PATTERNS OF THERMOREGULATION AND SEASONAL METABOLIC ADJUSTMENTS IN SMALL OWLS IN AN ARID ENVIRONMENT

By

BEN SMIT

Submitted in fulfilment of the requirements for the degree of

Master of Science

in the

School of Animal, Plant and Environmental Sciences

The University of the Witwatersrand

Johannesburg

2008

PREFACE

The experimental work described in this thesis was carried out in Molopo Nature Reserve, North West Province, South Africa, between May 2007 and March 2008. The study was conducted under the supervision of Professor Andrew E. McKechnie and Professor Graham Alexander.

These studies present original work by author and have not been submitted in any other form for any other degree or diploma to any other University. Where use has been made of work of others it is duly acknowledged in the text.

A manuscript based on chapter 2 has been accepted for publication in *Physiological and Biochemical Zoolog*y.

All procedures related to the use of animals in these studies were approved by the Animal Ethics Screening Committee of the University of the Witwatersrand (clearance certificate 2007/31/'01).

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Ben Smit

Johannesburg

November 2008

ABSTRACT

A high, approximately constant normothermic body temperature is associated with elevated maintenance energetic requirements. However, many small endotherms offset the energetic demands of thermoregulation through heterothermy (e.g., daily torpor and hibernation) and/or phenotypic adjustments in maintenance metabolic requirements. In terms of their significance in energy conservation, there are limited data on the above mentioned physiological responses in birds, compared to mammals.

Torpor appears to be common in species that rely on unpredictable food resources. However, to better understand the adaptive value and evolution of avian torpor, a better understanding of the phylogenetic distribution of this trait is needed. The first aim of this dissertation was to investigate the occurrence of torpor in free-ranging Pearl-spotted Owlets (*Glaucidium perlatum*) and African Scops-Owls (*Otus senegalensis*). Although heterothermic responses have been recorded in a number of avian taxa, the occurrence of this phenomenon in owls (Strigidae) remains unknown.

I investigated winter patterns of thermoregulation in the crepuscular 80-g Pearl-spotted Owlet and the strictly nocturnal 61-g African Scops-Owl by obtaining telemetric measurements of skin temperature (T_{skin}) from free-ranging individuals in the Kalahari Desert of southern Africa. Pearl-spotted Owlets remained normothermic ($T_{\mathrm{skin}} > 37°\mathrm{C}$) throughout the study period, whereas African Scops-Owls routinely used shallow torpor, with T_{skin} reduced by 3° to 9°C below normothermic levels for 1.5 to 5 h after sunrise. The mean lowest T_{skin} in three African Scops-Owl individuals was $29.0° \pm 0.1°\mathrm{C}$. The reductions in T_{skin} in African Scops-Owls are, to the best of my knowledge, the most

pronounced T_{skin} reductions yet observed in owls. The thermoregulatory differences between these two species may be related to their diets and activity patterns. African Scops-Owls are almost exclusively insectivorous and experience a marked reduction in food availability on cold winter nights, and are therefore likely to undergo energy stress. In contrast, Pearl-spotted Owlets have more flexible activity patterns and include larger and/or diurnal vertebrate prey in their diet, which is a more reliable food resource.

On the other hand, there is increasing evidence that birds can adjust their minimum maintenance metabolic requirements (i.e. basal metabolic rate, BMR) over short time scales in response to changing environmental conditions. However, there has been very little emphasis on the role of metabolic adjustments at reducing energy requirements in birds. Reductions in BMR would facilitate greatest energy savings during winter when increased thermoregulatory demands coincide with low food availability. The second aim of this dissertation was to investigate seasonal adjustments in basal metabolic rate of birds resident year round in the Kalahari Desert of southern Africa. Our current understanding on the role of these adjustments is largely limited to small birds inhabiting cold temperate regions in the northern Hemisphere, where winter BMR is typically elevated.

I measured winter and summer BMR in the field for five species resident in the Kalahari Desert of southern Africa, using a portable respirometry system. I found that winter BMR was generally lower than in summer. Mass-specific BMR was significantly lower in winter in the nocturnal African Scops-Owl (*Otus senegalensis*; 23%), the diurnal Fork-tailed Drongo (*Dicrurus adsimilis*; 35%), Crimson-breasted Shrike (*Laniarius atrococcinneus*; 29%), White-browed Sparrow-Weaver (*Plocepasser mahali*; 17%), and

the crepuscular Pearl-spotted Owlet (*Glaucidium perlatum*; 30%). In African Scops-Owls, however, the lower winter BMR (23%) was largely explained by lower winter body mass (12%). These results suggest that seasonal adjustments in BMR in both nocturnal and diurnal species are related to winter energy savings, and possibly also water savings, rather than cold tolerance.

The limited data on seasonal BMR adjustments that are currently available suggest that whereas most small northern Hemisphere birds up-regulate winter BMR, the opposite is generally true in southern Hemisphere species. However, north-south comparisons are complicated by differences in body mass and latitudes of acclimatization, and the finding that mid-winter temperatures explained 57% of the variation in global patterns of seasonal BMR adjustments. More data are therefore required before global patterns can be reliably identified. Nevertheless, my data reveal a dichotomy in the direction of seasonal BMR adjustments, and raises the possibility that in regions where winters are milder, adjustments are related to energy savings in winter.

In summary, I found that African Scops-Owls use shallow torpor, presumably to reduce energy requirements. These data represent the first description of shallow torpor in free-ranging individuals of a member of the suborder Strigi. I also found that African Scops-owls, Pearl-spotted Owlets and three diurnal bird species exhibit significant BMR reductions during winter. These winter reductions in BMR are opposite in direction to those exhibited by most northern Hemisphere species.

ACKNOWLEDGMENTS

The University of the Witwatersrand and the DST/NRF Centre of Excellence at the Percy FitzPatrick Institute (University of Cape Town), provided funding for this study. I am also grateful to the University of the Witwatersrand and Percy FitzPatrick Institute for providing funds to attend an international conference during 2008. The North West Parks Board and the staff of the Molopo Nature Reserve are thanked for their support of the study and for the use of the facilities at Molopo Nature Reserve.

My supervisor, Professor Andrew McKechnie, has been an excellent mentor and guide towards the world of academia during the two years of my masters. I have learned immensely from Andrew about undertaking research, writing and publishing. I am incredibly grateful for his support and enthusiasm for this project during the last two years and for his never-ending patience with my absentmindedness. Andrew also paid for me to attend three international conferences. These conferences where of invaluable academic experience to me and I greatly appreciated it. Andrew, Australia was awesome, Kaokoland was an adventure of a life-time, and thanks for sending me to the Kalahari! To Amanda, thanks for reminding repeatedly what a home cooked meal should taste like.

I am also sincerely grateful to Professor Graham Alexander for acting as my supervisor at the University of the Witwatersrand after Andrew moved to the University of Pretoria. I am indebted to Ms Carol Sam and Mrs Shena Kennedy at the School of Animal, Plant and Environmental Sciences, for being immensely helpful during the last two years. Barry Lovegrove and two anonymous referees are thanked for providing useful comments on earlier drafts on parts of the dissertation.

Without the help of my field assistants I would not have been able to obtain the data for this project. The field work component of this project involved many sleepless nights – often in the freezing cold, while trying to trap and radio-track owls. I am unfathomably grateful to David Potgieter, Helen Carter, Helen Place, Jolanda Smit, Kate Meares, Luke Duncan, Matthew Brennan, Megan Mackay, Nicholas Tye and Robyn Bruyns. Matt, you were quite lazy and irresponsible, but redeemed yourself to some extent when you found the first Scops-Owl for the project. Jolanda, thanks for nursing me and taking over the cooking duties when I got sick in winter. Kate, thanks for your determination at catching owls and motivating me to keep on trying. Meg, thanks for your assistance during both seasons and your excitement about the project. Rob, thanks for your enthusiasm, the great pictures, the Kalahari tunes and the magnificent *Kalahari-fix-me* video. I am also grateful to Gerald and Ina Botha at Molopo Nature Reserve for ice-cold refreshments, *stoep*-stories and *potjie-kos*. I greatly appreciate the hospitality of Mrs Louise Bloom for offering me free lodging in Johannesburg, and I am also very thankful towards Mrs Margaret Place for organising this accommodation.

