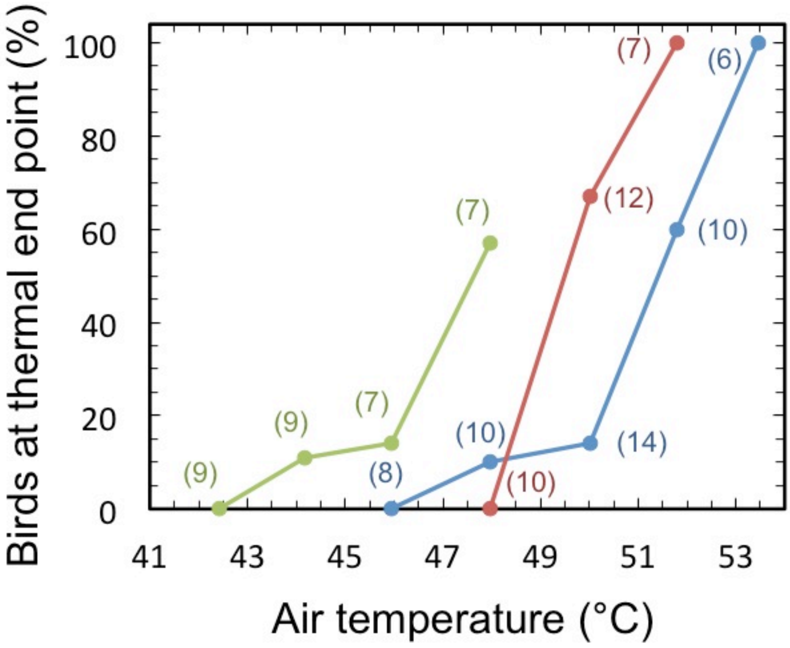

**Figure 7.** Percentage of individuals that reached their thermal end point for scaly-feathered weavers (n=15, green), sociable weavers (n=25, red) and white-browed sparrow-weavers (n=31, blue) over a range of air temperatures ($T_a$). Numbers in brackets indicate the total birds tested at each $T_a$.

*Sociable weavers*

Between 25 and 35 °C, RMR generally decreased, although there was considerable scatter (Fig. 1). Above 35 °C, RMR increased linearly with increasing $T_a$ from 13.2 ± 0.8 at $T_a$ = 40 °C to 15.2 ± 2.8 mg $g^{-1}$ $h^{-1}$ at $T_a$ = 48 °C (Fig. 1, Table 1). At $T_a$ = 52 °C, RMR had increased to 17.7 ± 3.8 mg $g^{-1}$ $h^{-1}$. The relationship between $T_a$ above 35 °C and RMR was statistically significant ($t_{1,22}$ = 3.25, $p < 0.01$), with RMR increasing at a rate of 0.33 when $T_a$s up to 48 °C were included (Fig. 6), or 0.41 mW $g^{-1}$ °$C^{-1}$ (Fig. 1) when $T_a$s up to 52 °C were included.

At $T_a < 40$ °C, EWL was stable and low, averaging 3.4 ± 1.8 mg $g^{-1}$ $h^{-1}$ (Fig. 2). Above 40 °C, EWL increased linearly with increasing $T_a$ up to 37.5 ± 3.8 mg $g^{-1}$ $h^{-1}$ at $T_a$ = 48 °C (Fig. 2, Table 1). By $T_a$ = 52 °C, EWL had increased 20 fold from the low levels when $T_a < 40$ °C up to $62.6 \pm 16.1$ mg $g^{-1}$ $h^{-1}$ (Fig. 2). This relationship was statistically significant, with a rate of 5.05 mg $g^{-1}$ °$C^{-1}$ ($t_{1,14} = 10.37$, $p < 0.001$).

Above $T_a = 40$ °C, evaporative capacity increased linearly and significantly ($t_{1,22} = 9.85$, $p < 0.001$) at a rate of 12 % °$C^{-1}$, from $12 \pm 8$ % to $161 \pm 44$ % at $T_a = 48$ °C (Fig. 3, Table 1). At $T_a = 52$ °C, $222 \pm 26$ % of metabolic heat load was being dissipated by evaporative means (Fig. 3). Evaporative capacity increased by 41 % between $T_a = 48$ and 50 °C, and by 20 % between $T_a = 50$ and 52 °C.

Mean $T_b$ averaged $41.3 \pm 1.1$°C at $T_a < 40$ °C, and increased significantly ($t_{1,19} = 11.19$, $p < 0.001$) above $T_a = 40$ °C at a rate of 0.32 °C °$C^{-1}$ (Fig. 4). At $T_a = 48$ °C, mean $T_b$ was $44.3 \pm 0.3$ °C (Fig. 4, Table 1), and this increased up to $44.7 \pm 0.5$ °C when $T_a = 52$ °C (Fig. 4).

Over ~ 10 min at a specific $T_a$, $T_b$ remained fairly constant, increased slightly, or decreased, averaging a rate of $0.003 \pm 0.033$ °C $min^{-1}$ when $T_a < 48$ °C (Fig. 5). The slope of the rate of $T_b$ increase when $T_a > 48$ °C was 0.023 °C $min^{-1}$ °$C^{-1}$ ($t_{1,4} = 4.37$, $p < 0.05$; Fig. 5). At $T_a = 48$ °C, rate of $T_b$ increase averaged $0.03 \pm 0.02$ °C $min^{-1}$ (Fig. 5, Table 1), and increased to $0.12 \pm 0.04$ °C $min^{-1}$ at $T_a = 52$ °C (Fig. 5).

For sociable weavers, EHL began to increase significantly at a rate of 3.96 mW $g^{-1}$ °$C^{-1}$ when $T_a - T_b \approx 0$, ($t_{1,9} = 8.48$, $p < 0.001$), with an average of $24.1 \pm 2.0$ mW $g^{-1}$ when $T_a$ exceeded $T_b$ by 3-5 °C (at $T_a \approx 48$ °C) (Fig. 6). At $T_a = 52$ °C, when $T_a$ exceeded $T_b$ by 6-8.5 °C, EHL was $39.3 \pm 10.1$ mW $g^{-1}$ (Fig. 6).

Thermal end points were reached by 67 % of sociable weavers at $T_a = 50$ °C, increasing to 100 % at $T_a = 52$ °C (Fig. 7). Of the birds that reached thermal end point at $T_a = 52$ °C, mean $T_b$, mean $T_{b,\max}$ and evaporative capacity were $44.5 \pm 0.5$ °C, $45.3 \pm 0.4$ °C, and $2.09 \pm 0.30$ respectively (Table 1).

*White-browed sparrow-weavers*

Between $T_a$ = 25 and 40 °C, RMR remained fairly constant, averaging 13.4 ± 1.4 mW $g^{-1}$ (Fig. 1). Above $T_a$ = 40 °C, RMR increased with increasing $T_a$ up to 16.8 ± 2.1 mg $g^{-1}$ $h^{-1}$ at $T_a$ = 48 °C (Fig. 1, Table 1). By $T_a$ = 54 °C, RMR had increased up to 21.3 ± 0.4 mg $g^{-1}$ $h^{-1}$ (Fig. 1). This linear increase in RMR was statistically significant ($t_{1,19}$ = 7.55, $p < 0.001$) with RMR increasing at a rate of 0.58 when $T_a$s up to 48 °C were included (Fig. 6), or 0.81 mW $g^{-1}$ °$C^{-1}$ (Fig. 1) when $T_a$s up to 54 °C were included.

When 25 < $T_a$ < 39 °C, EWL was consistently low, averaging 4.1 ± 2.5 mg $g^{-1}$ $h^{-1}$ (Fig. 2). Above $T_a$ = 40 °C, EWL increased linearly with increasing $T_a$ up to 38.5 ± 4.8 mg $g^{-1}$ $h^{-1}$ at $T_a$ = 48 °C (Fig. 2, Table 1). By $T_a$ = 54 °C, EWL had increased up to 65.5 ± 1.8 mg $g^{-1}$ $h^{-1}$. This 16 fold increase in EWL at a rate of 4.02 mg $g^{-1}$ $h^{-1}$ °$C^{-1}$ was statistically significant ($t_{1,24}$ = 16.65, $p < 0.001$).

Above $T_a$ = 35 °C, evaporative capacity increased linearly and significantly ($t_{1,33}$ = 23.6, $p < 0.001$) with increasing $T_a$, at a rate of 9 % °$C^{-1}$, from 14 ± 6 % to 146 ± 23 % at $T_a$ = 48 °C (Fig. 3, Table 1). By $T_a$ = 54 °C, 193 ± 8 % of metabolic heat was being dissipated by evaporative means (Fig. 3). Evaporative capacity increased by 17 % between $T_a$ = 50 and 52 °C, and 14 % between $T_a$ = 52 and 54 °C.

Mean $T_b$ averaged 41.2 ± 0.9°C at $T_a$ < 40 °C, but began to increase significantly ($t_{1,12}$ = 7.18, $p < 0.001$) at $T_a$ > 40 °C at a rate of 0.21 °C °$C^{-1}$ (Fig. 4). At $T_a$ = 48 °C, mean $T_b$ was 43.0 ± 0.5 °C (Fig. 4, Table 1). At $T_a$ = 49.3 °C, a significant second breakpoint was found ($t_{1,68}$ = 8.47, $p < 0.001$), and the slope of mean $T_b$ increased significantly ($t_{1,5}$ = 8.98, $p < 0.001$) at a rate of 0.53 °C °$C^{-1}$. At $T_a$ = 54 °C, mean $T_b$ was 44.8 ± 0.2 °C (Fig. 4).

Over ~ 10 mins at a specific $T_a$, $T_b$ remained fairly constant, increased slightly, or decreased, averaging a rate of 0.001 ± 0.027 °C $min^{-1}$ when $T_a$ < 48 °C

(Fig. 5). Rate of $T_b$ increased significantly when $T_a > 48$ °C ($t_{1,7} = 6.2$, $p < 0.001$) at a rate of 0.021 °C $min^{-1}$ °$C^{-1}$ (Fig. 5). At $T_a = 48$ °C, rate of $T_b$ increase averaged 0.03 ± 0.02 °C $min^{-1}$ (Fig. 5, Table 1), and this average increased up to 0.1 ± 0.03 °C $min^{-1}$ at $T_a = 54$ °C (Fig. 5).

For white-browed sparrow-weavers weavers, EHL began to increase significantly at a rate of 3.17 mW $g^{-1}$ °$C^{-1}$ when $T_a - T_b \approx -1.5$, ($t_{1,22} = 12.98$, $p < 0.001$), with an average of 24.2 ± 3.2 mW $g^{-1}$ when $T_a$ exceeded $T_b$ by 4-6 °C (at $T_a \approx 48$ °C) (Fig. 6). At $T_a = 54$ °C, when $T_a$ exceeded $T_b$ by 6-8.5 °C, EHL was 35.3 ± 5.0 mW $g^{-1}$ (Fig. 6).

Thermal end points were reached by 10 % of white-browed sparrow-weavers at $T_a = 48$ °C (Fig. 7). This increased to 14 % at $T_a = 50$ °C, to 60 % at $T_a = 52$ °C and to 100 % at $T_a = 54$ °C (Fig. 7). Of the birds that reached their thermal end point at $T_a = 54$ °C, mean $T_b$, mean $T_{b,\,max}$ and evaporative capacity were 44.4 ± 0.9 °C, 45.5 ± 0.1 °C and 1.79 ± 0.30 respectively (Table 1).

### *Species comparison*

I used $T_a = 48$ °C as an upper cutoff to compare the slopes of the regressions, as this was the highest $T_a$ shared by the three species. At any given $T_a$, scaly-feathered weavers had higher mass-specific RMR, by approximately 2 mW $g^{-1}$ than the other two species (Fig. 8A, Table 2). White-browed sparrow-weavers displayed the steepest increase in RMR, and sociable weavers the shallowest (Fig. 8A). At any given $T_a$, all three species had similar levels of EWL, although the slope of EWL was steeper in scaly-feathered weavers than in the other two species (Fig. 8B, Table 2). Sociable weavers had higher evaporative capacity than the other two species at any given $T_a$ (Table 2) by ~ 25%, with the slopes for sociable weavers and scaly-feathered weavers being higher than that of white-browed sparrow-weavers (Fig. 8C). However, when $T_a$ < 42, evaporative capacity in white-browed sparrow-weavers was comparable to that of sociable weavers (Fig. 8C). At $T_a$ = 40 °C, all three species had similar mean $T_b$, with scaly-feathered weavers increasing $T_b$ from this point at the steepest rate of the three species. White-browed sparrow-weavers had the shallowest slope, with mean $T_b$ at $T_a$ = 48 °C being ~ 1.5 °C lower than that of scaly-feathered weavers at the same $T_a$ (Fig. 8D, Table 2).

**Table 2.** Coefficients for a nonlinear relationship ($y = ax^2 + bx + c$) between air temperature ($T_a$) and evaporative water loss (EWL, mg $g^{-1}$ $h^{-1}$) for white-browed sparrow-weavers, sociable weavers and scaly-feathered weavers. For all three species, Akaike information criteria (AIC) are shown for polynomial and segmented models.

| | **white-browed sparrow-weaver** | **sociable weaver** | **scaly-feathered weaver** |
|---|---|---|---|
| a | 0.13 | 0.14 | 0.16 |
| b | -7.63 | -8.86 | -10.16 |
| c | 117.02 | 138.33 | 160.45 |
| AIC polynomial | 464.6 | 395.01 | 298.75 |
| AIC segmented | 469.4 | 396.83 | 295.89 |

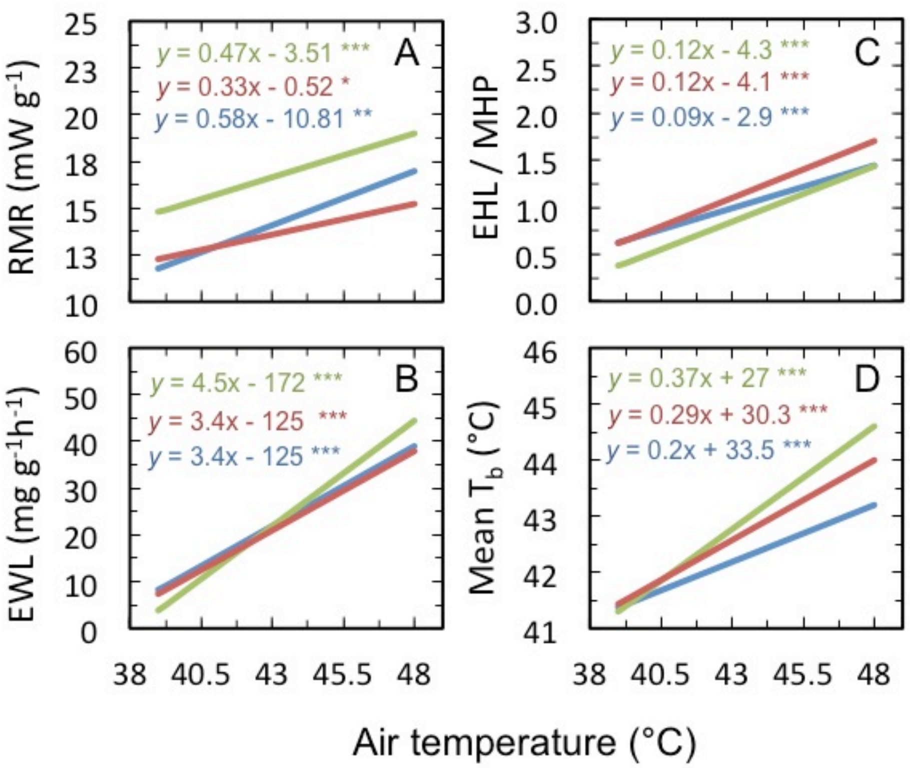

**Figure 8.** Linear regressions for the relationships between air temperature ($T_a$) and **A.** Resting metabolic rate (RMR), B. Evaporative water loss (EWL), C. Evaporative capacity [the ratio of evaporative heat lost (EHL) to metabolic heat produced (MHP)] and D. Mean body temperature ($T_b$) for scaly-feathered weavers (n=15, green), sociable weavers (n=25, red) and white-browed sparrow-weavers (n=31, blue) at $T_a < 48$ °C.

## Discussion

My data reveal a strong effect of body mass on thermal end point among three species of ploceid passerines, although the relationships between body mass and RMR, EWL and evaporative capacity were less clear. All three species I examined showed a pronounced capacity for facultative hyperthermia when experiencing $T_a$ values above normothermic $T_b$.

*Resting metabolic rate*

Resting metabolic rate at moderate $T_a$s was very similar for all three species, despite the differences in mass (Fig. 1). These findings are unexpected, and given the 4-fold range in body mass in the three study species I would have expected a stronger body mass effect. The slope of RMR when $T_a > T_b$ should be higher in smaller birds (Weathers 1981), so it was also unexpected for white-browed sparrow-weavers to exhibit a slope much steeper than that of the other two species (Fig. 1). All three species conform to the classic model of endotherm energetics (Scholander et al 1950) – there is a clear upper critical limit of thermoneutrality, above which metabolic rate increases linearly.

The temperature-dependent elevations in RMR as $T_a$ approaches and exceeds $T_b$ potentially demonstrate the high costs of heat dissipation associated with panting at higher temperatures, as has been previously suggested (Dawson 1958). At high $T_a$s, scaly-feathered weavers had a higher mass-specific RMR at any given $T_a$ compared to that of sociable weavers and white-browed sparrow-weavers (Fig. 6). These findings are in line with the expectation that smaller birds have higher mass-specific metabolic rates (Bartholomew and Cade 1963, Fig. 6). Sociable weavers, on the other hand, display lower mass-specific RMR than white-browed sparrow-weavers at $T_a$s above ~44 °C (Fig 6), despite being on average 35 % smaller. This suggests that sociable weavers were able to keep the metabolic costs of panting comparatively low at high $T_a$s compared to the other two species.

An increase in $T_b$ could have a $Q_{10}$ effect on RMR. Some species lack this effect, exhibiting an elevation in $T_b$ within the TNZ, without an increase in RMR (Tieleman and Williams 1999). Many authors have argued that the lack of a $Q_{10}$ effect contributes to water savings, because a lower RMR results in decreased respiratory

EWL. While $T_b$ remained fairly constant within the TNZ in all three of my study species, I did observe increases in both $T_b$ and RMR at $T_a > 40$ °C. I estimated the expected increases in RMR as a result of the increase in $T_b$ between $T_a = 35$ and 46 °C (assuming $Q_{10} = 2.5$). Whereas the increase in RMR was much lower than expected in scaly-feather weavers ($Q_{10} = 1.7$), the increase in RMR in sociable weavers was similar to expected from a $Q_{10}$ effect ($Q_{10} = 2.8$). In contrast, RMR increased substantially more in the white-browed sparrow weaver ($Q_{10} = 5.7$). However, interpreting $T_b$-related increases in metabolic rate in endotherms is very complex, because metabolic rate plays an active role in thermoregulation of endotherms, e.g. panting or gular fluttering (Tieleman and Williams 1999). Elucidating metabolic increases due to panting versus $Q_{10}$ effects warrants further study.

I compared the RMRs of my three study species to that of three ot.her desert species of similar size for which data are available. At $T_a = 44$ °C, scaly-feathered weavers exhibited an average RMR ~37 % lower than that exhibited by the 12-g spinifexbird (*Eremiornis carteri*; ~27.3 mW $g^{-1}$, an Australian desert passerine) at the same $T_a$ (Ambrose et al 1996). At $T_a = 48$ °C, RMR in the 27-g dune lark was almost double that of sociable weavers at the same $T_a$ (30.1 mW $g^{-1}$; *Mirafra erythrocephalus,* an African desert passerine) (Williams 1999). White-browed sparrow-weavers exhibited an RMR 14 % lower than that of the 38-g greater hoopoe lark (19.7 mW $g^{-1}$, *Alaemon alaudipes*), a desert passerine from the Sahara and Arabian deserts, at the same $T_a$ (Tieleman et al 2002a). These data suggest large variation in the metabolic costs associated with heat dissipation in desert passerines at a global scale. The large discrepancy between dune lark and sociable weaver RMR could, however, be attributed to the fact that the absolute humidity levels in Williams (1999) were much higher (20–25 mmHg at $T_a$s > 40 °C) than those in my study. This could have lead to agitated behavior (Gerson et al. in press) in the unmonitored dune larks, which could in turn have resulted in elevated metabolic rates.