I am also sincerely grateful to the Department of Zoology and Entomology at the University of Pretoria, in particular the head of school, Professor Sue Nicolson, for providing me with office space to write this dissertation when I moved to Pretoria during 2008. I thank Angela Kohler for sharing her office with me at UP.

Lastly, and most importantly, I wholeheartedly thank my parents, John and Hettie, my sister, Jolanda, and my brother, Neels, for their unfailing love, supporting me in every possible manner, and for tolerating bird-like noises for the past 20 years.

TABLE OF CONTENTS

CHAPTER 1:

INTRODUCTION

Endothermy allows for the regulation of a high, approximately constant normothermic set-point body temperature (T_b) that is independent of environmental temperature (T_e) (i.e., endothermic homeothermy). The evolution of endothermy improved physiological efficiency, increased enzymatic action and activity levels, and facilitated major thermal niche expansion in birds and mammals (Schmidt-Nielsen 1990). However, for an endotherm to maintain a high T_b within a narrow normothermic range requires a sufficient energy supply from the environment to meet maintenance energy requirements (Withers 1992). In broad terms, an endotherm's maintenance energy demands can be subdivided into (1) basal- (i.e. minimum maintenance metabolic rate for a normothermic endotherm), (2) thermoregulatory- (i.e. metabolic heat production or thermogenesis at low T_e) and (3) locomotory (metabolic rate during activity) energy requirements (Lovegrove 2006).

A normothermic T_b is energetically costly to maintain, particularly during the rest phase of an animal's circadian cycle, when T_e may be well below T_b, and no metabolic heat is produced through activity (Withers 1992). During cold weather thermoregulatory energy demands are increased, especially for smaller endotherms, since they have a larger surface area per unit body mass (M_b) over which heat is lost (Schmidt-Nielsen 1990). Small endotherms therefore may need to increase metabolic heat production to several times basal levels when T_e is below thermoneutrality (range of T_e where no energy is expended on thermoregulation) (Schmidt-Nielsen 1990; Withers 1992).

The challenges that small endotherms face in terms of matching energy demand to supply can affect their behaviour, life-history and ultimately their evolution, particularly in environments where the availability of energy resources are low and/or unpredictable (Lovegrove 2006). Many small endotherms offset the energetic demands of thermoregulation behaviourally by selecting thermally-buffered micro-environments and/or by roosting communally, but also physiologically through (1) heterothermy (e.g. daily torpor and hibernation) and/or (2) phenotypic adjustments in maintenance metabolic requirements (Dawson and Whittow 2000; Lovegrove 2005). In this dissertation I focus on the latter two physiological responses and their roles in energy conservation.

Heterothermy

Heterothermy is probably the most studied physiological response in terms of its contribution to energy conservation and occurs widely amongst birds and mammals, although the majority of studies have focused on mammals. Heterothermic responses in endotherms involve controlled and precisely regulated departures from the normothermic state, by reducing metabolic rate and T_b during daily torpor and hibernation (Withers 1992). Many small birds in which heterothermic responses have been investigated show moderate reductions in body temperature (1° to 5°C), referred to as nocturnal- or rest-phase hypothermia (Prinzinger et al. 1991; Reinertsen 1996). In contrast, daily torpor and hibernation involve more pronounced reductions in metabolic rate and T_b (generally T_b reduction below 30°C), and can lead to substantial energy savings (Geiser 2004). During daily torpor, the bout duration is restricted to a single circadian cycle, whereas hibernation involves multi-day bouts of torpor (McKechnie and Lovegrove 2002; Geiser

2004). These physiological responses reduce an endotherm's energy requirements below the levels required for normal physiological maintenance or activity.

Hibernation has been reported in only one avian species, the Common Poorwill (*Phalaenoptilus nuttalli*) (Jaeger 1948; Brigham 1992), whereas daily torpor appears to be more common in birds than previously thought, especially in semi-tropical and tropical environments (Merola-Zwartjes and Ligon 2000; McKechnie and Lovegrove 2002). Torpor is widely used by small birds whose food resources exhibit large spatial and/or temporal fluctuations in availability, e.g. frugivores (Coliidae and Columbidae), nectarivores (Trochilidae and Nectariniidae) and aerial insectivores (Todidae, Apodidae, Caprimulgidae and Hirundinidae) (McKechnie and Lovegrove 2002; Schleucher 2004). In some species, at least under laboratory conditions, torpor appears to be an emergency response when food intake rates are too low to match energy demands (Dawson and Whittow 2000). However, a number of species also show spontaneous torpor that is not necessarily an emergency response related to energy stress (Carpenter and Hixon 1988; Bech et al. 1997; Merola-Zwartjes and Ligon 2000; Maddocks and Geiser 2007).

Avian taxa in which the presence of torpor is established include mousebirds [order Colliformes (Prinzinger et al. 1981; McKechnie and Lovegrove 2001)], swifts [family Apodidae (Koskimies 1948; Bartholomew et al. 1957)], hummingbirds [family Trochillidae, (Lasiewski 1963; Wolf and Hainsworth 1972; Carpenter and Hixon 1988; Calder 1994)], caprimulgids [i.e. nightjars and allies, sub-order Caprimulgi (Bartholomew et al. 1957; Peiponen 1965; Dawson and Fisher 1969; Brigham 1992; Hickey 1993; Brigham et al. 2000; Körtner et al. 2000; Fletcher et al. 2004; Lane et al. 2004)], doves and pigeons [order Columbiformes (MacMillen and Trost 1967;

Schleucher 2001)], a tody and a kingfisher [order Coraciiformes (Merola-Zwartjes and Ligon 2000; Cooper et al. 2008)], and a few passerines [families Hirundinidae and Nectariniidae (Cheke 1971; Prinzinger and Siedle 1988; Downs and Brown 2002)]. Pronounced torpor, in which T_b is reduced by > 30°C below normothermic levels, has only been reported in hummingbirds and caprimulgids (McKechnie and Lovegrove 2002).

However, to better understand the adaptive value and evolution of heterothermic responses in birds, a more thorough assessment of the phylogenetic distribution of this trait is needed (McKechnie and Lovegrove 2002; Schleucher 2004). Malan (1996) hypothesized a monophyletic, plesiomorphic origin for torpor in endotherms, a hypothesis that predicts that torpor should be wide-spread in phylogenetically older taxa. The latter prediction seems to hold for mammals, since torpor is widespread throughout the mammalian phylogeny, and is present in almost all the oldest (or basal) taxa (Lovegrove et al. 1999; Lovegrove and Génin 2008). In birds, on the other hand, conclusions concerning the phylogenetic distribution and evolution of avian torpor have proved more elusive because, (1) data on the capacity for torpor are lacking for many phylogenetically older avian taxa (McKechnie and Lovegrove 2002), and (2) investigations of the capacity for heterothermy in many of the most basal avian taxa (i.e. Paleognathae, which includes the ratites) are complicated by their relatively large body masses (Geiser 1998).