### *Evaporative water loss and evaporative capacity*

I fitted linear relationships to EWL data at $T_a < 48$ °C (Fig. 6). However, if all EWL data for sociable weavers (up to $T_a = 52$ °C) and white-browed sparrow weavers (up to $T_a = 54$ °C) were included, the slopes were substantially steeper (5.0 and 4.0 respectively; Fig. 2). In white-browed sparrow-weavers, a polynomial relationship between $T_a$ and EWL was most parsimonious, while for sociable weavers, linear and nonlinear relationships fitted equally well (Table 2).

These findings could complicate interspecific comparisons assessing the scaling of the slope of mass-specific EWL at high $T_a$s [as in (McKechnie and Wolf 2010)], especially when maximum $T_a$s exceed 50 °C. McKechnie and Wolf (2010) compiled data from the literature on birds tested at maximum $T_a$s, which varied from 42.5 to 56.5 °C. This may have influenced the relationship of expected slope of mass-specific EWL vs. body mass, by underestimating the slope in species subjected to comparatively low maximum $T_a$s, and potentially overestimating slope for species subjected to higher maximum $T_a$s. For example, black-bellied sandgrouse (*Pterocles orientalis*) and pin-tailed sandgrouse (*Pterocles alchata*) (Hinsley et al 1993) exhibited mass-specific EWL slopes that were 68 and 48 % lower respectively than what was expected for birds of their mass from (McKechnie and Wolf 2010). The highest test $T_a$ that these two species experienced was 45 °C, whereas the spotted nightjar (*Eurostopodus argus*) (Dawson and Fisher 1969), which experienced a maximum $T_a$ of 56.5 °C, exhibited a slope roughly equal to that expected for a bird of its mass from (McKechnie and Wolf 2010).The latter comparison highlights a potential experimental source of variation that should be taken into consideration in future comparative analyses.

The expected slopes of mass-specific EWL for birds of similar mass to scaly-feathered weavers, sociable weavers and white-browed sparrow-weavers are 4.52, 2.90 and 2.33 mg $g^{-1}$ $h^{-1}$ °$C^{-1}$ respectively. Whereas scaly-feathered weaver evaporated water at the approximate rate predicted for a bird of its mass, the slopes for the sociable weaver and white-browed sparrow weaver were 17.4 and 45.9% higher respectively ($T_a$ = 48 °C cut-off) or 72.4 and 71.7 % higher respectively (entire $T_a$ range) than the expected values. At $T_a$ = 44 °C, scaly-feathered weavers evaporated water at an average rate very similar to that exhibited by spinifexbirds (~28.9 mg $g^{-1}$ $h^{-1}$) at the same $T_a$ (Ambrose et al 1996). At $T_a$ = 48 °C, EWL in sociable weavers was half that of dune larks (Williams 1999). White-browed sparrow-weavers exhibited similar EWL to the greater hoopoe lark at $T_a$ = 50 °C (Tieleman et al 2002a).

Observed minimum and maximum values of individual EWL at the highest test $T_a$ were vastly different in all three species (by as much as double in the two larger weaver species). These values represent individuals that were calm inside respirometry chambers, and I argue that the variation observed is therefore unlikely to represent variation in stress levels. Variation in physiological traits can be either genetic or phenotypic. Phenotypically plastic responses driving variation could be the result of seasonal acclimatisation (e.g. birds tested in early summer versus late summer), age, breeding status or developmental plasticity (environmental conditions during chick development) (McKechnie et al 2006; Tieleman 2007; McKechnie 2008). An important avenue for future research would be to determine to what extent inter-individual variation is driven by genetic adaptation or phenotypic responses, both of which could mediate the effects of climate change on arid-adapted populations. Phenotypic responses would be especially important for long-lived species where the effects of climate change will be experienced within an individual's life-time (Boyles et al. 2011). In contrast, genetic variation will provide a larger gene pool for natural selection to act on in wild populations in hotter climates, especially for short-lived species.

Evaporative capacity increased linearly in all three species above their respective inflection points (Fig. 3), with similar efficiencies (140–160 %) across species at $T_a$ = 48 °C (Table 1). At the highest $T_a$s experienced (48, 52 and 54 °C respectively), calm scaly-feathered weavers, sociable weavers and white-browed sparrow-weavers were dissipating ~140, 220 and 190 % of their metabolic heat through evaporative means (Fig. 3). Birds at their thermal limit at these $T_a$s (both active and inactive) exhibited lower evaporative capacity, due to the increased metabolic costs associated with high activity levels (Table 1).

I expected to see evaporative capacity plateau as maximum EWL rates were reached. This was to some extent the case in scaly-feathered weavers and sociable weavers, with both species exhibiting a slowing down in the rate of evaporative capacity increase at high $T_a$s. White-browed sparrow-weavers, however, exhibited similar rates of increase in evaporative capacity between $T_a$ = 50 and 52 °C, and $T_a$ = 52 and 54 °C (Fig 3.). Thermal limits are reached when $T_b$ approaches lethal levels, when lethal dehydration is reached, or a combination of the two. It is therefore likely that dehydration played a role in thermal limits being reached in scaly-feathered weavers and sociable weavers, while it may not have been as important in white-browed sparrow weavers.

The evaporative efficiencies demonstrated by our study species were roughly similar to other desert birds of similar mass. Evaporative capacity at $T_a$ = 48 °C was

~162 % in dune larks (Williams 1999), similar to that of sociable weavers at the same $T_a$. In order for these two species to dissipate heat at similar efficiencies at $T_a = 48$ °C, dune larks had to evaporate water at double the rate of sociable weavers. White-browed sparrow-weavers dissipated a similar percentage of metabolic heat load to the greater hoopoe lark, which dissipated ~170 % at $T_a = 50$ °C (Tieleman et al 2002a). Both species had higher than expected rates of EWL increase for their mass, and their similar evaporative efficiencies were as a result of similar RMR and EWL levels. At $T_a = 44$ °C, scaly-feathered dissipated ~33 % more metabolic heat through evaporative means than the ~67 % dissipated by spinifexbirds at the same $T_a$ (Ambrose et al 1996). The higher RMR of the Spinifexbirds at this $T_a$ leads to lower evaporative capacity, despite similar rates of EWL.

### *Body temperature and thermal end points*

Birds have been shown to elevate their $T_b$ 2-4 °C above normothermic levels during extreme heat and/or dehydration, with water conservation thought to be the primary function of such facultative hyperthermia (Tieleman and Williams 1999). During acute exposure to heat (1 h), birds ranging in size from 10-1000 g may conserve up to 50% of total evaporative water loss by becoming hyperthermic, whereas during chronic exposure (5h), only small birds benefit (Tieleman and Williams 1999). Hyperthermia conserves water by enhancing the loss of heat from bird to environment when $T_a < T_b$, but when $T_a > T_b$, it presents another advantage by reducing the rate of heat gain from the environment (Kilgore et al 1976). The patterns of hyperthermia shown by my study species were generally characterized by a stable $T_b$ elevated above normothermic levels, which increased in a step-wise fashion with each increment in $T_a$ up to $T_a = 48$ °C. Above $T_a = 48$ °C, however, $T_b$ appeared no longer to be regulated at stable levels, as indicated by the steeper rates of $T_b$ increase at extremely high $T_a$s (Fig. 4). At $T_a$ = 44 and 46 °C, average $T_b$s in scaly-feathered weavers, sociable weavers and white-browed sparrow-weavers were between ~42.5 and ~43.8 °C (Fig. 5).

Leon (2006) categorised three patterns of $T_b$ which most endotherms adhere to during heat stress. Initial exposure to heat results in a rapid increase in $T_b$ above normothermic levels, which is followed by an equilibrium phase, during which a hyperthermic $T_b$ is maintained at relatively stable levels (Leon 2006). It is during this phase that behavioural and physiological heat dissipation mechanisms are actively implemented to balance heat load. The equilibrium plateau is followed by "thermoregulatory breakdown", which results in a rapid, uncontrolled increase in $T_b$ toward lethal levels (Leon 2006). Individual variation is observed in the slope of the equilibrium plateau, as well as the time taken to reach lethal $T_b$ levels (Leon 2006). The patterns of $T_b$ regulation observed in the three passerines in my study largely conformed to this model.

Sociable weavers and white-browed sparrow-weavers were unable to maintain a stable $T_b$ at the highest $T_a$s, which suggests that they were dissipating heat at maximum capacity (Fig. 5). At these $T_a$s, $T_{b,max}$ was close to what is typically considered lethal levels [46-47 °C (Schmidt-Nielsen 1964)] (Table 1). Scaly-feathered weavers at $T_a$ = 48 °C (both calm birds at their thermal limit and not), were dissipating heat at near maximum capacity, as exhibited by the plateauing of evaporative capacity (Fig. 3), and mean $T_{b, max}$ was, if not yet approaching lethal limits, very high. However, the rate of $T_b$ increase was comparatively low (Fig. 5), which is likely due to only 14 % of birds being active at $T_a$ = 48 °C. In contrast, at their thermal end points, 57 % of white-browed sparrow-weavers and 29 % of sociable weavers were active.

I would expect controlled hyperthermia to involve a stable elevated $T_b$ when $T_a$ is maintained at a stable set point. The apparent inability to maintain $T_b$ at constant levels at the highest test temperatures could be a combined result of high activity levels and thermal limits being approached. This could also have been confounded by the short measurement period (~10 mins) at the highest $T_a$, raising the possibility that $T_b$ may not have had sufficient time to stabilize. However, it was difficult to obtain data for longer periods at test temperatures since the birds became restless. Clarifying the differences between controlled and uncontrolled hyperthermia would be a useful avenue for future research.

Scaly-feathered weaver $T_b$ was on average 0.6 °C lower at $T_a = 44$ °C than that of spinifexbirds (Ambrose et al 1996). At $T_a = 48$ °C, Sociable weaver $T_b$ was ~0.6 °C lower than dune larks at the same $T_a$ (44.7 °C , Williams 1999), and white-browed sparrow-weavers exhibited an average $T_b$ 1.5 °C lower at $T_a = 50$ °C than that of greater hoopoe larks (45 °C, Tieleman et al. 2002a). Previous studies have not monitored behaviour of birds during runs and it is difficult to tell whether the higher $T_b$ recorded in other species may have been affected by activity levels.

At $T_a = 48$, 52 and 54 °C, 57, 100 and 100 % of scaly-feathered weavers, sociable weavers and white-browed sparrow-weavers respectively had reached their thermal end point, as defined by the criteria set out at the beginning of the experiment. These criteria include both active and inactive birds that exhibit steep rates of $T_b$ increase and high overall $T_b$. Extreme agitation or escape behavior at low $T_a$s often results in outlying data points, making removal of these data from analyses an obvious necessity. However, at high $T_a$s, this behaviour is equally likely to be a consequence of thermal end point being reached, as it is to be the cause of thermal end point being reached. Distinguishing between cause and consequence in this sense was not possible in this study, and the numbers of birds that were calm at their thermal limit were too low to allow for independent analysis. In future studies, however, it would be worthwhile to exclude active data completely.

Thermal end point was well-defined in white-browed Sparrow-weavers, as evaporative capacity had peaked, and $T_b$ was increasing steeply as a result of external heat load. In sociable weavers, capacity was still increasing, but because this species is smaller, this increase in capacity was possibly not enough to combat external heat gain, and $T_b$ increased to near-lethal levels. For scaly-feathered weavers at $T_a = 48$ °C, capacity was plateauing, but average $T_{b,\,max}$ was not yet at lethal levels. The fact that I did not determine the $T_a$ where 100% of birds were at their thermal end point reflects a combination of small sample size and caution on my part. I was more likely to prematurely end an experimental run for a scaly-feathered weaver than for a white-browed sparrow-weaver, as sudden jumping from a scaly-feathered weaver was more likely to cause a fatal increase in metabolic rate and heat load.

### *Species comparisons*

Interspecific comparisons of heat dissipation capacity are difficult with such limited data at high $T_a$s. Until more research has been done, this makes two-species comparisons largely unavoidable, though caution must be taken when drawing conclusions. Overall, scaly-feathered weavers seemed better able to cope with a $T_a$ of 44 °C than a species of similar mass, the spinifexbird. The impressive ability to cope with heat in the small scaly-feathered weaver could be due to the relatively long evolutionary period that this species has had to evolve heat tolerance mechanisms, as

African deserts are geologically very old (van Zinderen Bakker 1975), and this species is found only in arid-zone areas of Southern Africa. It has been suggested that the mesic evolutionary history of the genus *Eremiornis* has resulted in the lack of physiological adaptation to arid conditions in the desert-dwelling spinifexbird (Schodde 1982). On the other hand, the high RMR and low evaporative capacity at high $T_a$s found in spinifexbirds (Ambrose et al 1996) could possibly be due to relatively high chamber humidity (the authors do not specify the humidity levels within the chambers, or mention attempting to keep humidity as low as possible), or due to high activity (birds were not monitored during experiments). Sociable weavers seemed to manage a $T_a$ of 48 °C better than dune larks, which had to evaporate double the water to get the same evaporative capacity as the sociable weaver. Dune larks live in the comparatively cool Namib desert, which may explain their higher RMR at both low and high $T_a$s (Williams 1999). White-browed sparrow-weavers and hoopoe larks exhibited similar RMR, EWL and evaporative capacity at $T_a = 50$ °C, although the latter had an average $T_b$ 1.5 °C higher than the former. The desert environments occupied by the hoopoe larks are more climatically extreme than the Kalahari, which could potentially affect the evolution of heat dissipation capacity in this species.

My findings do not support a clear effect of body mass on evaporative cooling capacity between the three ploceid species. At $T_a = 48$ °C, scaly-feathered weavers had higher mass-specific RMR and EWL than sociable weavers and white-browed sparrow-weavers (Table 1), as is expected in a smaller bird. Sociable weavers at $T_a =$ 52 °C exhibited an average mass-specific RMR lower than that of white-browed sparrow weavers (~17.7 compared to ~22.4 mW $g^{-1}$), but with similar average EWL (~62 mg $g^{-1}$ $h^{-1}$), both of which were unexpected. The ecology and evolutionary history of these three species could have played a more important role than body mass in shaping evaporative cooling capacities. It is also possible that the relatively narrow body mass range of our species (white-browed sparrow-weavers are only ~30 g heavier than scaly-feathered weavers) is too small to detect the expected body mass effects on RMR and EWL.

My data do, however, support the prediction that thermal end point increases with increasing mass, though this result is likely specific to the artificial situation of a ramped $T_a$ profile, where birds are exposed to stable $T_a$s for a relatively short time, after which $T_a$ is increased to a higher setpoint. The mass effect on thermal end point in my study could be partly due to small birds not meeting their higher mass-specific water requirements, subsequently leading to earlier peaking of evaporative capacity and potentially lethal dehydration, as seen in my study and outlined by the literature (McKechnie and Wolf 2010). It is also due to the steeper rate of environmental heat gain in smaller birds leading to an increase in $T_b$ to near-lethal levels (Wolf and Walsberg 1996b). Larger birds are more likely at risk of pathological hyperthermia than dehydration (Weathers 1981). My finding that white-browed sparrow-weavers exhibited lower average $T_b$s overall at high $T_a$s than the other species could potentially support this idea, as these birds may have been attempting to minimize hyperthermia.

### *Methodological limitations and closing remarks*

The methodologies utilized to investigate the effects of $T_a$ on an animal's EWL, RMR and $T_b$ in this and many other studies place certain limitations on ecological extrapolation, and care must be taken in interpreting the results. A number of aspects in the experimental setup provide a set of controlled conditions that test subjects would likely not experience in a natural setup. For instance, the ramped $T_a$ profile, in which $T_a$ is stabilized for short periods before being increased again, could cause stress responses in birds and artificially influence physiology. During my experiments, birds were subjected to a maximum ramp in $T_a$ of ~20 °C over a period of ~ three hours. While this may seem extreme, I would argue that a bird actively foraging in a desert environment can experience huge changes in operative temperature simply by moving in and out of the sunlight (Add Wolf and Walsberg 1996). I therefore do not believe that ramping Ta results in unreliable physiological estimates, besides which, data from stressed and agitated birds were excluded from analysis.

It is important to realize, however, that the estimates I obtained likely reflect maximum heat dissipation capacity, due to the relatively short exposure time to the high $T_a$s along with the artificially low humidity levels within experimental chambers. The short exposure times likely minimized the effects of hydration state on EWL, and under natural conditions, when birds are exposed to heat stress and water intake is halted, EWL would decrease over time (Menon et al 1989; Maloney and Dawson 1998). While deserts are by definition characterized by heat and aridity, natural humidity levels, which are likely to fluctuate far above the levels used in this study, would reduce the efficiency of EWL. Maintaining humidity at extremely low and standardized levels during experiments, is, however, crucial if we aim to effectively compare maximal EWL rates between species. While we cannot apply the absolute physiological values obtained during these experiments to ecological scenarios, we can use the data qualitatively in inter-specific comparisons of maximal heat dissipation abilities.

It is thus important to continue with species-specific laboratory-based research into the thermoregulatory abilities of birds at extremely high $T_a$s, as it lays the foundation for larger-scale mechanistic modeling of overall vulnerability to current and future climate scenarios. Heat waves, which are predicted to increase in frequency, duration and intensity by 2080 (IPCC 2011), have already caused mass die-offs of birds (Finlayson 1932; Keast 1960; Miller 1963; Towie 2009; Albright et al 2010). Birds influence food-webs as they occupy a range of trophic levels (Whelan et al 2008), and provide critical ecosystem services such as pollination and seed dispersal. They are thus important members of animal communities. Consequently, changes in avian community structure as a result of heat waves could have considerable effects on ecosystems. From the results of this study, I can suggest that smaller desert passerines may be less resilient to heat waves than larger birds, due to an inability to meet high water requirements in arid areas, and a resultant lower thermal end point.

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# CHAPTER 3: COMPARING HEAT TOLERANCE AND EVAPORATIVE COOLING CAPACITIES OF DOVES AND PASSERINES

## Abstract

The roles of phylogeny and body size in avian heat stress physiology, and how they interact to set the upper limits to heat dissipation capacity, remain largely unexplored. I measured evaporative water loss (EWL), resting metabolic rate (RMR) and body temperature ($T_b$) in three arid-zone columbids spanning a range of body mass, namely Namaqua dove (*Oena capensis*, ~37 g), laughing dove (*Spilopelia senegalensis*, ~89 g) and Cape turtle dove (*Streptopelia capicola*, ~148 g) at air temperatures ($T_a$) of up to 55-60 °C. At $T_a$ = 56 °C, mass-specific EWL was 9.6, 7.3 and 9.2 times higher than baseline levels at 35 °C in Namaqua, laughing and Cape turtle doves respectively. Mass-specific RMR increased by 27 and 24 % in Cape turtle- and laughing doves between $T_a$ = 35 and 56 °C, but decreased by 14 % in Namaqua doves. At 60, 58 and 56 °C, Namaqua, laughing and Cape turtle doves dissipated 498, 218 and 231 % of metabolic heat, respectively. All three species used facultative hyperthermia when experiencing $T_a$ values above normothermic $T_b$. I also compared thermoregulatory characteristics among six columbids and seven passerines to test the hypothesis that the metabolic costs of heat dissipation, and consequently $T_b$ at high $T_a$s, are lower in doves than they are in passerines. A conventional analysis found significant differences in slopes of EWL as well as the change in RMR, EWL and $T_b$ between $T_a$ = 35 and 48 °C between doves and passerines, though once phylogeny was controlled for, these differences were shown to be a result of phylogenetic inertia. Both a conventional analysis and a phylogenetic independent contrast (PIC) found a significant effect of body mass on slope of EWL, change in EWL (only the PIC) and change in $T_b$ between $T_a$ = 35 and 48 °C. From the results of this study, I argue that by utilizing high ratios of cutaneous EWL to respiratory EWL, doves generate much less metabolic heat at high $T_a$s than passerines. I suggest that larger passerines are better able to tolerate heat than smaller passerines, whereas the opposite is true in doves. The lack of data from small doves obscured this finding in the conventional and PIC analyses. Further studies on the

upper limits to the avian capacity for evaporative cooling and heat tolerance are critical for larger-scale mechanistic modeling of vulnerability to extreme heat events under current and future climate scenarios.

## Introduction

In the classic model of endotherm thermoregulation, metabolic rate increases as air temperatures ($T_a$) decrease below the thermoneutral zone (TNZ), or increase above the TNZ (Scholander et al 1950; Angilletta et al 2010). Many more studies have examined the energetic costs of thermoregulation at cold temperatures than those associated with very high $T_a$ far above the TNZ, when active cooling via evaporative heat loss is necessary. Although a substantial body of literature exists on the increases in evaporative water loss (EWL) and metabolic rate that occur with increasing $T_a$ (Dawson 1954; Cade et al 1964; Coulombe 1970; Weathers and Caccamise 1975; Weathers 1981; Maloney and Dawson 1994; Tieleman et al 2002a; McKechnie and Wolf 2004a), the extent to which the metabolic costs of maintaining $T_b < T_a$ varies with factors such as body mass and phylogenetic position remain largely unclear. Desert-dwelling birds, which are mostly diurnal and generally do not use burrows or other thermal refugia (but see (Williams et al 1999)), often need to defend a $T_b$ setpoint far below operative temperature observed in the environment. The metabolic costs of heat defense may be substantial, and the dune lark (*Mirafra erythrocephalus*), for example, doubles its resting metabolic rate (RMR) between $T_a$s of 35 and 48 °C (Williams 1999).

Increasing heat dissipation at high $T_a$ involves increasing rates of evaporative water loss (EWL), which occurs cutaneously (CEWL) or via the respiratory passages

(REWL) (Dawson 1982). An approximately linear increase can be seen in either of these avenues of EWL once $T_a$ exceeds $T_b$ (McKechnie and Wolf 2010). The cutaneous contribution to total avian EWL has been debated (Menon et al 1986) and was for a long time thought to be minimal, as birds have no sweat glands. It has since been shown, however, that evaporation of water from the skin is the major means of heat dissipation in certain avian lineages, especially the order Columbiformes (pigeons and doves) (Smith and Suthers 1969; Bernstein 1971; Dawson 1982; Marder and Ben-Asher 1983; Marder and Arieli 1988; Withers and Williams 1990; McKechnie and Wolf 2004). In contrast, passerines appear to rely primarily on increases in respiratory evaporation at high $T_a$ (Dawson 1982; Wolf and Walsberg 1996a; McKechnie and Wolf 2004a). Several researchers have shown that heat dissipation via CEWL may be less energetically costly than dissipation via respiratory pathways such as panting, as CEWL appears to be passive and diffusional in nature (Withers and Williams 1990b; Hoffman and Walsberg 1999; McKechnie and Wolf 2004a). As a consequence, heat dissipation that relies on the use of cutaneous EWL in preference to respiratory EWL could provide an advantage, especially at extremely high $T_a$s. Doves acclimated to high $T_a$s exhibit adaptive increases in the relative contribution of CEWL compared to doves acclimated to lower $T_a$s (Marder and Arieli 1988; McKechnie and Wolf 2004a). It has been suggested that this phenotypic flexibility could reflect the lower metabolic costs associated with CEWL (Marder and Arieli 1988; McKechnie and Wolf 2004). In contrast, thermal acclimation does not seem to cause an increase in the ratio of CEWL to REWL in passerines (Tieleman and Williams 2002a), though this area of research is largely unexplored. The increase in CEWL observed in heat-acclimated doves is attributable to a decrease in whole-body water vapour diffusion resistance, which is brought about by structural changes increasing the permeability of the skin, as well as changes in peripheral blood supply (McKechnie and Wolf 2004a). The latter may allow for adjustments in the contribution of CEWL over much shorter time scales (Hoffman and Walsberg 1999), which could possibly aid a bird in preventing uncontrolled loss of body water in a situation when dehydration is a greater risk than elevated $T_b$.

In this study, I investigated the scaling of resting metabolic rate (RMR), EWL, evaporative capacity and changes in $T_b$ at high $T_a$ in three columbids varying approximately 4-fold in mass. In Chapter 2, I found that because of higher mass-specific EWL coupled with limited body water supply, smaller birds became dehydrated quickly, and reached near-lethal $T_b$ levels at lower $T_a$s than larger birds. Larger birds reached their thermal end points at higher $T_a$s, possibly as a consequence of avoiding dehydration limits for longer. However, I predict that this would not be the case in columbids. In smaller doves, a higher surface area to volume ratio presumably results in more skin per unit body volume from which to evaporate water cutaneously and dissipate heat effectively. In larger doves, cutaneous EWL may be supplemented by respiratory EWL (panting and/or gular fluttering), which could lead to increased metabolic heat load, lower evaporative capacity and consequently a lowering of the $T_a$ at which thermal end points are reached, though these predictions may be specific to the artificial situation of the ramped $T_a$ profile used in this study. In addition, dehydration during acute heat exposure may not be as critical a factor in columbiformes as it is in passerines, due to the ability of pigeons and doves to store water in their enlarged crops. I therefore expected to see smaller doves tolerating higher $T_a$s, and exhibiting smaller increases in mass-specific RMR, EWL and $T_b$ between TNZ and extremely high $T_a$s.

I expected mass-specific RMR to increase in the doves above the upper critical limit of thermoneutrality ($T_{uc}$), due to the costs of heat dissipation mechanisms such as gular fluttering, although I expected the fractional increases to be smaller than those I observed in passerines. I also expected the slope of RMR vs $T_a$ to be negatively related to body mass (Weathers 1981). I further predicted that the slope of mass-specific EWL vs $T_a$ would be steeper in smaller doves (McKechnie and Wolf 2010), and that mass-specific RMR and EWL of smaller doves would be higher at any given $T_a$ than in larger doves (Bartholomew and Cade 1963).

I also compared heat tolerance variables (the slope of mass-specific EWL as a function of $T_a$, and the magnitude of change in mass-specific RMR, EWL, evaporative capacity and $T_b$ between $T_a = 35$ and 48°C) between Passeriformes and Columbiformes using seven passerine and six columbid species (the six species from the present study together with data from other sources), in order to test the hypothesis that the primary avenue of EWL is a significant predictor of the magnitude of change in mass-specific RMR, EWL and $T_b$ between moderate and high $T_a$s, due to the lower metabolic costs of high ratios of CEWL to REWL in doves.

## Materials and methods

Field sites and experimental protocol are described in Chapter 2, with methodological differences highlighted below.

### *Study species*

Rates of EWL, RMR and $T_b$ were measured at a range of $T_a$ in three species from the family Columbidae, namely *Oena capensis* (Namaqua dove, ~40 g), *Spilopelia senegalensis* (laughing dove, ~100 g; formerly *Streptopelia senegalensis*) and *Streptopelia capicola* (Cape turtle dove, ~153 g) (Hockey et al 2005). All three species are granivorous, and occur widely throughout sub-Saharan Africa in almost all habitats except forests. All three species are common year-round in the Kalahari desert, although their numbers decrease during dry periods (Hockey et al 2005).

Birds were captured using mistnets at various times of the day, and initially held in cloth bags. All birds used in the study were adults and appeared to be in good condition. The mean body masses of *O. capensis S. senegalensis*, and *S. capicola* were 37.1 ± 3.2 g (mean ± SD; n = 29), 89.4 ± 13.0 g (n = 33) and 147.5 ± 17.6 g (n = 26) respectively.

### *Gas exchange measurements*

Birds were placed individually in sealable plastic chambers with volumes of 4 L (*O. capensis*) or 9 L (*S. senegalensis*, and *S. capicola*). Depending on $T_a$ and the body mass of the bird, flow rates ranging 6 - 85 L $min^{-1}$ were used. Birds tended to remain calmer when flow rates were higher, and chamber humidity lower (personal observation). Due to the high flow rates used, fractional depletion of oxygen within the chamber was below the resolution of my oxygen analyser (FC-10A, Sable Systems, Las Vegas NV, USA), and could therefore not be measured accurately. By massaging the crop of a dove, I could feel whether or not seed was present. If seed was present before commencing an experimental run, I assumed a respiratory exchange ratio (RER) of 1, and if no seed was present, I assumed an RER of 0.71, representative of lipid metabolism in post-absorptive birds (Walsberg and Wolf 1995). Birds were exposed to $T_a$s of 25–60 °C in 5 °C increments, except above 40 °C, where $T_a$ was increased in increments of 2 °C.

*Data extraction and analyses*

Voltage outputs from the analysers, thermistor probe and pit tags were digitised using a Universal Interface (model UI2-1101-33, Sable Systems, Las Vegas NV, USA) and recorded with a sampling interval of 5 s using a personal computer with Expedata software (Sable Systems, Las Vegas NV, USA). $\dot{V}_{CO_2}$ and $\dot{V}_{H_2O}$ were calculated using equations 10.5 and 10.9 respectively (Lighton 2008), assuming 0.803 mg $H_2O$ per ml of water vapour. Metabolic heat gain (mW) was calculated as in (Walsberg and Wolf 1995) assuming an RER of 0.71. Evaporative heat loss (mW) was calculated using 2.26 J mg$^{-1}$. Evaporative capacity is the ratio of metabolic heat produced to evaporative heat lost. Resting metabolic rates and rates of EWL were calculated from steady-state traces of $\dot{V}_{CO_2}$ (combined with assumed RERs) and $\dot{V}_{H_2O}$ in ExpeData, with the lowest 1-min mean values considered to be representative of resting values. Rate of $T_b$ increase (°C min $^{-1}$) was calculated as the difference between the first and last $T_b$ measurement during the final ten minutes of a test $T_a$, divided by the amount of time between the first and last measurement (~ 10 mins).

Broken stick analyses were performed in R3.0 (R Development Core Team 2011b) using the package *segmented* (Muggeo 2008) to estimate inflection points for $\dot{V}_{H_2O}$, $\dot{V}_{CO_2}$, evaporative capacity, mean $T_b$ and rate of $T_b$ increase. All data points associated with agitation or activity in the metabolic chambers were excluded from statistical analyses. I did not test for the effect of activity on response parameters since I seldom had enough active data to conduct conclusive statistics for this factor, and because of the difficulty in interpreting and standardising the manner of activity observed between individuals. Data above the inflection point were used to obtain slopes for the relationships of $\dot{V}_{H_2O}$, $\dot{V}_{CO_2}$, evaporative capacity, mean $T_b$ and rate of $T_b$ increase as function of increasing $T_a$. For these subsets of the data I performed generalised mixed-effect models, with package nlme (Pinheiro et al 2009) to test for an effect of $T_a$ on the above parameters. I used individual as a random factor. In addition to the linear regression, a polynomial relationship between $T_a$ and EWL was fitted using a generalised linear regression, and the coefficients for this polynomial regression, along with the Akaike Information Criterion (AIC) for both the segmented and polynomial regressions are shown in Table 4. For comparative purposes, however, only the linear regressions are presented in the results.

All results are mass-specific, and expressed as mean ± SD for inactive birds, unless otherwise stated.

### *Comparative analysis: columbids vs passerines*

I used both conventional analyses (generalised linear models) and phylogenetically independent contrasts [PIC, in R2.15.2 (R Development Core Team 2011a)] to test for differences in physiological heat tolerance parameters between columbids and passerines. I used the package *car* (Fox et al 2013) for conventional analyses and *ape* (Paradis et al 2004) for PIC analyses. I tested the slope of mass-specific EWL as a function of $T_a$, and the magnitude of change in mass-specific RMR, EWL, evaporative capacity and $T_b$ between $T_a = 35$ and 48°C. I selected this range of $T_a$s for comparison on the basis of 35°C representing baseline RMR and EWL at thermoneutrality and 48°C being the highest test $T_a$ shared by all the species in the analysis. Whereas the magnitude of change in mean values of RMR and EWL were calculated as ratios, changes in evaporative capacity and $T_b$ were calculated as differences in absolute values. I sampled 100 phylogenies for the 13 species included in the data set (Table 1) sampled from http://www.birdtree.org (Jetz et al 2012) using the Hackett et al. (2008) phylogeny as a backbone. The majority consensus tree was identified using the programme Mesquite (Maddison and Maddison 2011).

Null models of the parameters tested were used to establish phylogenetic signal, using the parameter *K* (Blomberg et al 2003). Statistically significant phylogenetic signal was not detected in any of the parameters (slope of EWL: $K = 1.831$, $p = 0.051$; log Mb: $K = 1.246$, $p = 0.089$; RMR: $K = 0.516$, $p = 0.303$; EWL: $K = 1.6$, $p = 0.091$; capacity: $K = 0.61$, $p = 0.27$ and $T_b$: $K = 0.227$, $p = 0.6523$). However, for comparisons involving less than 20 species, it has been noted that while the *K*-statistic itself (indicating the extent to which phylogenetic signal is detected) is reliable, the test for its statistical significance is not (Blomberg et al 2003). Significant *K*-values are often in the range of 0.4 and 0.8, and are found to not be significantly greater than zero simply because of the small size of the sample being tested. It is therefore advisable not to simply assume that phylogenetic signal is absent, but to perform both conventional statistical analyses and phylogenetically independent contrasts (PIC), which is similar to the phylogenetic generalised least-squares analysis (PGLS) but involves no branch length transformations (Blomberg et al 2003). Hence, I present both conventional and phylogenetically-corrected results (Table 2).

**Table 1.** The seven passerines and six doves included in the conventional and phylogenetic independent contrast (PIC) models to explain the differences in heat tolerance parameters between the two avian orders. Slope of mass-specific evaporative water loss (log transformed) (Log Slope of EWL), and the change in resting metabolic rate ($RMR_{Ta=48}$ / $RMR_{Ta=35}$), evaporative water loss ($EWL_{Ta=48}$/ $EWL_{Ta=35}$), evaporative capacity (Δ Eff) and body temperature ($\Delta T_b$) are shown for each species.

| **Species** | **Mass (g)** | **Log Slope of EWL ($mg^{-1}g^{-1}h^{-1}°C^{-1}$)** | **$RMR_{Ta=48}$ / $RMR_{Ta=35}$** | **$EWL_{Ta=48}$ / $EWL_{Ta=35}$** | **Δ Eff ($Eff_{Ta=48}$ - $Eff_{Ta=35}$)** | **Δ $T_b$ ($T_{b[Ta=48]}$ - $T_{b[Ta=35]}$)** | **Reference** |
|---|---|---|---|---|---|---|---|
| Columbiformes: | | | | | | | |
| spinifex pigeon<br>*Geophaps plumifera* | 89.0 | 1.20 | 1.49 | 4.82 | 1.48 | 1.60 | (Withers and Williams 1990b) |
| Namaqua dove<br>*Oena capensis* | 37.1 | 0.96 | 2.50 | 5.21 | 1.18 | 1.43 | (Present study) |
| laughing dove<br>*Stigmatopelia senegalensis* | 89.4 | 1.11 | 1.87 | 4.36 | 1.20 | 1.43 | (Present study) |
| Cape turtle dove<br>*Streptopelia capicola* | 147.5 | 1.03 | 1.62 | 4.83 | 1.19 | 1.60 | (Present study) |
| white-winged dove<br>*Zenaida asiatica* | 147.3 | 1.13 | 1.47 | 3.66 | 1.26 | 1.68 | (McKechnie and Wolf 2004a) |
| mourning dove<br>*Zenaida macroura* | 104.0 | 1.12 | 1.30 | 3.36 | 1.66 | 1.15 | (Hoffman and Walsberg 1999) |

| **Species** | **Mass (g)** | **Log Slope of EWL ($mg^{-1}g^{-1}h^{-1}°C^{-1}$)** | **$RMR_{Ta=48}$ / $RMR_{Ta=35}$** | **$EWL_{Ta=48}$ / $EWL_{Ta=35}$** | **Δ Eff ($Eff_{Ta=48}$ - $Eff_{Ta=35}$)** | **Δ $T_b$ ($T_{b[Ta=48]}$ - $T_{b[Ta=35]}$)** | **Reference** |
|---|---|---|---|---|---|---|---|
| Passeriformes: | | | | | | | |
| hoopoe lark<br>*Alaemon alaudipes* | 37.7 | 1.64 | 4.32 | 13.19 | 1.52 | 4.70 | (Tieleman et al 2002a) |
| verdin<br>*Auriparus flaviceps* | 6.7 | 1.24 | 5.33 | 7.88 | 1.19 | | (Wolf and Walsberg 1996a) |
| Dunn's lark<br>*Eremalauda dunni* | 20.6 | 1.72 | 4.54 | 10.30 | 1.08 | 3.20 | (Tieleman et al 2002a) |
| Burchell's starling<br>*Lamprotornis australis* | 108.4 | 1.33 | 1.93 | 4.29 | 0.93 | 1.53 | (Smit et al. unpublished data) |
| sociable weaver<br>*Philetairus socius* | 24.9 | 1.09 | 3.17 | 8.95 | 1.43 | 2.73 | (Present study) |
| white-browed sparrow-weaver<br>*Plocepasser mahali* | 39.4 | 1.27 | 4.01 | 7.94 | 1.23 | 1.53 | (Present study) |
| scaly-feathered weaver<br>*Sporopipes squamifrons* | 10.5 | 1.36 | 3.67 | 10.17 | 1.20 | 4.43 | (Present study) |

**Table 2.** Models explaining differences in heat tolerance parameters between the six doves (order Columbiformes) and seven passerines (order Passeriformes) for which data are currently available at hot air temperatures ($T_a$) (see Table 1 for details). The importance of log body mass (Log Mb) and order in explaining slope of mass-specific EWL (log transformed) as a function of $T_a$, and the change in resting metabolic rate ($RMR_{Ta=48}$ / $RMR_{Ta=35}$), evaporative water loss ($EWL_{Ta=48}$/ $EWL_{Ta=35}$), evaporative capacity ( Δ Capacity) and body temperature ( Δ $T_b$), between $T_a$ = 35 and 48 °C (see methods for details on the parameters), was investigated. The models with the lowest Akaike Information Criteria corrected for small samples (AICc) are in bold text. In cases where the lowest AICc values did not differ by more than two units, both models are presented. Both conventional and phylogenetic independent contrast (PIC) models are shown for each parameter.

| Model | AICc Conventional | AICc PIC |
|---|---|---|
| **Log Slope of EWL (mg$^{-1}$g$^{-1}$h$^{-1}$°C$^{-1}$)** | | |
| logSlopeEWL ~ Log Mb*Order | -12.16 | -32.97 |
| logSlopeEWL ~ LogMb + Order | **-17.41** | -39.07 |
| logSlopeEWL ~ LogMb | -14.55 | **-43.49** |
| logSlopeEWL ~ Order | -10.53 | -34.56 |
| **$RMR_{Ta=48}$ / $RMR_{Ta=35}$** | | |
| RMR ~ Log Mb*Order | 7.53 | -25.36 |
| RMR ~ LogMb + Order | 2.10 | -29.73 |
| RMR ~ LogMb | 3.71 | **-32.66** |
| RMR ~ Order | **-1.91** | **-33.95** |
| **$EWL_{Ta=48}$ / $EWL_{Ta=35}$** | | |
| EWL ~ Log Mb*Order | 70.41 | 34.68 |
| EWL ~ LogMb + Order | 64.87 | 29.96 |
| EWL ~ LogMb | 65.19 | **25.34** |
| EWL ~ Order | **62.49** | 33.03 |
| **Δ Capacity ($Cap_{Ta=48}$ - $Cap_{Ta=35}$)** | | |
| Capacity ~ Log Mb*Order | 10.86 | 5.43 |
| Capacity ~ LogMb + Order | 5.61 | 1.41 |
| Capacity ~ LogMb | **2.14** | **-1.18** |
| Capacity ~ Order | **1.37** | **-1.97** |
| **Δ $T_b$ ($T_{b[Ta=48]}$ - $T_{b[Ta=35]}$)** | | |

| **Model** | **AICc Conventional** | **AICc PIC** |
|---|---|---|
| Tb ~ Log Mb*Order | 45.06 | 8.87 |
| Tb ~ LogMb + Order | 41.42 | 1.55 |
| Tb ~ LogMb | **37.98** | **-1.64** |
| Tb ~ Order | **40.31** | **4.96** |

* indicates an interaction effect

## Results

### *Namaqua doves*

All Namaqua doves at their thermal end points were active, and therefore not included in the results below. Mass-specific RMR decreased from 12.5 ± 2.3 at 25 °C to 8.9 ± 1.4 mW $g^{-1}$ at 35 °C (Fig. 1). At 56 °C and 60 °C, RMR was 8.6 ± 1.8 mW $g^{-1}$ (Table 3), and 8.0 ± 1.9 mW $g^{-1}$ (Fig. 1) respectively. However, the mixed model, which takes individuals' changes in RMR into account, revealed that there was a slight but significant linear increase in RMR (Fig. ($t_{1,27} = 2.02$, $p = 0.048$).