It is noteworthy that the majority of studies in which the capacity for torpor was investigated involved birds held under artificial laboratory conditions (McKechnie and Lovegrove 2002). Accumulating evidence suggests that free-ranging endotherms are significantly more likely to show torpor than their captive counterparts, and the extent and importance of torpor can be greatly underestimated under artificial conditions (Geiser and Ferguson 2001). These findings reiterate the importance of ecological factors as important proximate determinants of heterothermy (Brigham 1992; Geiser et al. 2000; Cooper et al. 2008). To test predictions concerning evolutionary and ecological determinants, and further, provide answers to the energy saving role of heterothermic responses, it is therefore essential to focus future studies on free-ranging birds.

Seasonal metabolic adjustments

There is increasing evidence that birds can adjust their maintenance metabolic machinery over short time scales in response to environmental conditions such as temperature (West 1972; Weathers and Caccamise 1978; Dawson and Marsh 1988; Swanson 1991; Cooper and Swanson 1994; Dawson and O'Conner 1996; Liknes et al. 2002; Dawson 2003; Saarela and Hohtola 2003), but in contrast to studies on heterothermy, there has been very little emphasis on the role of metabolic adjustments in reducing energy requirements in birds. In mammals, phenotypic adjustments in body mass (Mb) and subsequently basal metabolic rate (BMR) that are related winter energy savings - a phenomenon known as the Dehnel effect - are well established (Mezhzherin 1964; Lovegrove 2005). In small mammals, seasonal thermoregulatory patterns typically involve winter reductions in M_b, and BMR, to reduce overall energy requirements (Mezhzherin 1964; Lovegrove 2005).

Adjustments in metabolic rate can be driven by physical conditions in natural environments (acclimatization), by controlled changes in specific climatic factors under laboratory conditions (acclimation), and/or involve physiological changes associated with intense and/or sustained activity, such as long distance migratory flights (Dawson and Whittow 2000).

For instance, acclimation to cold temperatures (−14° to +10°C) led to increases of 10 to 55% in standard metabolic rate in Domestic Fowl (*Gallus gallus*), Rock Dove (*Columba livia*) and Eurasian Collared Dove (*Streptopelia decaocto*), and up to 85% in the Eurasian Siskin (*Carduelis spinus*) (Dawson 2003). Basal metabolic rate, in particular, is known to be flexible and can be up- or down-regulated over time scales as short as two to three weeks (Williams and Tieleman 2000; Klaassen et al. 2004; McKechnie et al. 2007). Laughing Doves (*Streptopelia senegalensis*) provide a good example of flexibility in BMR: birds initially acclimated to an ambient temperature (T_a) = 10°C up-regulated BMR over a period of three weeks, but then down-regulated BMR over the same time scale when they were subsequently acclimated to T_a = 35°C (McKechnie et al. 2007).

Considering that BMR is flexible under acclimation experiments in most birds that have been investigated, it is not surprising that BMR varies with seasonal acclimatization, especially in regions where winters are severely cold (Bech 1980; Cooper and Swanson 1994; Liknes and Swanson 1996; Cooper 2000; Liknes et al. 2002; Dawson 2003; Swanson and Liknes 2006). The majority of data on BMR adjustments reveal that BMR is invariably up-regulated during winter or in response to cold exposure (McKechnie 2008). These responses suggest that BMR adjustments are involved in facilitating thermogenic capacity when thermoregulatory demands are higher. In wild, free-living populations of American Goldfinches (*Carduelis tristis*), for instance, winter BMR and summit metabolism (M_{sum}, maximum rate of cold-induced thermogenesis) were

46% and 31% higher, respectively, and they tolerated low air temperatures substantially better than in summer (Liknes et al. 2002).

Winter elevations in BMR are mostly associated with increased M_{sum} and improved cold tolerance (Cooper and Swanson 1994; Liknes and Swanson 1996; Swanson and Olmstead 1999; Cooper 2000; Liknes et al. 2002; Swanson and Liknes 2006), suggesting that BMR adjustments might contribute to improvement in cold tolerance. However, there is still much uncertainty on the role of BMR adjustments and suggestions that an up-regulation of BMR could serve as an emergency response, protecting peripheral tissue against cold injury, and/or lower the threshold temperature for initiating of shivering thermogenesis (Dawson and O'Conner 1996), have been considered unlikely (Swanson in press). Swanson (in press) argued that shivering thermogenesis would provide sufficient protection against cold injury, and that an increased BMR entails high energetic costs that are at least as costly as initiating shivering thermogenesis at slightly higher temperatures. Moreover, in environments where environmental conditions are more unpredictable, a higher winter BMR would be energetically costly, especially if winter ambient temperatures that require sustained increased thermogenesis, are not experienced throughout the day, e.g. in arid subtropical environments.

Most data on winter increases in BMR come from species that over-winter in the Holarctic region at high latitudes in the Northern Hemisphere where winters are severely cold (West 1972; Swanson 1990, 1991; Cooper and Swanson 1994; Swanson and Weinacht 1997; Liknes et al. 2002). It is likely that an up-regulated BMR represents a by-product of increased machinery needed for improved cold tolerance (Swanson in press).

If this is the case, the direction of seasonal patterns of BMR adjustment should be different in regions where winter temperatures are milder (Maddocks and Geiser 2000).

With the exception of a few studies (Dawson et al. 1983; Ambrose and Bradshaw 1988; Maddocks and Geiser 2000), the role of seasonal metabolic adjustments in species from tropical and semitropical latitudes remains unknown. There are also very limited data on the role of BMR adjustments in energy conservation. A reduction in BMR should facilitate greatest energy savings when low/unpredictable food availability coincides with mild to cool temperatures in winter. It is therefore possible that patterns of seasonal metabolic adjustments in tropical and subtropical regions reflect the requirement for energy conservation in winter, rather than improved cold defense.

Deserts as study environments

Desert environments provide the ideal habitats to answer questions related to heterothermy and phenotypic responses in metabolism because of the extreme fluctuations in daily and seasonal temperature and unpredictable food resources that characterize most arid regions (Lovegrove 1993). Desert environments in southern Africa, such as the Kalahari Desert, experience large seasonal fluctuations in ambient conditions, and rainfall occurs mainly in the form of unpredictable, isolated thunderstorms during summer (Lovegrove 1993). Winters are typically very dry, with frequent sub-zero temperatures at night, contrasting with temperatures exceeding 30°C during the day (Lovegrove 1993). During summer, day-time air temperatures may exceed 45°C. Climatic conditions in southern African deserts, particularly the Kalahari, are also strongly influenced by the EL Niño Southern Oscillation (ENSO), resulting in greater unpredictability of rainfall and frequent droughts (Stone et al. 1996). Thus, conditions that impose increased energetic demands for thermoregulation often coincide with periods of decreased primary activity during winter. Desert environmental conditions therefore pose tremendous thermal challenges and energetic demands to small endotherms, and are thus the typical environments in which selection for heterothermy and more flexible- and conservative metabolic phenotypes would be favoured (Lovegrove 1993; Tieleman and Williams 2000; Tieleman et al. 2003; Williams and Tieleman 2005). For instance, Tieleman et al. (2003) has shown that BMR decreased with increasing aridity in 12 species of lark (Alaudidae).

Small owls as model species

In terms of the questions about heterothermy and phenotypic flexibility in metabolic rates outlined above, small owls inhabiting desert regions are of particular interest. In this study, I explore the occurrence of torpor and seasonal metabolic adjustments in two small owl species, the crepuscular Pearl-spotted Owlet and the strictly nocturnal African Scops-Owl (*Otus senegalensis*), resident in the Kalahari Desert of southern Africa. These two species feed predominantly on arthropods, although Pearl-spotted Owlets frequently include large vertebrate prey in their diets (Hockey et al. 2005). In winter it is likely that these two species experience periods of energetic stress, as they forage when reduced levels of ectotherm prey activity coincide with low air temperatures.