At $25 < T_a < 40$ °C, EWL was consistently low, averaging 4.2 ± 2.5 mg $g^{-1}$ $h^{-1}$ (Fig. 2). Above $T_a \approx 40$ °C, EWL increased linearly (Table 4) and significantly ($t_{1,27} = 10.81$, $p < 0.001$) by ~15-fold to 44.0 ± 8.2 mg $g^{-1}$ $h^{-1}$ at $T_a = 56$ °C and 62.4 ± 12.7 mg $g^{-1}$ $h^{-1}$ at 60 °C (Fig. 2, Table 3). Evaporative capacity increased linearly and significantly from 0.25 ± 0.15 below $T_a = 40$ °C to 3.36 ± 1.00 and 4.98 ± 0.44 at $T_a = 56$ and 60 °C respectively ($t_{1,27} = 13.43$, $p < 0.001$, Fig. 3, Table 3). Though a linear regression was fitted for comparative purposes, average evaporative capacity appeared to increase nonlinearly at the higher $T_a$s, increasing by 0.69 between $T_a = 56$ and 58 °C, and by 0.93 between 58 and 60 °C (Fig. 3).

**Table 3.** Mean (± SD) maximum body temperature ($T_{b,max}$), rate of $T_b$ increase (~ 10 minute period), evaporative water loss (EWL), resting metabolic rate (RMR) and evaporative capacity in Namaqua doves (n = 8), laughing doves (n = 5) and Cape turtle doves (n = 7) at firstly, the highest shared air temperature ($T_a$)* at which all species were tested (~ 56 °C), and secondly, Namaqua doves (n = 2) and Cape turtle doves (n = 1) that had reached their thermal end point** at the highest air temperature ($T_a$) at which each species was tested (~ 56 and ~ 60 °C for Namaqua doves and Cape turtle doves, respectively). For Namaqua doves, the ranges instead of the means are shown. No laughing doves reached their thermal end point at the highest $T_a$ at which this species was tested.

| | **Namaqua doves** | **Laughing doves** | **Cape turtle doves** |
|---|---|---|---|
| **Birds at $T_a$ = 56°C** | **(n=8)** | **(n=5)** | **(n=7)** |
| mean $T_b$ ± SD (°C) | 42.5 ± 0.7 | 43.6 ± 1.0 | 44.7 ± 0.3 |
| mean $T_{b,\ max}$ ± SD (°C) | 42.7 ± 0.7 | 43.8 ± 1.0 | 45.0 ± 0.3 |
| mean rate of $T_b$ increase ± SD (°C $min^{-1}$) | 0.02 ± 0.05 | 0.03 ± 0.01 | 0.06 ± 0.04 |
| mean EWL ± SD (mg $g^{-1}$ $h^{-1}$) | 44.0 ± 8.2 | 39.9 ± 11.1 | 32.8 ± 9.0 |
| mean RMR ± SD (mW $g^{-1}$) | 8.6 ± 1.8 | 11.0 ± 3.6 | 8.9 ± 0.7 |
| mean evaporative capacity ± SD | 3.4 ± 1.0 | 2.3 ± 0.5 | 2.3 ± 0.6 |
| **Birds at thermal end point** | **(n=2)** | | **(n=1)** |
| mean $T_b$ ± SD (°C) | 44.2 – 44.5 | | 44.7 |
| mean $T_{b,\ max}$ ± SD (°C) | 45.1 | | 45.5 |
| mean rate of $T_b$ increase ± SD (°C $min^{-1}$) | 0.1 – 0.2 | | 0.13 |
| mean EWL ± SD (mg $g^{-1}$ $h^{-1}$) | 43.02 – 50.14 | | 21.11 |
| mean RMR ± SD (mW $g^{-1}$) | 9.64 – 9.73 | | 8.18 |
| mean evaporative capacity ± SD | 2.8 – 3.23 | | 1.62 |

* Only inactive birds were included.

** Active and inactive birds were included, as extreme escape behavior was considered a behavioural signal of thermal end points being reached.

Mean $T_b$ averaged 40.3 ± 0.9 °C at 25 °C < $T_a$s < 35 °C, but increased significantly ($t_{1,27} = 9.13$, $p < 0.001$) at higher $T_a$ (Fig. 4). At $T_a$ = 56 and 60 °C, mean $T_b$ was 42.5 ± 0.7 °C and 43.4 ± 1.0 °C respectively (Fig. 4, Table 3). The relationship between $T_a$ and the rate of $T_b$ increase was not significant ($t_{1,9} = 0.68$, $p = 0.52$), but there was much more variation in the data at higher $T_a$s, ranging from -0.1 to 0.25 °C $min^{-1}$ (Fig. 5).

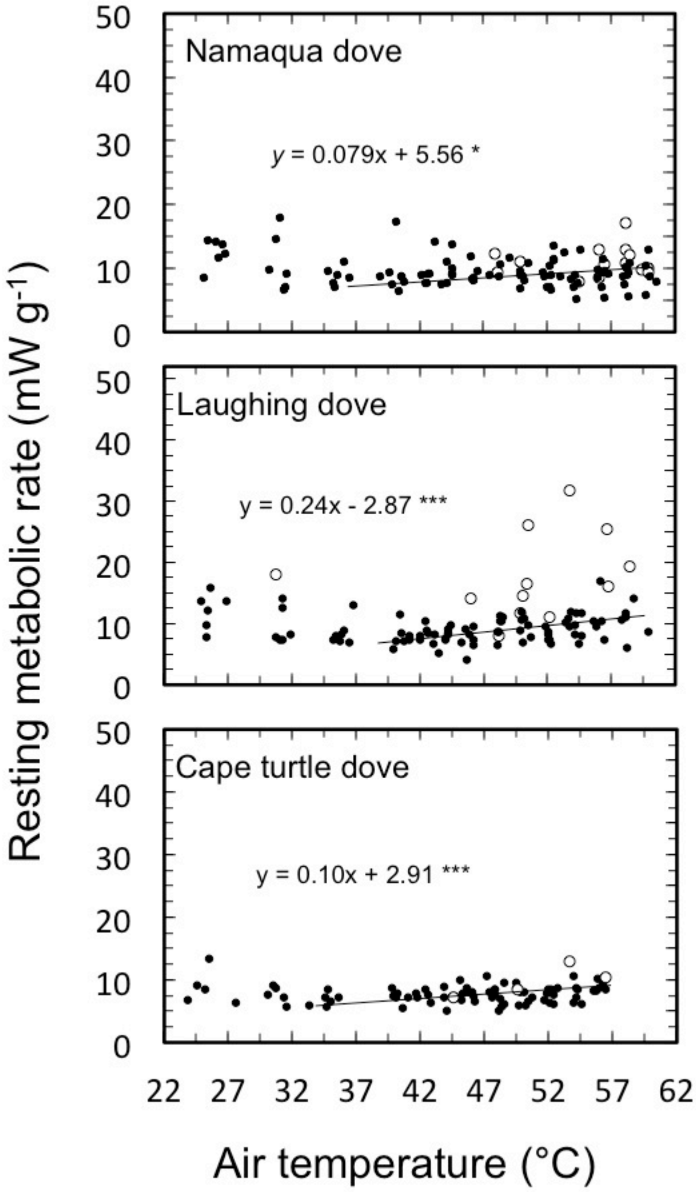

**Figure 1.** Resting metabolic rate (RMR) in Namaqua doves (n=29), laughing doves (n=33) and Cape turtle doves (n=26) over a range of air temperatures ($T_a$). Data from calm and active birds are shown by solid and unfilled circles respectively. Segmented regressions were used to estimate the inflection point in the relationship between RMR and $T_a$ for calm birds only. Statistical analyses were performed on data from calm birds to determine coefficients for the linear relationships above inflection points. Significant relationships are represented by asterisks.
Significance levels: * = < 0.05, ** = < 0.01, *** = < 0.001

**Table 4.** Coefficients for a nonlinear relationship ($y = ax^2 + bx + c$) between air temperature ($T_a$) and evaporative water loss (EWL, mg $g^{-1}$ $h^{-1}$) for Cape turtle doves, laughing doves and Namaqua doves. For all three species, Akaike information criteria (AIC) are shown for polynomial and segmented models.

| | **Cape turtle doves** | **laughing doves** | **Namaqua doves** |
|---|---|---|---|
| a | 0.04 | 0.03 | 0.06 |
| b | -2.28 | -1.48 | -3.44 |
| c | 35.6 | 20.8 | 51.4 |
| AIC polynomial | 468.5 | 592.5 | 664.3 |
| AIC segmented | 472.1 | 590.7 | 659.9 |

For Namaqua doves, when $T_a$ was 3-5 °C lower than $T_b$, EHL was low, averaging 3.9 ± 3.2 mW $g^{-1}$ (Fig. 6). As $T_a$ approached $T_b$, EHL increased, averaging 4.8 ± 2.8 mW $g^{-1}$ when $T_a \approx T_b$ (Fig. 6), and increasing linearly and significantly ($t_{1,26} = 9.58$, $p < 0.001$), to 34.7 ± 7.2 mW $g^{-1}$ when $T_a$ exceeded $T_b$ by 15-18 °C (Fig. 6). The number of Namaqua doves that reached thermal end points increased from zero at $T_a = 56$ °C to 18 % at $T_a = 58$ °C, and 29 % at $T_a = 60$ °C (Fig. 7). In the two birds that had reached their thermal end point at 60 °C, mean $T_b$ was 44.2 and 44.5 °C and $T_{b,\ max}$ was 45.1 °C in both birds. Mean $T_b$ is the average across the last ~ten minutes at a given $T_a$, whereas $T_{b,\ max}$ is the single highest recorded $T_b$ within the same ten minute period.

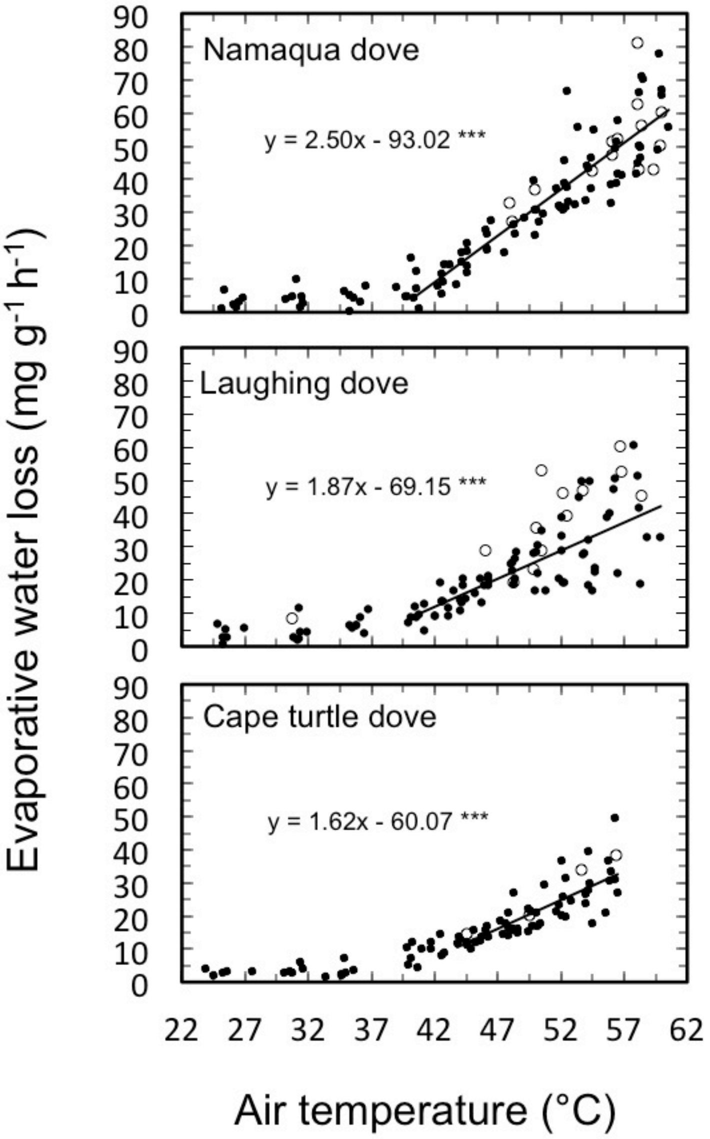

**Figure 2.** Evaporative water loss (EWL) in Namaqua doves (n=29), laughing doves (n=33) and Cape turtle doves (n=26) over a range of air temperatures ($T_a$). Data from calm and active birds are shown by solid and unfilled circles respectively. Segmented regressions were used to estimate the inflection point in the relationship between EWL and $T_a$ for calm birds only. Statistical analyses were performed on calm birds to determine coefficients for the linear relationships above inflection points. Significant relationships are represented by asterisks.
Significance levels: * = < 0.05, ** = < 0.01, *** = < 0.001

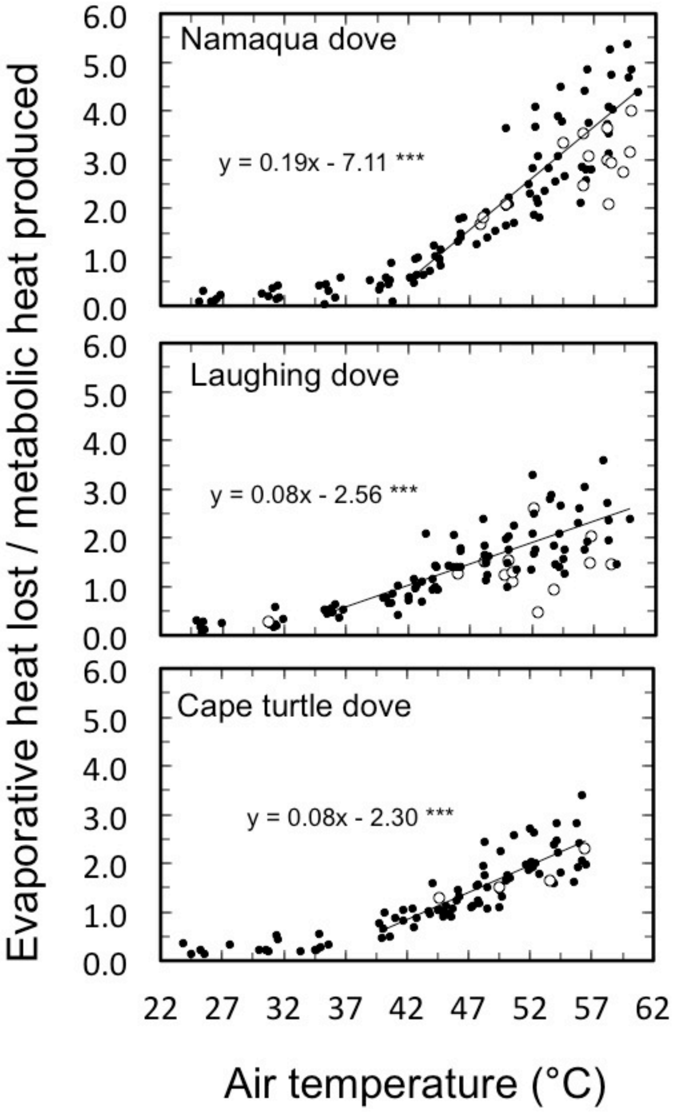

**Figure 3.** Evaporative capacity (the ratio of evaporative heat lost to metabolic heat produced) for Namaqua doves (n=29), laughing doves (n=33) and Cape turtle doves (n=26) over a range of air temperatures ($T_a$). Data from calm and active birds are shown by solid and unfilled circles respectively. Segmented regressions were used to estimate the inflection point in the relationship between evaporative capacity and $T_a$ for calm birds only. Statistical analyses were performed on calm birds to determine coefficients for the linear relationships above inflection points. Significant relationships are represented by asterisks.
Significance levels: * = < 0.05, ** = < 0.01, *** = < 0.001

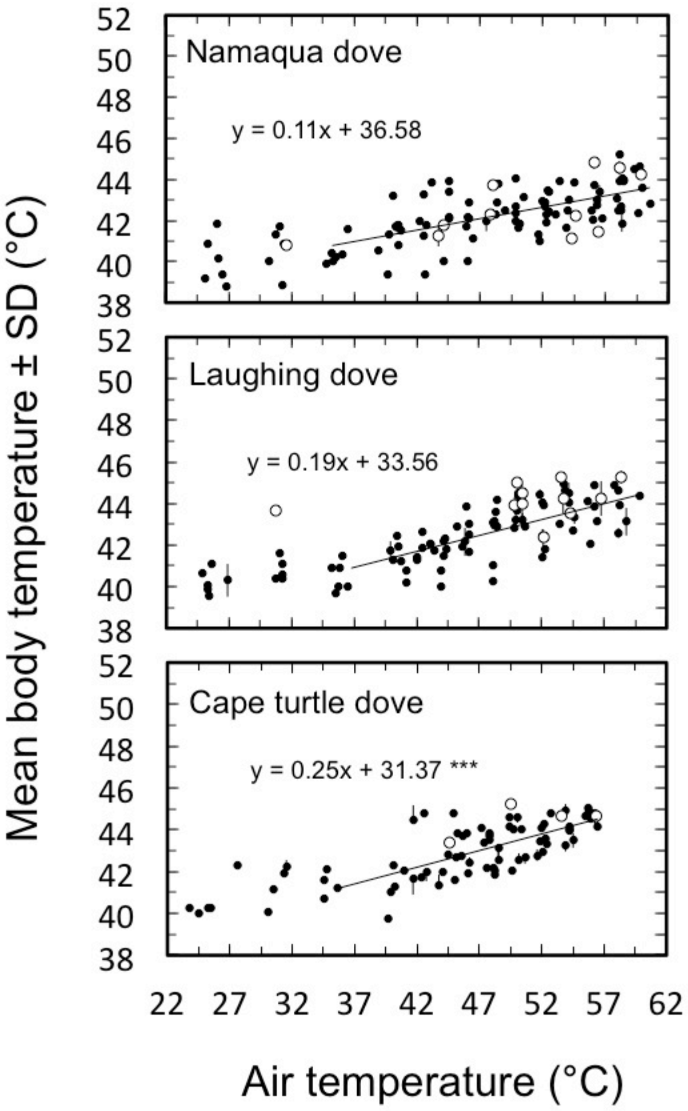

**Figure 4.** Mean (± SD) body temperature ($T_b$) for Namaqua doves (n=29), laughing doves (n=33) and Cape turtle doves (n=26) over a range of air temperatures ($T_a$). Data from calm and active birds are shown by solid and unfilled circles respectively. Segmented regressions were used to estimate the inflection point in the relationship between mean $T_b$ and $T_a$ for calm birds only. Statistical analyses were performed on calm birds to determine coefficients for the linear relationships above inflection points. Significant relationships are represented by asterisks.
Significance levels: * = < 0.05, ** = < 0.01, *** = < 0.001

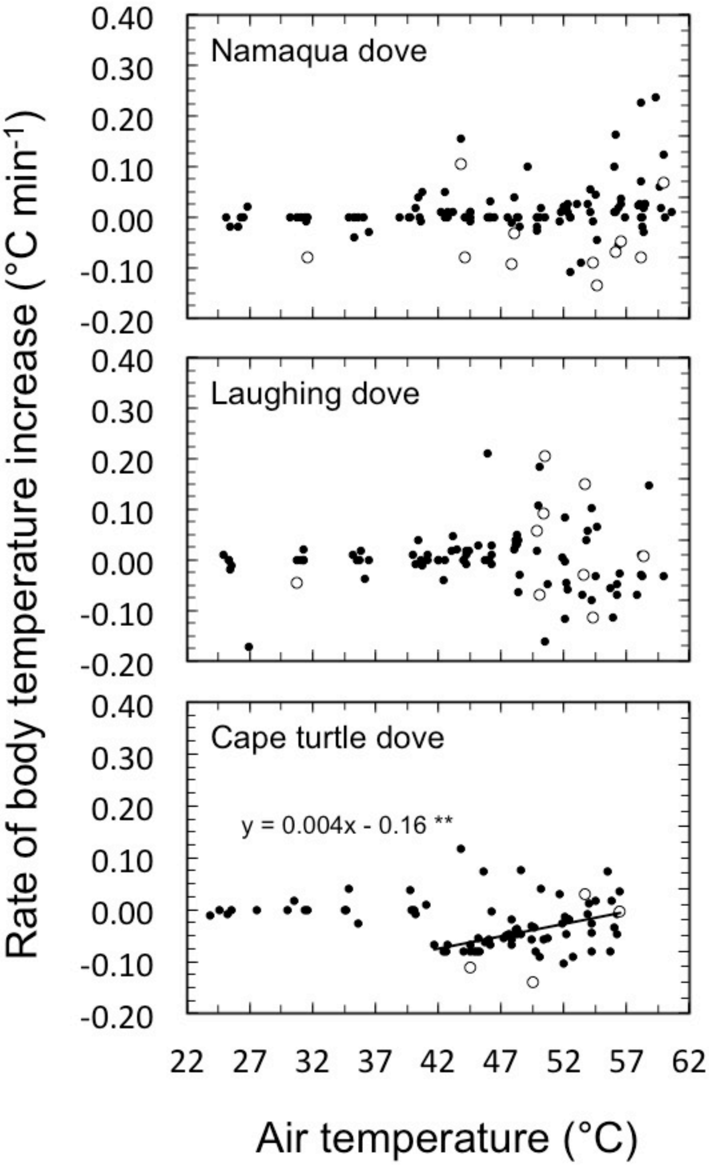

**Figure 5.** Rate of body temperature ($T_b$) increase over ~ 10 mins for Namaqua doves (n=29), laughing doves (n=33) and Cape turtle doves (n=36) over a range of air temperatures ($T_a$). Data from calm and active birds are shown by solid and unfilled circles respectively. Segmented regressions were used to estimate the inflection point in the relationship between the rate of $T_b$ increase and $T_a$ for calm birds only. Statistical analyses were performed on calm birds to determine coefficients for the linear relationships above inflection points. Significant relationships are represented by asterisks. In the case of Namaqua doves and laughing doves, the relationship was not statistically significant, and so is not shown.
Significance levels: * = < 0.05, ** = < 0.01, *** = < 0.001

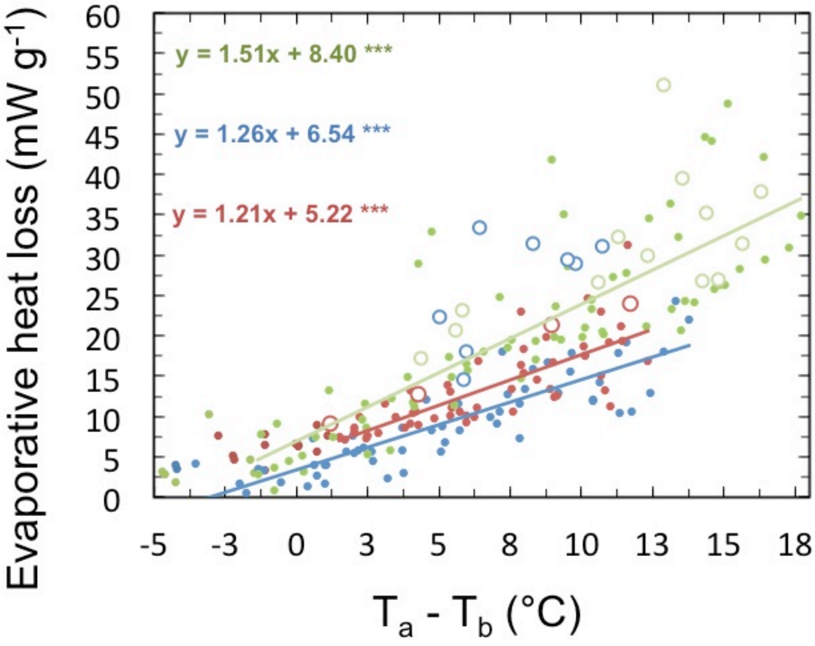

**Figure 6.** Evaporative heat loss (EHL) as a function of the gradient between air and body temperature ($T_a - T_b$) for Namaqua doves (n=29, green), laughing doves (n=33, blue) and Cape turtle doves (n=26, red). Segmented regressions were used to estimate the inflection point in the relationship between EHL and $T_a - T_b$. Data from calm and active birds are shown by solid and unfilled circles respectively. Statistical analyses were performed on calm birds to determine coefficients for the linear relationships above inflection points. Significant relationships are represented by asterisks.
Significance levels: * = < 0.05, ** = < 0.01, *** = < 0.001

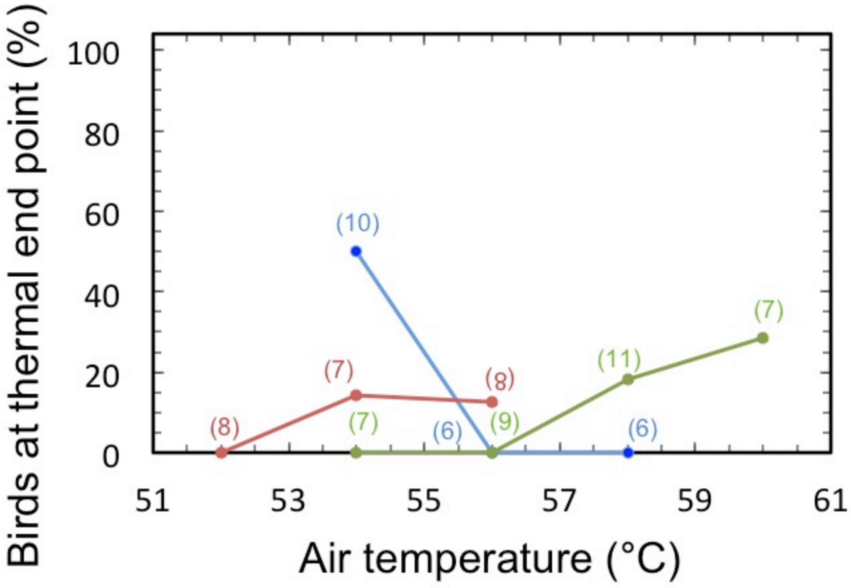

**Figure 7.** Percentage of individuals that reached their thermal end points for Namaqua doves (n=29, green), laughing doves (n=33, blue) and Cape turtle doves (n=26, red) over a range of air temperatures ($T_a$). Numbers in brackets indicate the total birds tested at each $T_a$.

Namaqua doves commenced gular fluttering at $T_a$ = 55.1 ± 3.6 °C (Fig. 8A). At $T_a \approx$ 50 °C, 215 ± 76 % of metabolic heat was being dissipated evaporatively (Fig. 8B). At this $T_a$, RMR was 7 % lower than RMR within the moderate $T_a$ range of 30-35 °C (Fig. 9).

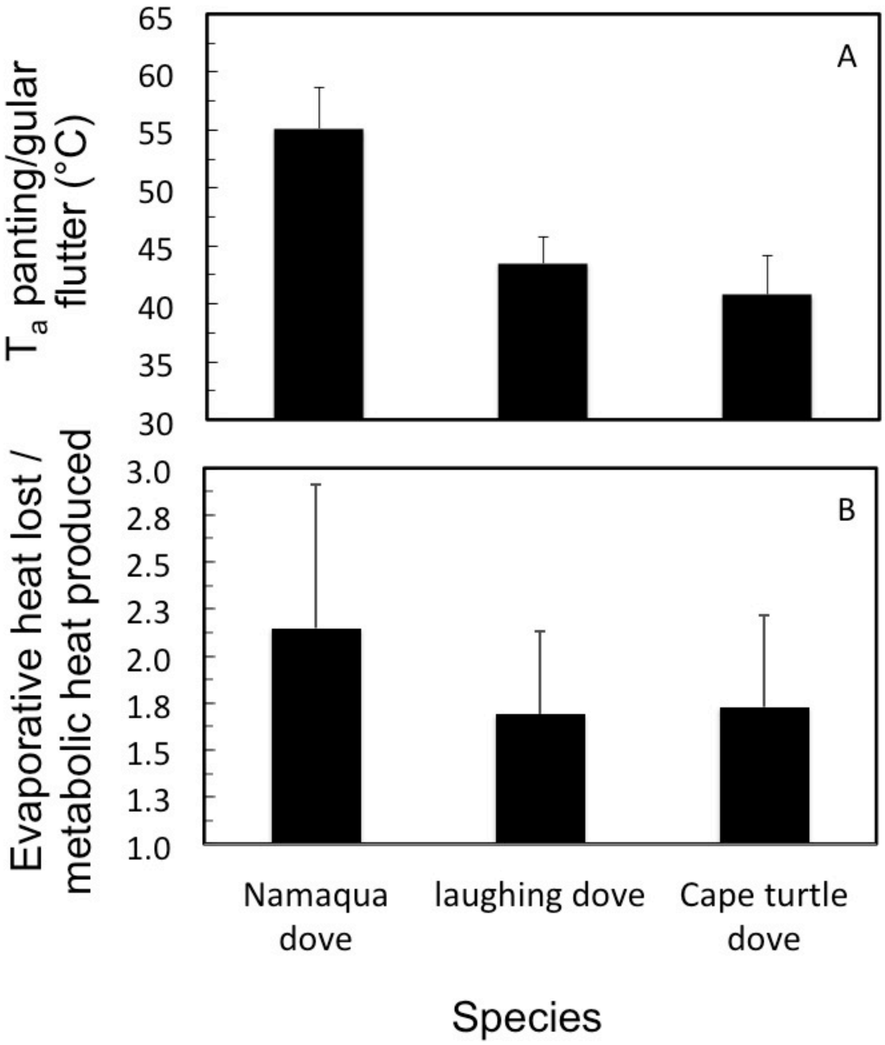

**Figure 8**. (A) Air temperature ($T_a$) at which Namaqua doves (n=12), laughing doves (n=19) and Cape turtle doves (n=14) were observed to commence gular fluttering. Data were considered reliable if birds were exposed to $T_a$s below 42 °C at the beginning of the experimental run, and had not yet started gular fluttering. The $T_a$ at which birds first started gular fluttering, even if it was intermittently, was used. These data are estimates only, as $T_a$ within the chambers sometimes increased by up to 3 °C between behavioural observations. When this occurred, and a bird could possibly have commenced gular flutter before the last behavioural observation, an average between the $T_a$ at which gular flutter was observed and the last $T_a$ at which gular flutter was not observed, was taken.
(B) Evaporative capacity of Namaqua doves (n=7), laughing doves (n=7) and Cape turtle doves (n=8) at $T_a$ = 50 °C, a $T_a$ at which Namaqua doves were utilizing predominantly cutaneous evaporative water loss (CEWL), but laughing and Cape turtle doves had already commenced gular fluttering.

*Laughing doves*

Inactive laughing doves that reached their thermal end points at high $T_a$s were included in the results below. There was a decrease in RMR from 12.2 ± 2.9 at 25 °C to 7.8 ± 0.7 mW $g^{-1}$ at 35 °C (Fig. 1). A linear increase in RMR at a rate of 0.24 mW $g^{-1}$ $°C^{-1}$ (Fig. 1), was found ($t_{1,68} = 5.47$, $p < 0.001$), with RMR averaging 11.0 ± 3.6 mW $g^{-1}$ (Table 3), and 10.4 ± 3.1 mW $g^{-1}$ (Fig. 1) at 56 °C and 58 °C respectively. It is interesting to note that in the case of laughing doves, active birds exhibited metabolic rates up to 3 times higher than resting birds at the same $T_a$ (Fig 1).

At $T_a < 40$ °C, EWL was stable and low, averaging 5.4 ± 2.9 mg $g^{-1}$ $h^{-1}$ (Fig. 2). Above 40 °C, EWL increased linearly (Table 4) with increasing $T_a$ ($t_{1,30} = 11.60$, $p < 0.001$) by ~6.5-fold to 39.9 ± 11.1 (Table 3) and 35.6 ± 12.0 mg $g^{-1}$ $h^{-1}$ (Fig. 2) at $T_a$ = 56 and 58 °C respectively. At these higher $T_a$s, however, a large amount of scatter in the EWL data was observed. Above 35 °C, evaporative capacity increased approximately linearly ($t_{1,76} = 12.36$, $p < 0.001$) from 0.5 ± 0.1 at 35 °C to 2.33 ± 0.52 at 56 °C and 2.18 ± 0.49 at 58 °C (Fig. 3, Table 3). Though a linear regression was fitted for comparative purposes, average evaporative capacity appeared to plateau at the higher $T_a$s, increasing by 0.69 between $T_a$ = 54 and 56 °C, but actually decreasing by 0.15 between $T_a$ = 56 and 58 °C, suggesting that the relationship may be a nonlinear one.

Mean $T_b$ averaged 40.8 ± 0.8 °C at $T_a < 40$ °C, and increased linearly ($t_{1,28} = 8.14$, $p < 0.001$) above this $T_a$ (Fig. 4). At $T_a$ = 56 and 58 °C, mean $T_b$ was 43.6 ± 1.0 °C (Table 3) and 43.7 ± 0.8 °C (Fig. 4) respectively. There was no relationship found between $T_a$ and the rate of $T_b$ increase ($t_{1,15} = 1.67$, $p = 0.12$), and a large amount of variation was observed above $T_a = 56$ °C (Fig. 5), ranging from -0.07 to 0.21 °C $min^{-1}$.

For laughing doves, EHL began to increase significantly when $T_a – T_b \approx -3$ °C, ($t_{1,28} = 8.66$, $p < 0.001$), with an average of 24.8 ± 10.7 mW $g^{-1}$ when $T_a$ exceeded $T_b$ by ~12 °C (at $T_a \approx 56$ °C) and 22.8 ± 6.8 mW $g^{-1}$ when $T_a$ exceeded $T_b$ by ~14 °C, (at $T_a \approx 58$ °C) (Fig. 6).

Five out of ten laughing doves reached their thermal end points at $T_a = 54$ °C (Fig. 7), whereas at $T_a = 56$ and 58 °C, no birds were at their thermal end points (Table 3, Fig. 7).

Laughing doves began to gular flutter at 43.5 ± 2.3 °C (Fig. 8A). At $T_a \approx 50$ °C, when laughing doves were already gular fluttering, 169 ± 44 % of metabolic heat was being dissipated (Fig. 8B). At this $T_a$, RMR was 11% higher than RMR within the moderate $T_a$ range of 30-35 °C.

*Cape turtle doves*

One inactive Cape turtle dove had reached its thermal end point at $T_a = 56$ °C and was included in the results below. There was a slight decrease in RMR from 8.8 ± 2.8 at $T_a = 25$ °C to 7.0 ± 1.0 mW $g^{-1}$ at $T_a = 35$ °C (Fig. 1), after which a linear increase in RMR (Fig. 1) was observed ($t_{1,25} = 3.94$, $p < 0.001$) with RMR averaging 8.9 ± 0.7 mW $g^{-1}$ at $T_a = 56$ °C (Table 3, Fig. 1).

At $T_a < 40$ °C, EWL was stable and low, averaging 3.4 ± 1.5 mg $g^{-1}$ $h^{-1}$ (Fig. 2). Above 40 °C, EWL increased approximately linearly with increasing $T_a$ ($t_{1,24} = 10.17$, $p < 0.001$), though a polynomial regression provided a slightly better fit for this relationship (Table 4). Water loss increased ~10-fold, averaging 32.8 ± 9.0 mg $g^{-1}$ $h^{-1}$ at $T_a = 56$ °C (Table 3). Above 39 °C, evaporative capacity increased linearly ($t_{1,25} =$

3.80, $p < 0.001$) from 3.20 ± 0.14 at $T_a$ = 35 °C to 2.31 ± 0.61 at $T_a$ = 56 °C (Fig. 3, Table 3). Average evaporative capacity increased only slightly at the higher $T_a$s, but closer to linearly than seen in the other two species, rising by 0.08 between $T_a$ = 52 and 54 °C, and by 0.10 between $T_a$ = 54 and 56 °C.

Mean $T_b$ averaged 41.1 ± 0.9 °C at Ta < 40 °C, and increased linearly ($t_{1,25}$ = 13.63, $p < 0.001$) above this $T_a$ (Fig. 4). At $T_a$ = 56, mean $T_b$ was 44.7 ± 0.3 °C (Table 3, Fig. 4). The rate of $T_b$ increase increased linearly ($t_{1,25}$ = 2.81, $p < 0.01$) with increasing $T_a$, though considerable variation was observed (Fig. 5).

For Cape turtle doves, EHL began to increase significantly when $T_a$ exceeded $T_b$ by ~1 °C, ($t_{1,22}$ = 8.36, $p < 0.001$), with an average of 18.9.8 ± 6.5 mW $g^{-1}$ when $T_a$ exceeded $T_b$ by ~11 °C (at $T_a \approx 56$ °C) (Fig. 6).

Only 13% of the 14 Cape turtle doves reached their thermal end points at $T_a$ = 54 °C and 56 °C respectively (Table 3, Fig. 7). The bird that reached its thermal end point at 56 °C exhibited a mean $T_b$, mean $T_{b,\ max}$, rate of $T_b$ increase and evaporative capacity of 44.7 °C, 45.5 °C, 1.27 °C $min^{-1}$ and 1.62 respectively (Table 3).

Cape turtle doves began to gular flutter at 40.8 ± 3.4 °C (Fig. 8A). At 50 °C, when Cape turtle doves were already gular fluttering, 173 ± 48 % of metabolic heat was being dissipated (Fig. 8B). At this $T_a$, RMR was 7.5 ± 1.3 mW $g^{-1}$, which is higher than RMR within the thermally neutral range of 30-35 °C (3.6 ± 1.8 mW $g^{-1}$, Fig. 9). Also at 50 °C, EWL was 20.1 ± 4.5 mg $g^{-1}$ $h^{-1}$, compared to 3.6 ± 1.8 mg $g^{-1}$ $h^{-1}$ between 30 and 35 °C (Fig. 9).