These two owl species are likely candidates to use torpor as (1) owls are phylogenetically closely related to the caprimulgids (Sibley and Ahlquist 1990), (2) they are small, and (3) they are resident in the Kalahari Desert where the availability of their prey is likely reduced during dry and cool winter months (Lovegrove 1993). Although torpor has not been shown in owls before, all species investigated so far were captive individuals in artificial, laboratory environments.

Pearl-spotted Owlets and African Scops-Owls are also useful model species for investigating the role of seasonal metabolic adjustments in subtropical environments. Owls, on account of their nocturnal activity patterns, provide opportunities to test hypotheses concerning the relative roles of energy conservation vs. improved cold tolerance in seasonal metabolic adjustments. Because they are active at night, metabolic heat generated as a by-product of activity and digestion can be expected to contribute significantly to thermoregulation. During the day, owls will require relatively little metabolic energy to thermoregulate since they can rest at a warmer T_e. Moreover, since the availability of terrestrial invertebrate prey generally decreases at low T_e, owls likely experience stronger selection for energy conservation. African Scops-owls are almost exclusively nocturnal (Hockey et al. 2005) and can be expected to show pronounced energy conservation in thermoregulation during winter. The requirement for energy conservation might be more moderate in Pearl-spotted Owlets, since they are often active during the day (Hockey et al. 2005) when the availability of invertebrate prey is likely to be higher. In contrast, diurnal species that also feed predominantly on invertebrates, such as the Fork-tailed Drongo (*Dicrurus adsimilis*), Crimson-breasted Shrike (*Laniarius atrococcineus*) and White-browed Sparrow-Weaver (*Plocepasser mahali*), are inactive at night and may thus be expected to experience stronger selection for improved cold tolerance during winter. Thus, I predict that whereas seasonal metabolic adjustments in diurnal species will reflect improved winter cold tolerance (i.e., winter elevations in

BMR), small owls, in particular the strictly nocturnal African Scops-Owl, will exhibit metabolic adjustments more indicative of energy conservation (i.e., winter decreases in BMR).

Throughout this dissertation I use the Sibley and Ahlquist (1990) avian phylogeny for bird families and orders, and phylogenetic analyses. The Sibley and Ahlquist (1990) phylogeny is widely accepted and has been used extensively during the past two decades in comparative studies on avian physiological traits (Reynolds and Lee 1996; Tieleman and Williams 2000; McKechnie and Lovegrove 2002; Rezende et al. 2002; McKechnie and Wolf 2004; Swanson and Liknes 2006). Although a radically different avian phylogeny has recently been proposed (Hackett et al. 2008), it remains to be seen whether this hypothesis of avian relationships will gain the widespread acceptance enjoyed by the Sibley and Ahlquist phylogeny.

Thesis structure

This dissertation is structured in a manuscript style as two stand-alone chapters based on empirical data plus a general introduction and conclusion. This inevitably leads to overlap in some details of the introductory material, materials and methods, and results. A shorter version of chapter 2 has been accepted for publication in *Physiological and Biochemical Zoology*.

Chapter 1 provides an overall introduction and some background on the two major topics of this dissertation.

In Chapter 2, I investigate the occurrence of torpor in free-ranging Pearl-spotted Owlets (*Glaucidium perlatum*) and African Scops-Owls (*Otus senegalensis*), resident in the Kalahari Desert of southern Africa.

In Chapter 3, I investigate the magnitude and direction of seasonal BMR adjustments in five bird species resident year-round in the Kalahari Desert of southern Africa: the nocturnal African Scops-Owl (*Otus senegalensis senegalensis*), crepuscular/nocturnal Pearl-spotted Owlet (*Glaucidium perlatum licua*), and diurnal Fork-tailed Drongo (*Dicrurus adsimilis apivorus*), Crimson-breasted Shrike (*Laniarius atrococcineus*) and White-browed Sparrow-weaver (*Plocepasser mahali mahali*). I also investigated global variation in patterns of avian seasonal BMR adjustments, by synthesizing literature data.

Chapter 4 provides general conclusions and suggestions for future research.

Literature cited

Ambrose S.J., and S.D. Bradshaw. 1988. Seasonal changes in standard metabolic rates in the white-browed scrubwren *Sericornis frontalis* (Acanthizidae) from arid, semi-arid and mesic environments. Comparative Biochemistry and Physiology 89A:79-83.

Bartholomew G.A., T.R. Howell, and T.J. Cade. 1957. Torpidity in the white-throated swift, anna hummingbird, and poor-will. The Condor 59:145-155.

Bech C. 1980. Body temperature, metabolic rate, and insulation in winter and summer acclimatized mute swans (*Cygnus olor*). Journal of Comparative Physiology 136:61-66.

Bech C., A.S. Abe, J.F. Steffensen, M. Berger, and J.E.P.W. Bicudo. 1997. Torpor in three species of Brazilian hummingbirds under semi-natural conditions. The Condor 99:780-788.

Brigham R.M. 1992. Daily torpor in a free-ranging goatsucker, the common poorwill (*Phalaenoptilus nuttallii*). Physiological Zoology 65:457-472.

Brigham R.M., G. Körtner, T.A. Maddocks, and F. Geiser. 2000. Seasonal use of torpor by free-ranging Australian owlet-nightjars (*Aegotheles cristatus*). Physiological and Biochemical Zoology 73:613-620.

Calder W.A. 1994. When do hummingbirds use torpor in nature? Physiological Zoology 67:1051-1076.

Carpenter F.L., and M.A. Hixon. 1988. A new function for torpor: fat conservation in a wild migrant hummingbird. The Condor 90:373-378.

Cheke R.A. 1971. Temperature rhythms in African montane sunbirds. Ibis 113:500-506.

Cooper C.E., G. Körtner, R.M. Brigham, and F. Geiser. 2008. Body temperature and activity patterns of free-living laughing kookaburras: the largest kingfisher is heterothermic. The Condor 110:110-115.

Cooper S.J. 2000. Seasonal energetics of mountain chickadees and juniper titmice. The Condor 102:635-644.

Cooper S.J., and D.L. Swanson. 1994. Seasonal acclimatization of thermoregulation in the black-capped chickadee. The Condor 96:638-646.

Dawson W.R. 2003. Plasticity in avian responses to thermal challenges - an essay in honor of Jacob Marder. Israeli Journal of Zoology 49:95-109.

Dawson W.R., and C.D. Fisher. 1969. Responses to temperature by the spotted nightjar (*Eurostopodus guttatus*). The Condor 71:49-53.

Dawson W.R., and R.L. Marsh. 1988. Metabolic acclimatization to cold and season in birds. Pp. 83-94 in C. Bech, and R.E. Reinertsen, eds. Physiology of cold adaptation in birds. Plenum Press, New York

Dawson W.R., R.L. Marsh, W.A. Buttermer, and C. Carey. 1983. Seasonal and geographic variation of cold resisitance in house finches. Physiological Zoology 56:353-369.

Dawson W.R., and T.P. O'Conner. 1996. Energetic features of avian thermoregulatory responses. Pp. 85-124 in C. Carey, eds. Avian energetics and nutritional ecology. Chapman and Hall, New York

Dawson W.R., and G.C. Whittow. 2000. Regulation of body temperature. Pp. 343-390 in P.D. Sturkie, eds. Avian Physiology. Academic Press, New York

Downs C.T., and M. Brown. 2002. Nocturnal heterothermy and torpor in the Malachite sunbird (*Nectarinia famosa*). Auk 119:251-260.

Fletcher Q.E., R.J. Fisher, C.K.R. Willis, and R.M. Brigham. 2004. Free-ranging common nighthawks use torpor. Journal of Thermal Biology 29:9-14.