*Columbid vs passerine comparison*

A conventional analysis found that the slope of mass-specific EWL as well as the change in $T_b$ between $T_a$ = 35 °C and $T_a$ = 48 °C, varied significantly with body mass

(Table 5, Fig. 9). Larger birds exhibited shallower EWL *vs* $T_a$ slopes, and smaller changes in $T_b$ (Fig. 9). The conventional analysis also revealed significant differences between columbids and passerines in terms of the slope of EWL, as well as the fractional increase in mass-specific RMR, mass-specific EWL, and $T_b$ between $T_a$ = 35 and $T_a$ = 48 °C (Table 5, Fig. 9), with doves exhibiting smaller changes than passerines. In the PIC analysis on the other hand, there were no significant differences between the two orders for any of the above parameters (Table 5), although slope of EWL *vs* $T_a$ and the change in mass-specific EWL and $T_b$ between $T_a$ = 35 °C and $T_a$ = 48 °C were significantly related to body mass when the columbid and passerine data sets were pooled (Table 5, Fig. 10).

**Table 5.** Parameters for the most parsimonious models explaining the differences in heat tolerance parameters between the avian orders Columbiformes and Passeriformes. Both conventional and phylogenetic independent contrasts (PIC) models are shown for each parameter. Heat tolerance parameters include slope of mass-specific EWL (log transformed) as a function of $T_a$, and the change in resting metabolic rate ($RMR_{Ta=48}$ / $RMR_{Ta=35}$), evaporative water loss ($EWL_{Ta=48}$/ $EWL_{Ta=35}$), evaporative capacity ( $\Delta$ capacity) and body temperature ( $\Delta T_b$), between $T_a$ = 35 and 48 °C. The contrasts (estimate), standard error (Std. error), t-value with residual degrees of freedom (df), p-value and significance are shown for each model. Significant differences are indicated by asterisks; NS = P > 0.05, * = P < 0.05, ** = P < 0.01, *** = P < 0.001

| | **Best-fitting models** | | | | | | |
|---|---|---|---|---|---|---|---|
| **Analysis** | **Model** | **Coefficients** | **Estimate** | **Std. Error** | **t-value (df)** | **p-value** | **Significance** |
| **Slope of EWL ($mg^{-1}g^{-1}h^{-1}°C^{-1}$)** | | | | | | | |
| Conventional | logSlopeEWL ~ LogMb + Order | Intercept | 0.794 | 0.158 | 5.011 (10) | 0.001 | *** |
| | | LogMb | -0.290 | 0.078 | -3.700 (10) | 0.004 | ** |
| | | Order | 0.178 | 0.066 | 2.717 (10) | 0.022 | * |
| PIC | logSlopeEWL ~ LogMb | Intercept | -0.005 | 0.009 | -0.60 (12) | 0.562 | NS |
| | | LogMb | -0.443 | 0.122 | -3.63 (12) | 0.005 | ** |
| **$RMR_{Ta=48}$ / $RMR_{Ta=35}$** | | | | | | | |
| Conventional | RMR ~ Order | Intercept | 1.092 | 0.072 | 15.269 (11) | 0.000 | *** |
| | | Order | 0.287 | 0.097 | 2.945 (11) | 0.013 | * |

| | Best-fitting models | | | | | | |
|---|---|---|---|---|---|---|---|
| **Analysis** | **Model** | **Coefficients** | **Estimate** | **Std. Error** | **t-value (df)** | **p-value** | **Significance** |
| PIC (a) | RMR ~ LogMb | Intercept | -0.014 | 0.014 | -0.987 (12) | 0.347 | NS |
| | | LogMb | -0.183 | 0.191 | -0.958 (12) | 0.361 | NS |
| PIC (b) | RMR ~ Order | Intercept | 0.005 | 0.020 | 0.267 (11) | 0.795 | NS |
| | | Order | -0.038 | 0.026 | -1.467 (11) | 0.173 | NS |
| **EWL$_{Ta=48}$ / EWL$_{Ta=35}$** | | | | | | | |
| Conventional | EWL ~ Order | Intercept | 4.373 | 0.851 | 5.138 (11) | 0.000 | *** |
| | | Order | 4.587 | 1.160 | 3.954 (11) | 0.002 | ** |
| PIC (a) | EWL ~ LogMb | Intercept | -0.278 | 0.156 | -1.788 (12) | 0.104 | NS |
| | | LogMb | -6.888 | 2.146 | -3.210 (12) | 0.009 | ** |
| **$\Delta$ capacity (Cap$_{Ta=48}$ - Cap$_{Ta=35}$)** | | | | | | | |
| Conventional | Capacity ~ LogMb | Intercept | 1.177 | 0.233 | 5.054 (12) | 0.000 | *** |
| | | LogMb | 0.058 | 0.136 | 0.426 (12) | 0.679 | NS |
| Conventional | Capacity ~ Order | Intercept | 1.328 | 0.081 | 16.376 (11) | 0.000 | *** |
| | | Order | -0.103 | 0.111 | -0.928 (11) | 0.373 | NS |
| PIC | Capacity ~ LogMb | Intercept | -0.009 | 0.011 | -0.854 (12) | 0.413 | NS |
| | | LogMb | -0.128 | 0.149 | -0.856 (12) | 0.412 | NS |
| PIC | Capacity ~ Order | Intercept | -0.021 | 0.016 | -1.277 (11) | 0.231 | NS |
| | | Order | 0.016 | 0.022 | -0.756 (11) | 0.467 | NS |
| **$\Delta$ T$_b$ (T$_{b[Ta=48]}$ - T$_{b[Ta=35]}$)** | | | | | | | |
| Conventional | Tb ~ LogMb | Intercept | 6.417 | 1.273 | 5.043 (11) | 0.001 | *** |
| | | LogMb | -2.408 | 0.721 | -3.342 (11) | 0.007 | ** |
| Conventional | Tb ~ Order | Intercept | 1.482 | 0.399 | 3.714 (10) | 0.004 | ** |
| | | Order | 1.538 | 0.564 | 2.727 (10) | 0.021 | * |
| Conventional | Tb ~ LogMb + Order | Intercept | 4.912 | 1.963 | 2.502 (9) | 0.034 | * |
| | | LogMb | -1.740 | 0.979 | -1.778 (9) | 0.109 | NS |
| | | Order | 0.701 | 0.696 | 1.007 (9) | 0.340 | NS |

| | Best-fitting models | | | | | | |
|---|---|---|---|---|---|---|---|
| Analysis | Model | Coefficients | Estimate | Std. Error | t-value (df) | p-value | Significance |
| PIC | Tb ~ LogMb | Intercept | 0.072 | 0.055 | 1.309 (11) | 0.223 | NS |
| | | LogMb | -2.810 | 0.962 | -2.921 (11) | 0.017 | * |

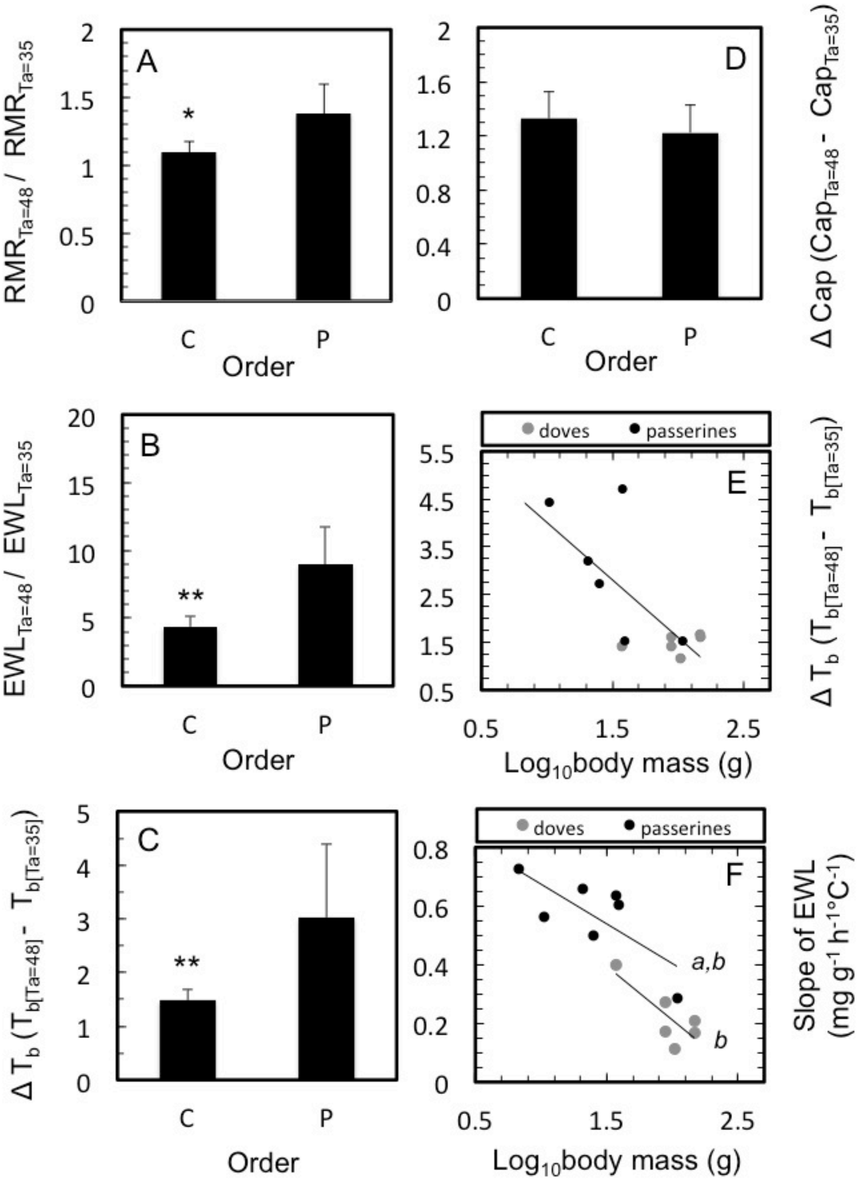

**Figure 9.** Comparisons of heat tolerance variables between seven passerines (Passeriformes, P) and six doves (Columbiformes, C) listed in Table 3, over air temperatures ($T_a$) ranging from 35 and 48° C (see Table 4 for details). The magnitude of change in A) resting metabolic rate ($RMR_{Ta=48}$/ $RMR_{Ta=35}$), B) evaporative water loss ($EWL_{Ta=48}$/ $EWL_{Ta=35}$), and C) body temperature [$\Delta T_b$ ($T_{b[Ta=48]}$ - $T_{b[Ta=35]}$)], was significantly higher in passerines. Over this range of $T_a$ there was no difference in D) evaporative capacity [$\Delta$ Cap ($Cap_{Ta=48}$ - $Cap_{Ta=35}$)] between orders. E) When pooling $T_b$ across the two taxa, log body mass ($Log_{10}$body mass) was significantly related to $\Delta T_b$. F) Slope of evaporative water loss [Log Slope of EWL ($mg^{-1}g^{-1}h^{-1}°C^{-1}$)] varied significantly as a function of body mass in both columbids and passerines, although passerines showed a significantly higher intercept. Significant differences are represented by asterisks. Trendlines indicate significant relationships, and “a” and “b” represent significant differences in intercept and gradient respectively. See Table 5 for coefficients of relationships.

Significance levels: NS = $P > 0.05$, * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$

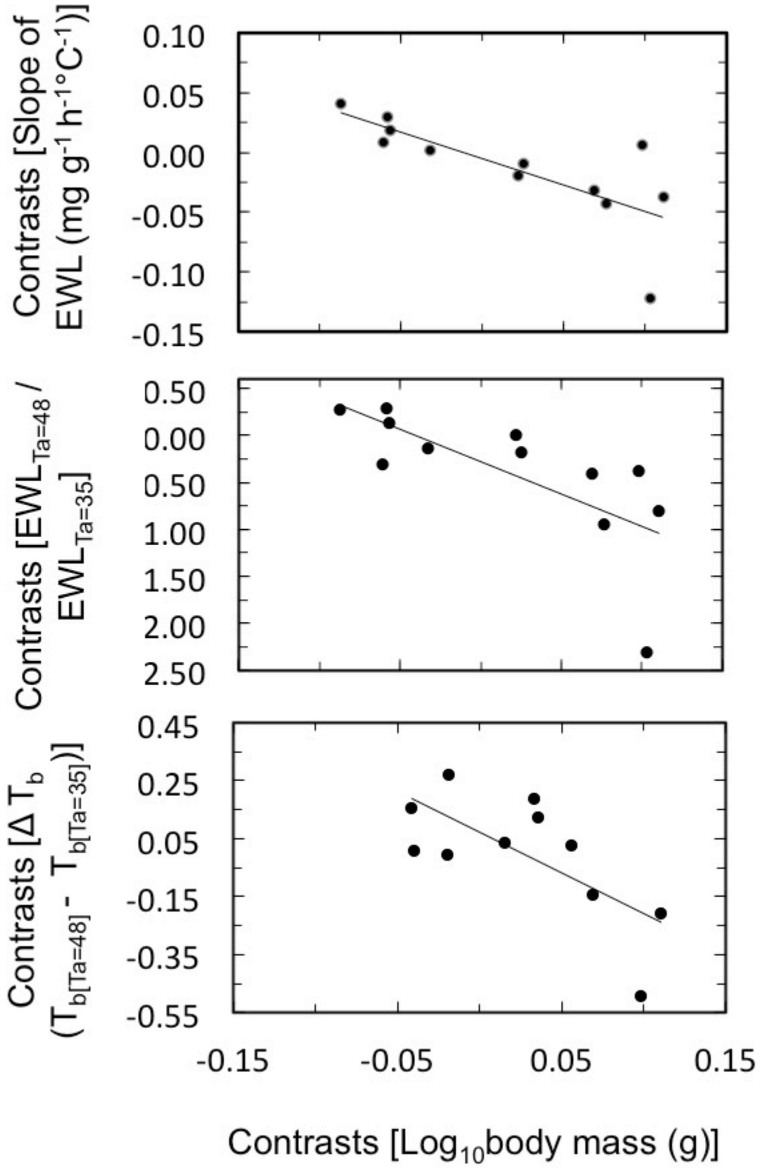

**Figure 10.** Phylogenetic independent contrasts of slope of evaporative water loss [Log slope of EWL ($mg^{-1}g^{-1}h^{-1}°C^{-1}$), and the magnitude of change in evaporative water loss ($EWL_{Ta=48}$/ $EWL_{Ta=35}$) and body temperature [ Δ $T_b$ ($T_{b[Ta=48]}$ - $T_{b[Ta=35]}$)] as a function of the phylogenetic independent contrast of body mass ($Log_{10}$body mass) for seven passerine and six dove species (listed in Table 3). Trendlines indicate significant relationships. See Table 5 for coefficients of relationships.

## Discussion

My data reveal an effect of body mass on mass-specific RMR, EWL, $T_b$, $T_a$ at which gular fluttering began and evaporative capacity among the three species of columbids. The relationship between body mass and thermal end point was less clear compared to the passerines (Chapter 2), with few individuals of any species reaching their thermal end points at the highest $T_a$ values to which they were exposed in this study. All three species showed a capacity for facultative hyperthermia at $T_a$ values above normothermic $T_b$. In the following paragraphs I will discuss the findings of my study in light of my theoretical predictions and relevant literature. The patterns in RMR, EWL, evaporative capacity, $T_b$ and thermal endpoints will be discussed in detail, followed by a discussion of the comparison of passerines and columbids in heat dissipation characteristics, and a general conclusion.

### *Resting metabolic rate*

Doves used in this study showed only small increases in RMR with increasing temperature above the UCT. Even when exposed to extremely high $T_a$s the birds of all three species exhibited only small increases in mass-specific RMR above the $T_{uc}$. This is consistent with the results of other researchers. In a study on North American desert columbids comparable in size to laughing- and Cape turtle doves, white-winged- and mourning doves exhibited even shallower slopes when tested up to $T_a$s of 65 °C (0.06 mW $g^{-1}$ °$C^{-1}$ in both species, Smith et al. unpublished data). Other desert-dwelling species have deviated similarly from the classic model of endotherm energetics (Scholander et al 1950), with Houbara bustards tolerating a $T_a$ of 55 °C for three hours without RMR increasing above that of the TNZ (Tieleman et al 2002b). Similarly, Spinifex pigeons and heat-acclimated rock pigeons maintained low RMR up to 50 and 60 °C respectively (Marder and Arieli 1988; Withers and Williams 1990b). Tieleman et al. (2002b) suggested that reducing metabolic heat production would be advantageous in desert birds, as it would lessen the need for evaporative cooling at high $T_a$s, thereby reducing water losses.

Both the slope of RMR and the mean mass-specific RMR at any given $T_a$ should be higher in smaller species (Bartholomew and Cade 1963; Weathers 1981). However, Namaqua doves, the smallest species used in our study exhibited the shallowest slope of mass-specific RMR (when accounting for individual responses in a mixed model), which is likely due to panting/gular fluttering being delayed until much higher $T_a$ (~55 °C) compared to the other two species (~44 and 41 °C in laughing and Cape turtle doves respectively) (Fig. 8). Panting/gular fluttering is said to commence in columbids when $T_b$ is between 42 and 43 °C (Randall 1943; Bartholomew and Dawson 1954). This was supported by my data, with $T_b = 42$ °C corresponding to a $T_a$ of ~ 44 and 42 °C in laughing- and Cape turtle doves respectively, and $T_b = 42.6$ °C corresponding to $T_a = 55$ °C in Namaqua doves. The higher surface area to volume ratio of smaller doves results in more skin per unit body volume from which to evaporate water cutaneously, while larger doves must supplement CEWL with panting/gular fluttering. My data support current suggestions that CEWL is a more energetically efficient pathway of heat dissipation than REWL (Fig. 11, Withers and Williams 1990; Hoffman and Walsberg 1999; McKechnie and Wolf 2004). Direct measurements of CEWL and REWL in these species are, however, needed to strengthen these conclusions. Adaptive phenotypic flexibility in CEWL/REWL as a result of heat acclimation further supports the notion of CEWL being more energetically efficient than REWL at high $T_a$ (Marder and Arieli 1988; Peltonen et al 1998; McKechnie and Wolf 2004a). The contribution of CEWL to total EWL in heat-acclimated white-winged doves at $T_a$ =45 °C was 25 % greater than in cool-acclimated doves, with cool-acclimated doves at this $T_a$ exhibiting 35 % higher RMR (McKechnie and Wolf 2004a). It is possible that my three study species were not fully acclimated to high temperatures since daily ranges in air temperatures fluctuated greatly (e.g. maximum $T_{air}$ of 42 °C versus minimum of 6 °C) during my study (personal observation); this $T_a$ range is not unusual during summer for the Kalahari desert (Lovegrove 1993). It is possible that if the Namaqua-, laughing- and Cape turtle doves that I tested had been exposed to persistently higher $T_a$s (Marder and Arieli 1988; McKechnie and Wolf 2004a), I would have observed lower metabolic rates and higher evaporative capacities at high $T_a$s, as well as further delay in the onset of panting/gular fluttering.

Given the obvious benefits of cutaneous evaporative cooling, one might ask why is it not more widespread amongst avian lineages? The high water demands associated with CEWL likely explain the rarity of high CEWL to REWL ratios amongst birds. While acclimatization can lead to adjustments in the contribution of CEWL to TEWL, it is unclear whether these changes can occur effectively over the short-term (i.e. hourly) (Hoffman and Walsberg 1999). I argue that in habitats where water sources are scarce, or the abundance of water-rich foods are low, excessive reliance on CEWL could lead to dehydration in the short term if birds do not have access to drinking water. Unlike passerines in arid areas, doves are able to store water in their crops, and their daily activities are tied around drinking regularly (Williams and Koenig 1980). Losing body heat by evaporating copious amounts of water through the skin would therefore be less disadvantageous to a dove than to a passerine with limited body-water supplies.

In Chapter 2 I discussed the potential $Q_{10}$ effects of increasing $T_b$ on RMR in hyperthermic birds. Increases in RMR with elevations in $T_b$ were lower than expected for a $Q_{10}$ of 2.5 in Namaqua doves ($Q_{10}$ = 2.0) and laughing doves ($Q_{10}$ = 0.7), but not for Cape turtle doves ($Q_{10}$ = 3.0). In all three species of doves increases in RMR were accompanied by increased levels of gular fluttering (similar to panting observed in passerines; Chapter 2), complicating the interpretation of RMR and $T_b$ correlations as purely a $Q_{10}$ effect. One possible way to further determine the $Q_{10}$ effect of $T_b$ on RMR would be to anaesthetise birds and observe the effect of thermal heat load on RMR in the absence of heat dissipation mechanisms.