Geiser F. 1998. Evolution of daily torpor and hibernation in birds and mammals: importance of body size. Clinical and Experimental Pharmacology and Physiology 25:736-740.

Geiser F. 2004. Metabolic rate and body temperature reduction during daily torpor. Annual Review of Physiology 66:239-274.

Geiser F., and C. Ferguson. 2001. Intraspecific differences in behaviour and physiology: effects of captive breeding on patterns of torpor in feathertail gliders. Journal of Comparative Physiology B 171:569-576.

Geiser F., J.C. Holloway, G. Körtner, T.A. Maddocks, C. Turbill, and R.M. Brigham. 2000. Do patterns of torpor differ between free-ranging and captive mammals and birds? Pp. 95-102 in G. Heldmaier, and M. Klingenspor, eds. Life in the cold: 11th International Hibernation Symposium. Springer, Berlin

Hackett S.J., R.T. Kimball, S. Reddy, R.C.K. Bowie, E.L. Braun, J.L. Chojnowski, W.A. Cox, K.-L. Han, J. Harshman, C.J. Huddleston, B.D. Marks, K.J. Miglia, W.S. Moore, F.H. Sheldon, D.W. Steadman, C.C. Witt, and T. Yuri. 2008. A phylogenetic study of birds reveals their evolutionary history. Science 320:1763-1768.

Hickey M.B.C. 1993. Thermoregulation in free-ranging whip-poor-wills. The Condor 95:744-747.

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

Jaeger E.C. 1948. Does the poor-will hibernate? The Condor 50:45-46.

Klaassen M., M. Oltrogge, and L. Trost. 2004. Basal metabolic rate, food intake, and body mass in cold- and warm-acclimated Garden Warblers. Comparative Biochemistry and Physiology A 137:639-647.

Körtner G., R.M. Brigham, and F. Geiser. 2000. Winter torpor in a large bird. Nature 407:318.

Koskimies J. 1948. On temperature regulation and metabolism in the swift, *Micropus a. apus* L. during fasting. Experimentia 4:274-276.

Lane J.E., R.M. Brigham, and D.L. Swanson. 2004. Daily torpor in free-ranging whip-poor-wills (*Caprimulgus vociferus*). Physiological and Biochemical Zoology 77:297-304.

Lasiewski R.C. 1963. Oxygen consumption of torpid, resting, and flying hummingbirds. Physiological Zoology 36:122-140.

Liknes E.T., S.M. Scott, and D.L. Swanson. 2002. Seasonal acclimatization in the American Goldfinch revisited: to what extent do metabolic rates vary seasonally? The Condor 104:548-557.

Liknes E.T., and D.L. Swanson. 1996. Seasonal variation in cold tolerance, basal metabolic rate, and maximal capacity for thermogenesis in white-breasted nuthatches *Sitta carolinensis* and downy woodpeckers *Picoides pubescens*, two unrelated arboreal temperate residents. Journal of Avian Biology 27:279-288.

Lovegrove B.G. 1993. The living deserts of southern Africa. Fernwood Press, Vlaeberg.

Lovegrove B.G. 2005. Seasonal thermoregulatory responses in mammals. Journal of Comparative Physiology B 175:231-247.

Lovegrove B.G. 2006. The power of fitness in mammals: perceptions from the African slipstream. Physiological and Biochemical Zoology 79:224-236.

Lovegrove B.G., and F. Génin. 2008. Torpor and hibernation in a basal placental mammal. the Lesser Hedgehog Tenrec *Echinops telfairi* Journal of Comparitive Physiology B 178:691-698.

Lovegrove B.G., M.J. Lawes, and L. Roxburgh. 1999. Confirmation of plesiomorphic daily torpor in mammals: the round-eared elephant shrew *Macroscelides proboscideus* (Macroscelidea). Journal of Comparative Physiology B 169:453-460.

MacMillen R.E., and C.H. Trost. 1967. Nocturnal hypothermia in the inca dove *Scardafella inca*. Comparative Biochemistry and Physiology 23:243-253.

Maddocks T.A., and F. Geiser. 2000. Seasonal variations in thermal energetics of Australian silvereyes (*Zosterops lateralis*). Journal of Zoology, London 252:327-333.

Maddocks T.A., and F. Geiser. 2007. Heterothermy in an Australian passerine, the Dusky Woodswallow (*Artamus cyanopterus*). Journal of Ornithology 148:571-577.

Malan A. 1996. The origins of hibernation: a reappraisal. Pp. 1-6 in F. Geiser, A.J. Hulbert, and S.C. Nicol, eds. Adaptations to the cold: Tenth International Hibernation Symposium. University of New England Press, Armidale

McKechnie A.E. 2008. Phenotypic flexibility in basal metabolic rate and the changing view of avian physiological diversity: a review. Journal of Comparative Physiology B 173:235-247.

McKechnie A.E., K. Chetty, and B.G. Lovegrove. 2007. Phenotypic flexibility in basal metabolic rate in Laughing Doves: responses to short-term thermal acclimation. Journal of Experimental Biology 210:97-106.

McKechnie A.E., and B.G. Lovegrove. 2001. Heterothermic responses in the speckled mousebird (*Colius striatus*). Journal of Comparative Physiology B 171:507-518.

McKechnie A.E., and B.G. Lovegrove. 2002. Avian facultative hypothermic responses: a review. The Condor 104:705-724.

McKechnie A.E., and B.O. Wolf. 2004. The allometry of avian basal metabolic rate: good predictions need good data. Physiological and Biochemical Zoology 77:502-521.

Merola-Zwartjes M., and J.D. Ligon. 2000. Ecological energetics of the Puerto Rican tody: heterothermy, torpor and intra-island variation. Ecology 81:990-1002.

Mezhzherin V.A. 1964. Dehnel's phenomenon and its possible explanation. Acta Theriologica 8:95-114.

Peiponen V.A. 1965. On hypothermia and torpidity in the nightjar (*Caprimulgus europaeus* L.). Annales Academiae Scientiarum Fennicae (Series A IV.Biologica) 87:1-15.

Prinzinger R., R. Göppel, A. Lorenz, and E. Kulzer. 1981. Body temperature and metabolism in the red-backed mousebird (*Colius castanotus*) during fasting and torpor. Comparative Biochemistry and Physiology 69A:689-692.

Prinzinger R., A. Preßmar, and E. Schleucher. 1991. Body temperature in birds. Comparative Biochemistry and Physiology 99A:499-506.

Prinzinger R., and K. Siedle. 1988. Ontogeny of metabolism, thermoregulation and torpor in the house martin *Delichon u. urbica* (L.) and its ecological significance. Oecologia 76:307-312.

Reinertsen R.E. 1996. Physiological and ecological aspects of hypothermia. Pp. 125-157 in C. Carey, eds. Avian energetics and nutritional ecology. Chapman & Hall, New York

Reynolds P.S., and R.M. Lee. 1996. Phylogenetic analysis of avian energetics: passerines and non-passerines do not differ. American Naturalist 147:735-759.

Rezende E.L., D.L. Swanson, F.F. Novoa, and F. Bozinovic. 2002. Passerines *versus* nonpasserines: so far, no statistical differences in the scaling of avian energetics. Journal of Experimental Biology 205:101-107.

Saarela S., and E. Hohtola. 2003. Seasonal thermal acclimatization in sedentary and active pigeons. Israeli Journal of Zoology 49:185-193.

Schleucher E. 2001. Heterothermia in pigeons and doves reduces energetic costs. Journal of Thermal Biology 26:287-293.

Schleucher E. 2004. Torpor in birds: taxonomy, energetics and ecology. Physiological and Biochemical Zoology 77:942-949.

Schmidt-Nielsen K. 1990. Animal physiology: adaptation and environment. Cambridge University Press, Cambridge.

Sibley C.G., and J.E. Ahlquist. 1990. Phylogeny and classification of birds. Yale University Press, New Haven.

Stone R.C., G.L. Hammer, and T. Marcussen. 1996. Prediction of global rainfall probabilities using phases of the Southern Oscillation index. Nature 384:252-255.

Swanson D.L. 1990. Seasonal variation in cold hardiness and peak rates of cold-induced thermogenesis in the dark-eyed junco (*Junco hyemalis*). Auk 107:561-566.

Swanson D.L. 1991. Seasonal adjustments in metabolism and insulation in the Dark-eyed Junco. The Condor 93:538-545.

Swanson D.L. in press. Seasonal metabolic variation in birds: functional and mechanistic correlates. Pp. in Current Ornithology.

Swanson D.L., and E.T. Liknes. 2006. A comparative analysis of thermogenic capacity and cold tolerance in small birds. Journal of Experimental Biology 209:466-474.

Swanson D.L., and K.L. Olmstead. 1999. Evidence for a proximate influence of winter temperatures on metabolism in passerine birds. Physiological and Biochemical Zoology 72:566-575.

Swanson D.L., and D.P. Weinacht. 1997. Seasonal effects on metabolism and thermoregulation in northern bobwhite. The Condor 99:478-489.

Tieleman B.I., and J.B. Williams. 2000. The adjustment of avian metabolic rates and water fluxes to desert environments. Physiological and Biochemical Zoology 73:461-479.

Tieleman B.I., J.B. Williams, and P. Bloomer. 2003. Adaptation of metabolic rate and evaporative water loss along an aridity gradient. Proceedings of the Royal Society of London 270:207-214.

Weathers W.W., and D.F. Caccamise. 1978. Seasonal acclimatization to temperature in monk parakeets. Oecologia 35:173-183.

West G.C. 1972. The effect of acclimation and acclimatization on the resting metabolic rate of the common redpoll. Comparative Biochemistry and Physiology 43A:293-310.

Williams J.B., and B.I. Tieleman. 2000. Flexibility in basal metabolic rate and evaporative water loss among hoopoe larks exposed to different environmental temperatures. Journal of Experimental Biology 203:3153-3159.

Williams J.B., and B.I. Tieleman. 2005. Physiological adaptation in desert birds. BioScience 55:416-425.

Withers P.C. 1992. Comparative animal physiology. Saunders College Publishing, Fort Worth.

Wolf L.L., and F.R. Hainsworth. 1972. Environmental influence on regulated body temperature in torpid hummingbirds. Comparative Biochemistry and Physiology 41A:167-173.

CHAPTER 2:

DO OWLS USE TORPOR? WINTER THERMOREGULATION IN FREE-RANGING PEARL-SPOTTED OWLETS AND AFRICAN SCOPS-OWLS

Introduction

Many birds are heterothermic endotherms and down-regulate body temperature (T_b) below normothermic levels during the rest-phase. Heterothermic responses have been reported in 11 orders, in species ranging in body mass (M_b) from < 3 to 6500 g, and in a much wider variety of ecological contexts than previously thought (Körtner et al. 2000; McKechnie and Lovegrove 2002). Within the Coraciiformes, for instance, heterothermy occurs in both the smallest and largest representatives, namely the 5-g Puerto Rican Tody (*Todus mexicanus*) and the 360-g Laughing Kookaburra (*Dacelo novaeguineae*) (Merola-Zwartjes and Ligon 2000; Cooper et al. 2008).

Torpor, mostly defined as a reduction in rest-phase T_b below 30°C (Hudson 1978; Reinertsen 1996; Schleucher 2001; reviewed by Barclay et al. 2001), appears to be particularly important in offsetting the energetic costs of thermoregulation in birds with specialized diets; it is most common in taxa whose food resources exhibit large spatial and/or temporal fluctuations in availability, e.g. frugivores (Coliidae and Columbidae), nectarivores (Trochilidae and Nectariniidae) and insectivores (Todidae, Apodidae, Caprimulgidae and Hirundinidae) (McKechnie and Lovegrove 2002; Schleucher 2004). However, to better understand the adaptive value and evolution of avian torpor, a more thorough assessment of the phylogenetic distribution of this trait is needed (McKechnie and Lovegrove 2002; Schleucher 2004).

One of the most puzzling phylogenetic patterns in the occurrence of avian torpor concerns the order Strigiformes (*sensu* Sibley and Ahlquist 1990, but see Hackett et al. 2008) which contains the suborders Caprimulgi (nightjars and allies) and Strigi (owls). Whereas the capacity for pronounced torpor is widespread in caprimulgids (Lane et al. 2004), it has not been reported in owls (Ligon 1969; Hohtola et al. 1994), an observation that is surprising in view of the close phylogenetic relationship of these two groups (Sibley and Ahlquist 1990). Only shallow reductions in T_b have been reported in two relatively large owl species, the Snowy Owl (*Nyctea scandiaca*) and Barn Owl (*Tyto alba*) (Gessaman and Folk 1969; Thouzeau et al. 1999). In the latter study, Barn Owls fasted in the cold for 8 days never reduced T_b by more than 5°C despite M_b loss of > 25% (Thouzeau et al. 1999). Several studies of smaller species, on the other hand, failed to document any evidence whatsoever for heterothermic responses, leading the authors to conclude that small owls can endure extended periods of energy stress without using torpor (Ligon 1969; Hohtola et al. 1994).

It is noteworthy, however, that all thermoregulatory studies on owls to date have been carried out under artificial conditions in laboratories and very little is known about how wild owls thermoregulate in natural habitats. Data from free-living birds are particularly important in the light of recent studies showing that many birds use torpor only under natural conditions (Brigham et al. 2000; Körtner et al. 2001; Fletcher et al. 2004; Lane et al. 2004; Cooper et al. 2008).

In arid environments with unpredictable and low productivity, torpor plays an important role of energy balance in many endotherms (Geiser 2004). I investigated patterns of thermoregulation in free-living Pearl-spotted Owlets (*Glaucidium perlatum*) and African Scops-Owls (*Otus senegalensis*) in the Kalahari Desert of South Africa to explore the occurrence of torpor within the owl taxon (Strigidae). The Kalahari Desert region is characterized by a wide range of temperatures, arid winters and unpredictable precipitation during summer (Lovegrove 1993). Small owls inhabiting this area seem likely to experience food shortages during cold and dry winter nights when the availability of arthropod prey is reduced.

Material and methods

Study site

Free-ranging Pearl-spotted Owlets and African Scops-Owls were studied at Molopo Nature Reserve (25° 47’ S, 22° 56’ E) at an elevation of 1000 meters above sea level in the Northwest Province, South Africa, from early June to mid August 2007 (austral winter). This reserve falls within the semi-arid Kalahari Desert region, where the climate varies seasonally between dry and cool winters (May to August) with frequent sub-zero temperatures at night, and hot summers (November to March) with spatially and temporally unpredictable patterns of rainfall (Lovegrove 1993). The mean ± SD annual rainfall recorded at Molopo Nature Reserve (MNR) over a 50-year period was 332 ± 105 mm (Meyer et al. 2007). This study took place in the southern part of the reserve, where the vegetation consisted mainly of mixed *Acacia* spp. and *Boscia albitrunca* savannah on deep red sand, and scrub on irregular dry calcrete pans.

Air temperature recording

Air temperature (T_{air}) was measured in the study area using two temperature-sensitive data loggers (iButton Thermochron, Dallas Semiconductor, Dallas, U.S.A.). The iButtons were housed in ventilated polystyrene cups suspended in the shade ~ 2 m above the ground, at two sites ~ 6 km apart (<10 m difference in altitude). Before the study the iButtons were calibrated in a temperature-controlled water bath (model ME, Julabo Labortechnik, Seelbach, Germany), using a mercury thermometer (resolution = 0.2°C) with an accuracy traceable to the US National Bureau of Standards, over the approximate T_{air} range experienced at the study site during winter.