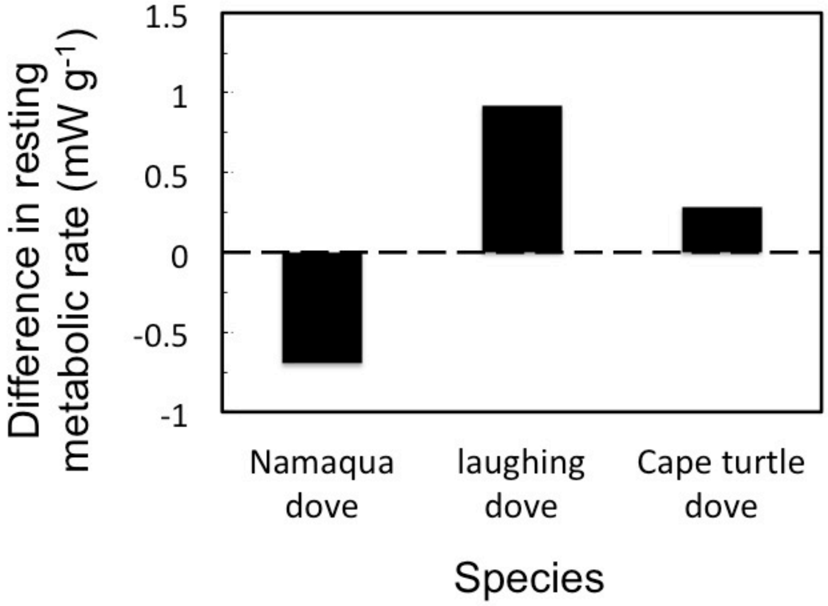

**Figure 11.** Difference in resting metabolic rate (RMR) between $T_a$ = 50 and 30–35 °C in Namaqua doves (n=7), laughing doves (n=7) and Cape turtle doves (n=8). The $T_a$ range of 30–35 °C represents a thermally neutral range of $T_a$s, and $T_a$ = 50 °C is a point at which Namaqua doves were utilizing only cutaneous evaporative water loss (CEWL) as a means of heat dissipation, but laughing and Cape turtle doves had commenced gular fluttering.

### *Evaporative water loss and evaporative capacity*

I used $T_a$ = 56 °C to compare mean values of the variables examined, as this was the highest $T_a$ experienced by all three species. Mass-specific EWL at 56 °C (and most other $T_a$s > $T_b$) was highest in Namaqua doves, followed by laughing doves, followed by Cape turtle doves, as expected from on the scaling of EWL in general (Bartholomew and Cade 1963) (Table 3). In all three dove species there was a large range between minimum and maximum values of EWL observed at high temperatures, similar to the two larger weavers (see discussion on the implications of this variation in Chapter 2).

McKechnie and Wolf (2010) compiled data from the literature on birds tested at $T_a > T_b$. Whereas Namaqua doves evaporated water at approximately the rate predicted for a bird of its mass, the slopes for the laughing doves and Cape turtle doves were 20 and 33 % higher, respectively, than the expected values. Similarly, white-winged- (*Zenaida asiatica mearnsii*) and mourning doves (*Zenaida macroura*, Smith et al. unpublished data) which are similar in mass to laughing- and Cape turtle doves respectively, yielded slopes 69 and 36 % higher than expected for their masses from (Mckechnie and Wolf 2010). The above-mentioned species were all tested up to $T_a$s > 56 °C. It is therefore possible that that the overall slopes of EWL for these species compiled in the analyses of Mckechnie and Wolf (2010) were underestimated since they were tested at comparatively low maximum $T_a$s [e.g. 42 °C in the double-banded sandgrouse *Pterocles bicinctus* (Hinsley 1992)], resulting in the predictive equation for EWL slope to yield lower values. A more detailed analysis of birds tested over similar temperature ranges would be necessary to conclude on the high EWL slopes reported in my study and those of Smith et al. (unpublished data).

Once acute dehydration limits are better understood, assessing the time period that a bird can maintain controlled $T_b$ before lethal dehydration sets in, will be useful. Studies of dehydration tolerance in the past have involved withholding water at moderate $T_a$s, and measuring mass loss over days to weeks (Bartholomew and MacMillen 1961). Given the long time periods, the above results are therefore confounded by tissue loss. Rock doves, for example, have been shown to handle mass loss of 16–18 % after being deprived of water for 48 hours, and food for 24 of those 48 hours (Arad et al 1989). Part of the described mass loss is therefore likely to be from tissue loss. Verdins have shown a loss of coordinated movement when they lost more than 11% of their body mass after relatively short periods (a few hours) of heat exposure (Wolf 2000). This mass loss can therefore be attributed to loss of body water alone. If the three dove species I tested were to experience an operative $T_a$ of 48 °C while foraging in the sun, with no access to water and no water stored in their crops, my data predict that Namaqua-, laughing- and Cape turtle doves would be able to survive 4.6, 4.6 and 6.4 hours before 11 % of body mass was lost. However, I suggest that using EWL rates collected during acute exposure to high $T_a$s, especially in a ramped $T_a$ setup, can be misleading. For example, at $T_a = 48$ °C, Namaqua doves in my study were regulating their $T_b$ close to normal levels (mean $T_b = 42$ °C). If they had been exposed to this $T_a$ for an extended period of time (i.e. > 2 hours), it seems likely that they would have become dehydrated enough to trigger facultative hyperthermia and therefore extend survival time by reducing EWL (Maloney and Dawson 1994). It is therefore difficult to link EWL rates obtained from laboratory studies to ecological situations. Moreover, these estimated survival times are probably optimistic, as it is unlikely that environmental humidity (dew point temperature of -20–25 °C in the Kalahari region during summer (unpublished data, A.E. McKechnie and P.A.R Hockey) will be as low as in my experimental setup (dew point temperature below -17 °C), and therefore evaporative heat dissipation will be less effective.

At $T_a = 50$ °C, when laughing- and Cape turtle doves were already panting/gular fluttering, Namaqua doves were dissipating a greater fraction of their metabolic heat (2.15) compared to the other two doves (~1.7 in both species). At this $T_a$, white-winged- (Smith et al. unpublished data) and Cape turtle doves, which are similar in mass, exhibited average $T_b$s of 42.1 and 43.6 °C, accompanied by evaporative capacities of ~250 and 173 % respectively. Mourning doves (Smith et al. unpublished data) and similarly sized laughing doves at $T_a$ = 50 °C exhibited average $T_b$s of 42.3 and 43.5 °C, with evaporative capacity of ~225 and 170 % respectively. The two larger Kalahari dove species appear to defend a higher $T_b$ setpoint with the accompanying lower metabolic costs of heat dissipation, while the North American desert doves defend a lower $T_b$ setpoint by increasing evaporation.

At the highest $T_a$s experienced (56, 58 and 60 °C respectively), Namaqua doves were dissipating metabolic heat more than twice as rapidly as the other two species. Namaqua doves were dissipating ~500 % of their metabolic heat load at $T_a$ = 60 °C, which is much higher than typically recorded for doves. Heat-acclimated rock doves (Marder and Arieli 1988), white-winged doves (Smith et al. unpublished data) and mourning doves (Smith et al., unpublished data) at the same $T_a$ dissipated ~286, 362 and 375 % of their metabolic heat loads respectively. Given that I found no effect of body mass on evaporative capacity (EHL/MHP) in either conventional analysis or PIC, I suggest it is reasonable to compare the evaporative capacities of these dove species at a given $T_a$. I also suggest, however, that evaporative capacity may be a misleading indicator of heat tolerance, as a higher evaporative capacity or steeper slope of evaporative capacity does not necessarily mean that a bird is handling heat better. For example, if RMR very low, it may be unnecessary for birds to greatly elevate evaporative water loss rates, and EHL/MHP will therefore be comparatively low. This was observed in acclimated rock doves (Marder and Arieli 1988), which exhibited a slope of EWL that was 27 % lower than expected for their mass from Mckechnie and Wolf (2010). Even if heat dissipation capacity may not directly indicate how well a bird is coping with extreme heat, evaporating 500 % of metabolic heat at a $T_a$ as high as 60 °C is impressive. It is likely that the high surface area to volume ratio of the small Namaqua dove makes cutaneous EWL very effective in this species, and despite the large volumes of water necessary for this mechanism of heat dissipation, water storage within the crop (Williams and Koenig 1980, personal observation) may make it possible over short time periods.

*Body temperature and thermal end points*

Birds have been shown to elevate their $T_b$ 2-4 °C above normothermic levels during extreme heat and/or dehydration, with water conservation thought to be the primary function of such facultative hyperthermia (Tieleman and Williams 1999). During acute exposure to heat (1 h), birds ranging in size from 10-1000 g may conserve up to 50% of total evaporative water loss by becoming hyperthermic, whereas during chronic exposure (5h), only small birds (<100) benefit (Tieleman and Williams 1999). Hyperthermia conserves water by enhancing rates of passive heat loss when $T_a < T_b$ (Calder and King 1974; Tieleman and Williams 1999), but when $T_a > T_b$, it presents another advantage by reducing the rate of heat gain from the environment (Kilgore et al 1976). In Chapter 1, the majority of passerine birds exposed to high $T_a$s exhibited steep rates of increase in $T_b$ alongside a very high mean $T_b$ (~45 °C). The patterns of hyperthermia shown by the three dove species in my study were characterized by a generally stable $T_b$ somewhat elevated above normothermic levels, as the relationship between $T_a$ and the rate of $T_b$ increase at each $T_a$ was absent in Namaqua and laughing doves, and not particularly clear in Cape turtle doves. Of the Namaqua, laughing and Cape turtle doves that exhibited high $T_b$s (> 45°C), 33, 44 and 50 % exhibited little to no increase in $T_b$ over the last ten minutes at a particular $T_a$.

At $T_a$ = 56 °C, hyperthermia was observed in Cape turtle doves (mean $T_b$ = 44.7 °C), to a certain extent in laughing doves (mean $T_b$ = 43.6 °C), but less so in

Namaqua doves (mean $T_b$ = 42.5 °C) (Table 3). This lack of pronounced hyperthermia in the smaller columbids at such a high $T_a$ demonstrates firstly that rates of EWL were high enough to defend lower $T_b$s, and that saving water through raising $T_b$ was probably not yet necessary in these birds. In contrast, five out of the seven Cape turtle doves that exhibited hyperthermic $T_b$ (with only one bird maintaining normothermic $T_b$ at $T_a$ = 56 °C) and also exhibited low rates of $T_b$ increase, suggesting that this species was utilising controlled hyperthermia at $T_a$ = 56 °C. Similar patterns involving the defense of high $T_b$ setpoints were observed in laughing- and Namaqua doves at $T_a$ = 58 °C (mean $T_b$ = 43.6 °C) and 60 °C (mean $T_b$ = 43.8 °C) respectively. Tieleman and Williams (1999) reported $T_b$s of 41.1 – 45.8 °C during facultative hyperthermia in 28 bird species, but questioned the direct role of high $T_b$ in water savings, since the higher temperatures at which air is exhaled will have a higher water holding capacity. This combined with increased tidal volume at high $T_a$s will lead to elevated respiratory water loss (Tieleman and Williams 1999). Boyles et al. (2011) further suggested that at $T_a$s above 45 °C, the water savings through passive heat loss accrued from hyperthermia are likely to decrease substantially, since $T_b$ cannot be maintained at much higher levels than ~ 45 °C due to biochemical constraints. Hyperthermia at extremely high $T_a$s, (for example $T_a$ > 50 °C) could theoretically be beneficial to water savings to a bird maintaining a $T_b$ of 45 °C, compared to a $T_b$ maintained 2–3 °C lower, given the smaller gradient over which $T_b$ is defended. However, the benefits of these water savings can easily be offset by increased respiratory water loss associated with higher temperatures of saturated exhaled air, and the risk of decreased physiological performance at near-lethal $T_b$ (Boyles et al 2011). Studies that have directly tested the extent to which hyperthermia during heat exposure represents a facultative increase in $T_b$ contributing to water savings, as opposed to being the result of reduced evaporative capacity (e.g., Maloney and Dawson 1994), are limited. In order to better elucidate the water-saving role of facultative hyperthermia at high $T_a$s, studies that investigate the effects of heat acclimation and hydration state (and how these factors interact) on patterns of $T_b$ regulation are necessary.

Although regulating a higher $T_b$ setpoint does not necessarily translate to an inability to tolerate heat, when coupled with a plateauing in the rate of evaporative capacity increase it may demonstrate that maximal EWL rates are reached. Beyond this point it seems unlikely that evaporative capacity can further increase to prevent elevations in $T_b$. This reduction in the rate at which evaporative capacity increased was observed in laughing doves between $T_a$ = 54 and 58 °C. Cape turtle doves were still increasing evaporative between $T_a$ = 52 and 56 °C, but at comparatively very low rates, suggesting that this species was also approaching maximal heat dissipation capacity.

The relationship between $T_a$ and rate of increase in $T_b$ in my study was sometimes obscure, and deserves closer inspection. Many active birds exhibited negative changes in $T_b$ over the last ten minutes at extremely high $T_a$s (Fig. 5). These decreases in $T_b$ are likely due to birds being active for the majority of the time, and then calming down towards the end of the ten minutes (air temperature was usually only increased to the next test temperature once birds were calm). I used the difference between the $T_b$ at the end of the tenth minute and the $T_b$ at the beginning of the first minute to calculate the rate of $T_b$ increase. Therefore even if a bird was active for nine of the ten minutes, the decrease in $T_b$ within the last minute could have been registered in the rate calculation. Many calm doves also exhibited negative changes in $T_b$ at high $T_a$s. It is possible that the ramp in $T_a$ caused an exaggerated hyperthermic response in these doves, which was later relaxed once $T_a$ had stabilized. Thus, the negative rates of $T_b$ increase at very high $T_a$ may simply represent an artifact of the ramped $T_a$ profile used during measurements.

I suggest that, of all the parameters I measured, $T_b$ regulation is the most direct measure of heat tolerance capabilities. Slopes and mean values of EWL, RMR and evaporative capacity are useful in exploring species-specific strategies of heat dissipation, but they do not provide insight into whether or not a bird is managing to maintain heat balance. From $T_b$ patterns at high $T_a$s, it is evident that $T_b$ follows three paths during heat stress: 1) it is either maintained at relatively low normothermic levels (~41–42 °C), 2) at high, near-lethal limits (probably to conserve water), or 3) on an uncontrolled trajectory towards lethal levels as observed in towhees (Dawson 1954). Of these, defending a normothermic $T_b$ setpoint with resultant greater water losses (Marder and Arieli 1988; Withers and Williams 1990b; Tieleman et al 2002b), and maintaining a stable, hyperthermic $T_b$ to conserve water (Tieleman and Williams 1999; Tieleman et al 2002a) are most likely to represent heat tolerance.

In this study, I was unable to observe the $T_a$ at which 100 % of each species had reached their thermal end points, due to a tendency of birds to become agitated at high $T_a$s. Criteria for thermal end points included both active and inactive birds that exhibited extremely high (>45 °C) average $T_b$. Extreme agitation or escape behavior at lower $T_a$s often resulted in outlying data points, making removal of these data from analyses an obvious necessity. However, these behaviours could, over time, lead to thermal end points being reached. Conversely, they are also likely to be expressed after thermal end points are reached (Dawson 1954). Distinguishing between cause and effect in this sense was not possible in this study, and the numbers of birds that were calm at their thermal end points were too low to allow for independent analysis. In future studies, however, it would be worthwhile to exclude active data completely.

There seems to be considerable variation in the maximum $T_a$s that different bird species can tolerate. For instance, brown towhees reached lethal $T_b$ (46.9 °C) after only a few hours of exposure to $T_a$s of 39 – 43 °C (Dawson 1954). On the other hand, Houbara bustards (Tieleman et al 2002b) and rock doves (Marder and Arieli 1988), maintained normothermic $T_b$ at $T_a$s of 55 - 60 °C. I was unable to continue testing Namaqua doves at higher $T_a$s due to our temperature control system not being able monitor $T_a$s higher than 60 °C. In the cases of laughing and Cape turtle doves, the majority of individuals exhibited maximum $T_b$s above 45 °C (four out of eight Cape turtle doves and three out of six laughing doves) and I stopped experiments early if birds were unsettled in order to prevent mortality. The loss of coordinated movement was observed in towhees when $T_b$ exceeded 45 °C, and death occurred at 46.9 °C (Dawson 1954). Fatal $T_b$ in California quail was somewhat lower, beginning at 45.7 °C, and these birds could only tolerate $T_b$s of 46 °C for relatively short periods (~15 minutes) (Brush 1965). Lethal $T_b$ was 46.8 °C in house wrens (Baldwin and Kendeigh 1932) and between 45.9 and 46.2 °C in four breeds of chicken (Arad and Marder 1982), though higher values up to 47.8 °C were reported previously (Randall 1943). The maximum $T_b$ I recorded in the three dove species was 45.8 °C in a calm Namaqua dove at $T_a = 60$ °C, and this $T_b$ is already above the lower end of the lethal $T_b$ range described above (45.7 – 47.8 °C). While I observed loss of coordinated movement in the passerines from Chapter 1 at around this $T_b$, this was not observed in the doves. This suggests that lethal $T_b$ in the three dove species I tested is likely closer to the mid- or higher values of the range reported in the literature.

### *Scaling and phylogenetic comparison of doves and passerines*

My findings support theoretical expectations on the effects of body mass on the thermoregulatory patterns of columbids at high $T_a$s. As was expected, smaller species exhibited higher mass-specific RMR and EWL at any given $T_a$ (Kleiber 1932; Bartholomew and Cade 1963). I also confirmed that the slope of mass-specific EWL versus $T_a$ was steeper in smaller birds (Mckechnie and Wolf 2010). The effect of body mass on thermal end points in doves was less clear, likely as a combined result of relatively short exposure times to high $T_a$s in my study, and a higher than expected lethal $T_b$. Both conventional and PIC analyses showed that body mass significantly affected the slope of EWL, as was expected (Mckechnie and Wolf 2010), as well as the change in EWL (only the PIC) and $T_b$ between 35 and 48 °C. Larger birds exhibited shallower slopes of EWL and smaller increases in EWL and $T_b$. This suggests that larger birds may be better able to maintain heat balance at high $T_a$s, as they are losing less water though heat dissipation but still manage to defend a lower $T_b$ setpoint. While this is likely true for passerines, I reiterate that within the three columbids studied here, the relationship between body mass and $T_b$ contradict these findings, with the larger species exhibiting larger changes in $T_b$, compared to smaller species. This was clear in the three dove species that I tested, with all three species starting off with similar $T_b$ at $T_a \approx 40$ °C, but above this $T_a$, the slope of the increase in $T_b$ was steeper in larger birds (Fig. 13). This contradictory finding warrants further investigation to establish if smaller doves, such as the Namaqua dove, are more heat tolerant than larger doves.