Capture of birds

Eight Pearl-spotted Owlets (three male, five females) and four African Scops-Owl (all males) were caught during June and July 2007 using mist nets and call playback, or spring-traps baited with mealworms. Neither species display sexual dimorphism in plumage colouration, but sexes can be distinguished by the females' softer and higher pitched calls (Hockey et al. 2005). All four individual African Scops-Owls were caught in adjacent territories (~ 1.5 km apart) and gave low pitched calls. They were also highly aggressive towards call playback and I strongly suspect that all these individuals were males.

Skin temperature recording

Skin temperature (T_{skin}) was measured using temperature-sensitive VHF transmitters (2.5g, model PD-2T, Holohil Systems, Carp, Ontario, Canada) emitting a frequency between 150.061 and 150.741 MHz. These transmitters were pre-calibrated in a temperature-controlled water bath at temperatures between 5° and 45°C (5°C intervals), using a mercury thermometer (resolution = 0.2°C). A broad-band communications receiver (IC-R10, Icom, Bellevue, WA) was used to obtain signals from the transmitters during calibration. The relationships between pulse rate and temperature were best described by second-order polynomial regressions, with all r^2 values > 0.995. Shortly after capture, each transmitter was secured dorsally, beneath the feathers in the interscapular region of each owl, using a harness constructed from clothing elastic inserted through a 6.5 mm Teflon ribbon (Telonics, Mesa AZ, USA), modified from Figure 18.2 of Kenward (2000), following McKechnie et al. (2007). This method has been widely used for the measurement of T_{skin} in free-ranging caprimulgids (Brigham 1992; Brigham et al. 2000; McKechnie et al. 2007), and loose harnesses can be readily detected from T_{skin} readings that vary unpredictably. Owls, however, are more likely to damage harnesses than nightjars, and if there were any indications that a harness had come loose, I excluded data from that individual.

The signals emitted by Holohil transmitters have been reported to drift, and they should be recovered after data collection and re-calibrated (J.B. Williams, pers. comm.). I recovered transmitters from two African Scops-Owls, five weeks after they were tagged, and recalibrated these at three temperatures (19°, 29° and 39°C) in the water bath. At 39°C the pulse rates of both transmitters were higher than during initial calibration (equivalent to a mean change in $\mathrm{T_{skin}}$ readings of 1.2°C), but at 19° and 29°C the pulse rates were identical to initial calibration. Since I was not able to retrieve transmitters from any of the Pearl-spotted Owlets, I examined T_{skin} values of the Pearl-spotted Owlets to investigate whether there were any consistent changes in T_{skin} that might be the result of transmitter drift. I compared an individual's night-time (18h00 to 5h00) T_{skin} data of the first four days to last four days of tracking, but found no significant differences.

I recorded T_{skin} from 31 May 2007 to 9 August 2007 in eight Pearl-spotted Owlets, (days of data collection per individual of 39, 39, 36, 32, 20, 12, 11, and 3) and four African Scops-Owls (28, 22, 6 and 4 days of data collection). I used a broad-band communications receiver (IC-R10, Icom, Bellevue, WA) to obtain signals from the transmitters. Readings from each transmitter were taken at 0.1 to 5 h intervals during the night and day. For each transmitter the duration of a minimum of 20 pulse intervals was timed manually using a stopwatch to obtain T_{skin} estimations. Manual measurement of T_{skin} using a stopwatch is widespread in such studies, and appear to be consistent with results obtained using digital data loggers (Rismiller and McKelvey 1996). I converted pulse intervals to T_{skin} values using the calibration curve previously determined for each transmitter. While measuring T_{skin}, the modulation of pulses allowed us to assess whether an individual was active and moving about (Brigham et al. 1999; Brigham et al. 2000).

One Pearl-spotted Owlet and two African Scops-Owls were held in a field laboratory for ~ 16 h prior to release in order to compare T_{skin}, T_b and air temperature (T_a) gradients. Skin temperature and cloacal T_b were measured simultaneously at $5° \leq T_a \leq 35°\mathrm{C}$. The owls were placed in 1.69L plastic chambers within an insulated environmental chamber, constructed by lining the interior of a 66.2L cooler box with copper tubing, through which water was pumped by a temperature-controlled circulator (model ME, Julabo Labortechnik, Seelbach, Germany). Air temperature within the plastic chamber was measured using a 21-gauge CU-CN (IT-18, Physitemp, Clifton NJ) thermocouple and a TC-1000 thermocouple meter (Sable Systems, Las Vegas, NV, USA). Body temperature was measured using a lubricated fine-gauge Teflon-coated Cu-Cn thermocouple (IT-18, Physitemp, Clifton NJ) inserted into the cloaca to a depth at which a slight withdrawal did not result in a change in the reading (~ 2 cm). The thermocouple was secured by attaching the thermocouple wire to the tail feathers, immediately behind the cloaca, using adhesive tape and a wire paperclip. Body temperature data were discarded if the thermocouple became dislodged during measurements. All the thermocouples were previously calibrated in the temperature-controlled water bath. Data from the thermocouples were digitized using a TC-1000 thermocouple meter (Sable Systems, Las Vegas, NV, USA) and recorded on a laptop computer using EXPEDATA software (Sable Systems).

Data analyses and defining departures from normothermy

Values are presented as mean ± SD for n = number of individuals and N = number of observations, unless stated otherwise. The relationships between T_{skin}, T_{b} and T_{a} were described using the regression model that provided the best fit to each data set, identified following Song et al. (1997). Changes in T_{skin} and T_{a} were described using least-squares linear regression models in STATISTICA version 7.0 (StatSoft, Inc. Tulsa, OK).

Considerable debate surrounds the terminology used to refer to down-regulation of T_{b} and metabolic rate below normothermic levels, and the approaches used to distinguish such states from normothermy (Barclay et al. 2001; Schleucher and Prinzinger 2006; Willis 2007). In free-ranging endotherms, the identification of heterothermic bouts from T_{skin} traces is further complicated by the effects of the thermal environment, and the fact that behavioural observations are seldom feasible in the field

(Barclay et al. 2001). In general, down-regulation of T_b below the set point T_b range that is associated with normal activity is considered to constitute heterothermy (Withers 1992). Traditionally, heterotherms were only considered to be in torpor if a state of lethargy and reduced responsiveness to external stimuli was associated with T_b well below the normothermic range (Bligh and Johnson 1973; IUPS 2003). However, whereas most small endotherms enter a state of lethargy when T_b is considerably below normothermic levels, e.g. $T_b < 20°C$, a number of endotherms show coordinated levels of activity at T_b well below normothermic levels (Choi et al. 1998; Geiser et al. 2002; Mzilikazi et al. 2002; Willis and Brigham 2003). For instance, the Fat-tailed Antechinus (*Pseudantechinus macdonnellensis*) is capable of coordinated movement at T_b of 22.6°C by running up a vertical cliff to bask in an exposed site in the sun (Geiser et al. 2002), and a small bat species (*Murina leucogaster ognevi*) is capable of biting and crawling at T_b as low as 8°C (Choi et al. 1998). Behavioural criteria can therefore not be used to define energy saving responses in a reliable and consistent manner (Willis 2007).