Many conventional analyses show that passerines have higher basal metabolic rates than non-passerines (Lasiewski and Dawson 1967; Aschoff and Pohl 1970), but these differences disappear once phylogenetic relatedness is controlled for, suggesting that they are a result of phylogenetic inertia rather than adaptation (McKechnie and Wolf 2004b; McKechnie et al 2006). Either way, the greater heat production in passerines compared to non-passerines within the TNZ could extend towards the higher $T_a$s, which partly explains why, in the data-set I used for my analysis (Table 3), the passerines exhibited higher RMR at high $T_a$s than similarly-sized doves (Fig. 12). I say partly, because these differences are also likely to be a result of passerines panting at high $T_a$s and generating more metabolic heat, though these two explanations cannot be untangled in this case. However, when using the fractional increase in mass-specific RMR between $T_a$ = 35 and 48 °C, meaning that the difference in RMR, and not the actual values of RMR are important, I was able to show that the metabolic costs of panting, and not the extended effects of a higher BMR, caused the significant differences between doves and passerines in my conventional analysis. These results seem to support my predictions that the dominant mechanism of heat dissipation used by these two taxa would affect heat tolerance. At high temperatures, panting requires an increase in ventilation rate and an increase in metabolic heat production (Dawson 1958). In contrast, the high ratios of CEWL to REWL from which doves are likely to benefit could greatly reduce metabolic heat load. A conventional analysis also revealed significant differences between doves and passerines in the slope of EWL and the magnitude in $T_b$ between $T_a$ = 35 and 48 °C. In one case of overlapping body mass, for example, Namaqua doves exhibited much steeper increases in evaporative capacity, but much smaller increases in mass-specific RMR and $T_b$ than the similarly sized white-browed sparrow-weaver (Figs 13 and 14). I argue that the differences between doves and passerines in these thermoregulatory characteristics will be heightened once more data from small doves are added to the analysis.

In my study, testing for phylogenetic signal was not possible, as the test for statistical significance associated with the *K*-statistic is not reliable for comparisons involving less than 20 species (Blomberg et al 2003). Given the uncertainty of the phylogenetic signal underlying the traits in these two taxa, it was important to consider the findings from both conventional and PIC analyses. However, once more data from more species, especially passerines and doves that overlap in body mass, we will be better equipped to determine whether or not the patterns of RMR observed in doves and passerines are adaptive or a result of phylogenetic inertia (as suggested by my PIC).

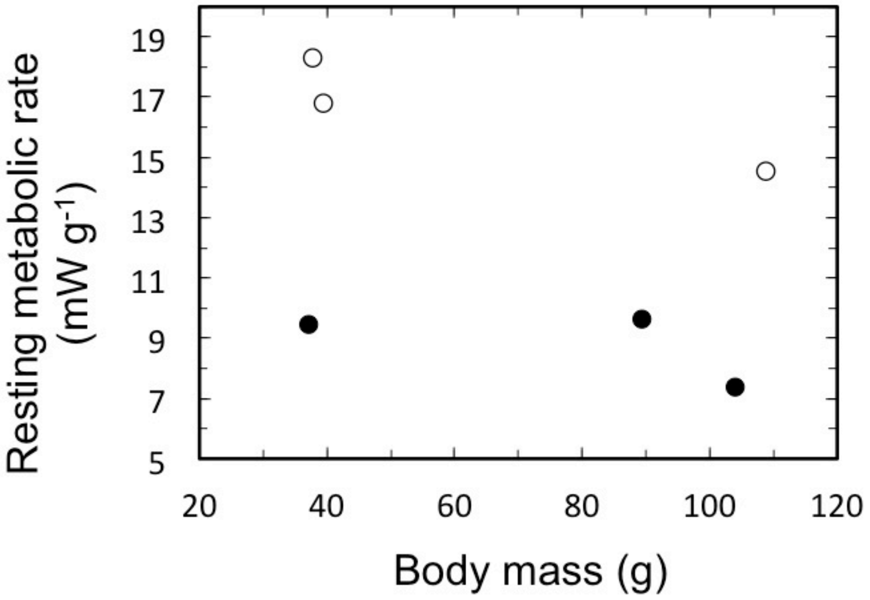

**Figure 12.** Mass-specific resting metabolic rate (RMR) as a function of body mass at an air temperature ($T_a$) of 48 °C for three passerines (open circles), namely the greater hoopoe lark (38 g), Burchell's starling (109 g) and white-browed sparrow-weaver (39 g) and three doves (closed circles), namely the Namaqua dove (37 g), laughing dove (89 g) and mourning dove (109 g).

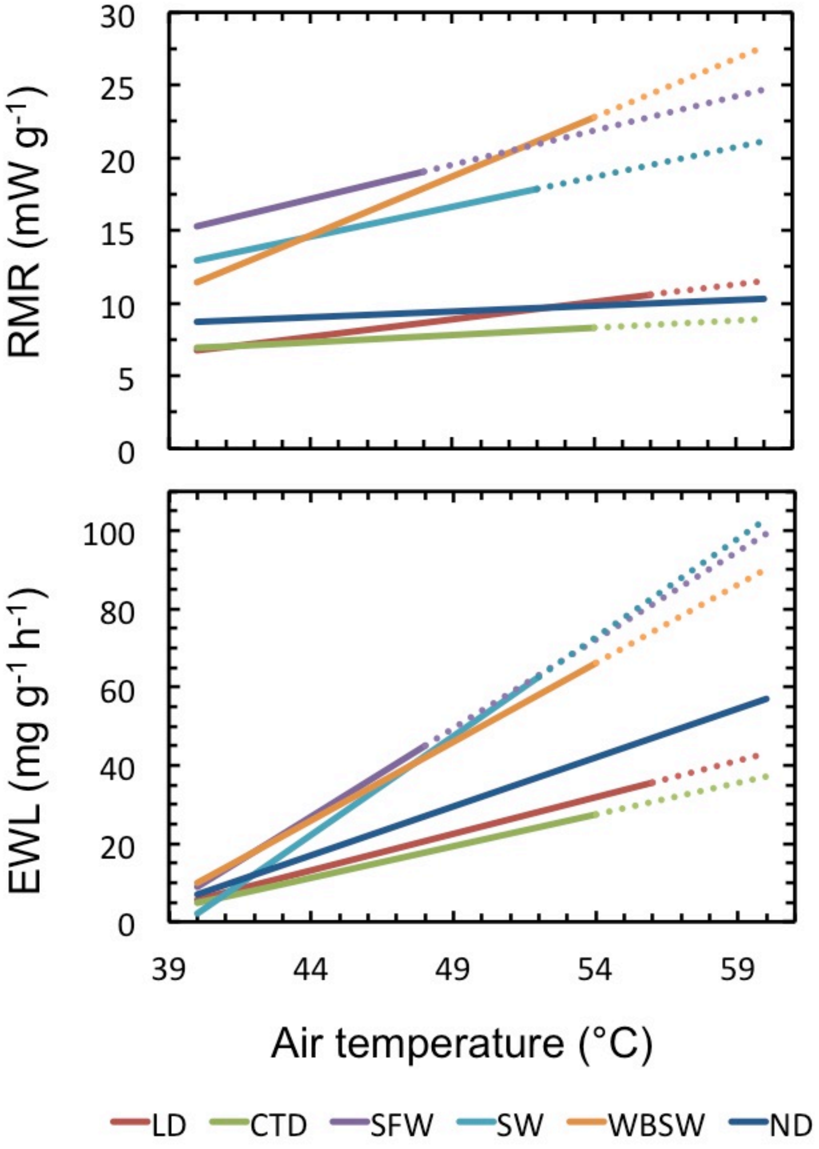

**Figure 13.** Trendlines for mass-specific resting metabolic rate (RMR) and evaporative water loss (EWL) as a function of air temperature ($T_a$) for three passerines [scaly-feathered weavers (SFW, n = 15), sociable weavers (SW, n = 25) and white-browed sparrow-weavers (WBSW, n = 31)] and three columbids [namaqua doves (ND, n = 29), laughing doves (LD, n = 33) and cape turtle doves (CTD, n = 26)]. Solid lines represent actual $T_a$s at which birds were tested, while dotted lines are extrapolations.

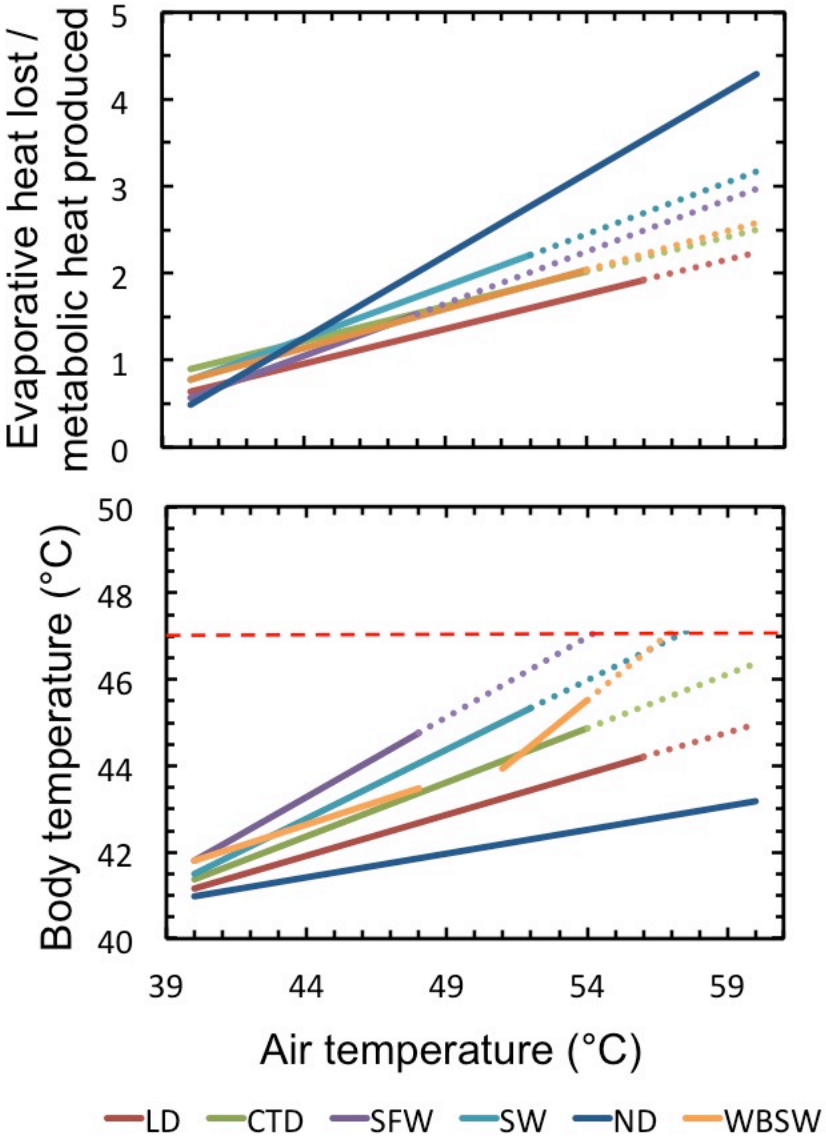

**Figure 14.** Trendlines for evaporative capacity and body temperature ($T_b$) as a function of air temperature ($T_a$) for three passerines [scaly-feathered weavers (SFW, n = 15), sociable weavers (SW, n = 25) and white-browed sparrow-weavers (WBSW, n = 31)] and three columbids [namaqua doves (ND, n = 29), laughing doves (LD, n = 33) and cape turtle doves (CTD, n = 26)]. Solid lines represent actual $T_a$s at which birds were tested, while dotted lines are extrapolations. The dotted red line through $T_b$ = 47 °C represents current estimates of lethal $T_b$.

*Conclusion*

It is important to continue with species-specific laboratory-based research into the thermoregulatory abilities of birds at extremely high $T_a$s, as it lays the foundation for larger-scale mechanistic modeling of overall vulnerability to current and future climate scenarios (Boyles et al 2011). It is evident that there can be great variation in heat dissipation capacity and heat tolerance both among species of varying evolutionary history, between closely related species depending on variables such as body mass and biogeographical origin, and even within species depending on acclimation history and phenotypic plasticity. Doves and passerines provide an interesting model for comparison since they differ greatly in the evaporative heat dissipation pathway employed. More studies, including a greater number of species with a wider range of body mass overlap between these taxa, is needed to investigate differences in physiological mechanisms of heat tolerance between these taxa, and how these traits can effect vulnerability of taxa to hot temperatures. From the results of this study, it seems that smaller desert columbiformes may be more resilient to direct effects of heat stress than larger birds, due to an ability to minimize the metabolic costs associated with active heat dissipation, most likely by relying predominantly on cutaneous EWL. Within the Passeriformes, larger birds appear better able to tolerate high $T_a$s. Doves appear able to handle short periods at high $T_a$s very well, but under natural conditions, their heat tolerance will be tightly linked to having access to free-standing water. As granivores, many doves obtain very little preformed water from their food (MacMillen 1990). I often observed doves drinking from water troughs at the hottest time of the day, underscoring their reliance on free-standing water sources (Williams and Koenig 1980). If water is readily available, doves appear to be strong candidates for survival during extreme heat events. Passerines, especially the insectivorous species, are less reliant on drinking water due to the high preformed-water content of their food sources. However, their higher

REWL to CEWL ratios combined with their inability to store water in their crops may make them more vulnerable to heat waves.

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# CHAPTER 4: CONCLUSIONS AND SUGGESTIONS FOR FURTHER RESEARCH

By statistically testing the effects of body mass in a pooled data set of seven passerines and six doves, I showed that body mass significantly affected the slope of EWL, as was expected (Bartholomew and Cade 1963; McKechnie and Wolf 2010), as well as the change in EWL and $T_b$ between 35 and 48 °C. Larger birds exhibited shallower slopes of EWL and smaller increases in EWL and $T_b$. This suggests that larger birds may better be able to maintain heat balance at high $T_a$s, as they lose less water, as a % of body mass, through heat dissipation but still manage to defend a lower $T_b$ setpoint. While this is likely true for passerines which rely mainly on respiratory evaporative cooling, and was observed in the three ploceids I tested, I argue that the opposite relationship between $T_a$ and $T_b$ could be found in columbids if more data from small doves were included. Among the three doves I tested, the larger species exhibited larger changes in $T_b$, and smaller increases in evaporative capacity, compared to smaller species. This is likely due to the larger doves beginning to pant/gular flutter at lower $T_a$s, resulting in increased metabolic heat loads. It seems reasonable to suggest that smaller doves benefit more from cutaneous evaporative cooling because of the larger surface-area to volume ratio that will facilitate heat loss across the skin.

A conventional analysis revealed that passerines exhibited significantly greater changes in RMR between $T_a$ = 35 and 48 °C than did doves, which provides further support for the notion of the metabolic costs associated with predominantly cutaneous evaporation being lower than those associated with reliance on respiratory cooling mechanisms such as panting. However, direct measurements of CEWL and

REWL in these species are needed to verify these conclusions. The fact that a PIC analysis did not reveal significantly greater changes in RMR between $T_a$ = 35 and 48 °C between doves and passerines suggests that these differences are due to phylogenetic inertia. Future research should include species representing greater body mass range, as well as measurements at $T_a$s as close to thermal limits as possible without causing any permanent damage. It would also be highly informative to test nonpasserine birds that use gular fluttering alone as their dominant form of heat dissipation, such as Caprimulgiformes, Strigiformes, Galliformes, Pelecaniformes, Cuculiformes and Gruiformes (Bartholomew et al 1962; Bartholomew et al 1968; Dawson and Whittow 2000). Measurements from these taxa will enable us to determine the relative costs and benefits of respiratory- versus cutaneous-dominated mechanisms for evaporative cooling.

All doves and passerines I examined showed a pronounced capacity for hyperthermia when experiencing $T_a$ values above normothermic $T_b$, and most birds were able to regulate $T_b$ as high as 45 °C. At very high $T_a$s (>48 °C), the passerines from Chapter 2 exhibited steep rates of increase in $T_b$ alongside a very high mean $T_b$ (>45 °C), suggesting that $T_b$ was increasing in an uncontrolled manner. The patterns of hyperthermia shown by the three dove species in Chapter 3 were characterized by a generally stable $T_b$ somewhat elevated above normothermic levels, and the relationship between $T_a$ and the rate of $T_b$ increase at each $T_a$ was absent in Namaqua and laughing doves, and not particularly clear in Cape turtle doves, suggesting that controlled hyperthermia was possible at even the highest $T_a$s (up to $T_a$ = 60 °C). Exploring more thoroughly the differences between controlled and uncontrolled hyperthermia would be a useful avenue for future research (Tieleman and Williams 1999). In order to better elucidate the water-saving role of facultative hyperthermia at high $T_a$s, studies that investigate the effects of heat acclimation and hydration state (and how these factors interact) on patterns of $T_b$ regulation are necessary. For example, continuous monitoring of $T_b$ at very high $T_a$ over time, under different levels of hydration state, should provide better insight into the water savings role of hyperthermia. Tieleman and Williams (1999) point out the critical importance of steady-state experimental conditions when investigating the significance of facultative hyperthermia for water balance, highlighting their separate study on crested larks (*Galerida cristata*), which involved 3–5 hour periods of exposure to constant $T_a$s. The ramped $T_a$ profiles used in my study likely did not allow for these conditions to be met. The findings on $T_b$ in my study provide insight into the upper limits of thermoregulation, and conclusions drawn on the potential for water savings through hyperthermia will be limited.

From the results of this study, it seems that smaller columbids may be more resilient to direct effects of heat stress than larger birds, while the opposite may be likely in passerines. Doves appear able to handle short periods at high $T_a$s very well, but under natural conditions, their heat tolerance will be strongly dependent on having access to free-standing water. Passerines, especially the insectivorous species, are less reliant on free-standing water due to the high preformed-water content of their food sources. However, their apparently less efficient evaporative cooling mechanism, combined with their limited storage of water in their crops may make them vulnerable to heat waves.

The predicted increase in frequency, intensity and duration of heat waves by 2080 (IPCC 2011) will likely become bottlenecks for avian survival and reproduction (McKechnie et al. 2012), and in desert environments, which are already extremely hot and arid, heat waves could have devastating consequences in the future. As we are no longer able to reverse or even slow the progress of climate change (IPCC 2011), understanding how future climate scenarios will affect species is of critical importance for biodiversity conservation (Root et al 2003). Williams et al. (2008) proposed that a species' vulnerability to climate change is determined by both sensitivity (intrinsic aspects of an organism's physiology) and exposure (extrinsic climatic or environmental factors), and species-specific studies, such as this one, that quantify thermal tolerance and heat dissipation abilities fall into this "sensitivity" category. It is imperative that we address the general lack of physiological data at high $T_a$s by repeating the methodologies of this study in many arid-zone taxa, taking into account body mass, phylogenetic history and aspects of physiology and ecology that relate to exposure to heat, and quantifying not only the temperature dependence of physiological variables, but of behavioural and reproductive variables too (McKechnie et al. 2012).

Although the physiological data were obtained under relatively controlled conditions, one might use these data to model minimum EWL costs and energy demands of birds under natural conditions. Relationships between resting rates of EWL and RMR with increasing $T_a$ under laboratory conditions can be related to the operative temperatures [measured through taxidermic mounts (Mahoney and King 1977; Walsberg and Wolf 1996) that birds experience under natural conditions. These estimates of RMR and EWL should be regarded as highly conservative, however, as water turnover rates and field metabolic rates are variable and complex in free-living birds, and depend strongly on activity patterns and microsite use (Wolf and Walsberg 1996). These laboratory based data can be incorporated into models of survival and reproductive success under future climate scenarios (McKechnie et al 2012), to improve predictions of inter-specific avian responses within desert environments.

Studying $T_b$ patterns under free-living conditions would be a particularly interesting avenue for further research. In this thesis I have shown that species can increase $T_b$ under hot conditions. However, the ecological and physiological costs of maintaining a high $T_b$ remain understudied. Detailed studies linking short-term fluctuations in $T_b$ under natural conditions are rare (Smit et al 2013). It is important to note that under field conditions birds may reach sub-lethal $T_b$ at lower $T_a$ for a number of reasons, including high levels of activity and field metabolic rate, or high solar radiation. Facultative hyperthermia likely plays an important role in water savings, but a high $T_b$ also leaves little room for error. For example, when escaping a predator, a bird may be forced into the sun, or become suddenly active, and this could cause an already high $T_b$ to breach lethal limits. Maintaining facultative hyperthermia during a period of heat will therefore likely influence activity choices (foraging, microsite selection etc.) of individuals (Tieleman and Williams 2002b). Comparing $T_b$ patterns under natural and laboratory conditions will therefore better elucidate the practical, instead of theoretical, adaptive value of facultative hyperthermia.

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