Rather than attempting to define torpor on the basis of behavioural criteria [which is rarely feasible in the field (Barclay et al. 2001)], or applying a specific T_b / T_{skin} threshold value, such as $T_{skin} = 30°C$ (Brigham 1992; Brigham et al. 2000), I used a method modified from that of (McKechnie et al. 2007), which identifies departures from normothermic T_b or T_{skin} by testing the fit of a normal distribution curve to the T_{skin} data of each individual. I used Komolgorov-Smirnov tests to check the fit of a normal distribution curve to the normothermic T_{skin} data within each individual. I included T_{skin} data irrespective of time of day since neither species exhibited clear circadian rhythms of normothermic T_{skin}. If there was a significant fit of normality to the T_{skin} data for an individual, I concluded that it did not deviate from normothermy during the study period. On the other hand, if an individual's T_{skin} data were significantly non-normal, I estimated the normothermic T_{skin} range for that individual by fitting a normal distribution to the upper modal and absolute maximum T_{skin}, following McKechnie et al.(2007). For each individual, the lower 99% confidence limit (C.L.) of the normothermic distribution was then determined and the upper threshold T_{skin} for departures from normothermy was calculated by subtracting 3°C from the lower 99% C.L. of normal T_{skin}, in order to account for the error associated with estimating T_{b} from T_{skin} measurements (see Figure 1).

Results

Mean M_{b} was 79.5 ± 5.4 g (n = 8) for Pearl-spotted Owlets and 60.6 ± 3.6 g (n = 4) for African Scops-Owls. Air temperature during the study period (31 May to 9 August 2007) ranged from −7.0° to 33.1°C, with a mean daily minimum and maximum T_{a} of 2.7° ± 3.8°C and 24.4° ± 3.0°C, respectively, and an overall mean air temperature of 12.7° ± 2.4°C (mean daily T_{a}, 31 May to 9 August 2007) (Figure 2A).

Skin temperature was predictably related to T_{b} in the one Pearl-spotted Owlet and two African Scops-Owls in which T_{skin} and T_{b} was simultaneously measured in the field laboratory (Figure 1). The relationships between $T_{\mathrm{b}} - T_{\mathrm{skin}}$ and $T_{\mathrm{b}} - T_{\mathrm{a}}$ were best described using polynomial regression models, where $T_{\mathrm{b}} - T_{\mathrm{skin}} = -0.006(T_{\mathrm{b}} - T_{\mathrm{a}})^2 + 0.489(T_{\mathrm{b}} - T_{\mathrm{a}}) - 7.356$, ($r^2 = 0.949$) in the Pearl-spotted Owlet, and $T_{\mathrm{b}} - T_{\mathrm{skin}} = -0.001(T_{\mathrm{b}} - T_{\mathrm{a}})^2 + 0.154(T_{\mathrm{b}} - T_{\mathrm{a}}) - 2.230$, ($r^2 = 0.955$) in African Scops-Owls (n = 2). At high T_{b}-T_{a} differentials (i.e. low T_{a}), T_{skin} typically remained 3^{o} and 2^{o}C below T_{b} for Pearl-spotted

Owlets and African Scops-Owls, respectively (Figure 1), and vice versa at low T_b-T_a differentials.

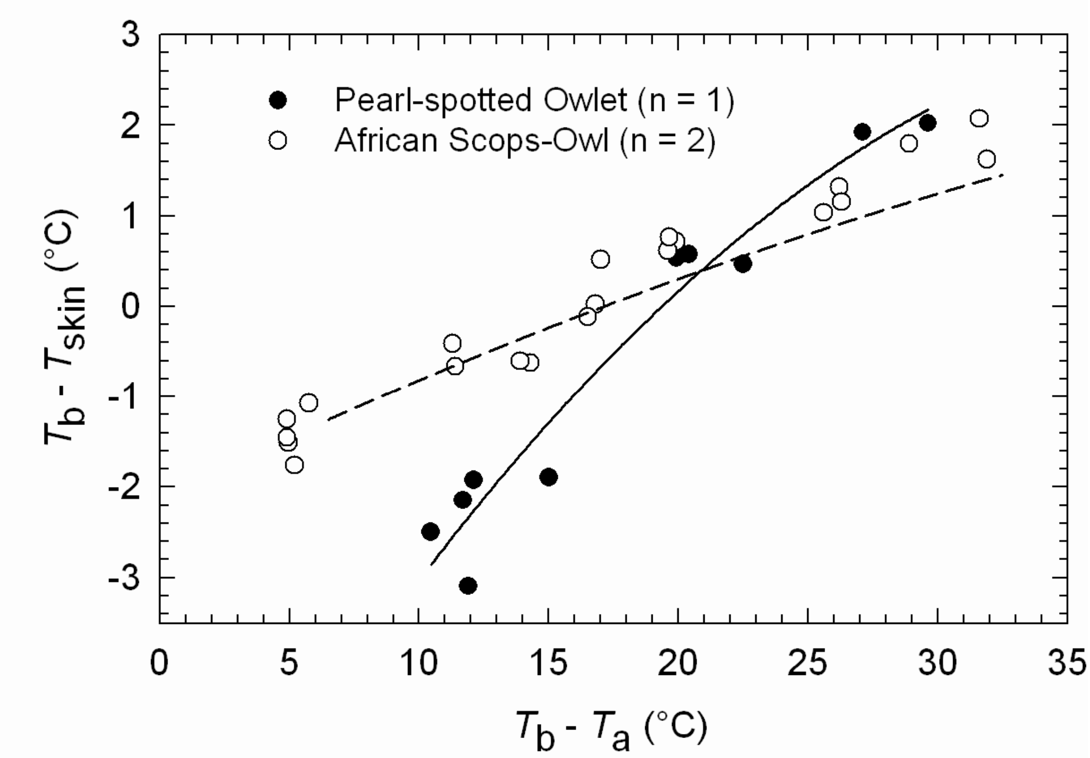

Figure 1: Simultaneous measurements of T_{skin}, T_b and T_a in a single Pearl-spotted Owlet (clear circles) and two African Scops-Owls (filled circles), held in a field laboratory. All birds remained normothermic ($T_b > 37°C$) during simultaneous measurements of T_{skin} and T_b.

Pearl-spotted Owlets

Pearl-spotted Owlets were active and heard calling during the day and night while they were radio-tracked, with the highest activity levels occurring around sunset and sunrise. I obtained reliable T_{skin} traces from four Pearl-spotted Owlets. Skin temperature in these individuals typically peaked at 38.5° to 42.5°C between 12h00 and 18h00, and was subsequently maintained at 38° to 39°C (mean night-time T_{skin} = 39.7° ± 1.0°C, n = 4, N = 850; Figures 2B & 3).

The Pearl-spotted Owlets showed significant normal distributions of T_{skin}, which was typically maintained between 36.5° and 41°C (Figure 4). At no time during the study did Pearl-spotted Owlets exhibit torpor, and the lowest T_{skin} I observed was 35.6°C.

African Scops-Owls

African Scops-Owls were active only at night and typically returned to the same roosting sites about 30 min before sunrise while radio-tracked. I obtained reliable T_{skin} traces from three African Scops-Owls. Only 9 hrs of data was obtained from the fourth individual since it moved to an inaccessible site shortly after it was released. Skin temperature typically peaked an hour before sunset at 38° to 39°C and were subsequently maintained between 34° and 38°C during the night (mean night-time T_{skin} = 36.0° ± 1.2°C, n = 3, N = 328; Figure 2B). After sunrise, the African Scops-Owls reduced T_{skin} below 34°C for 1.5 to 5 h (pooled mean of complete bouts = 2.8 ± 0.8 h, n = 3, N = 30) every day during the study period (Figure 3).

Reductions in T_{skin} (mean night-time T_{skin} − minimum T_{skin}) shortly after sunrise ranged from 3.3° to 8.6°C (pooled mean = 5.3° ± 1.1°C, n = 3, N = 36), and minimum T_{skin} (pooled mean of lowest daily T_{skin} readings) averaged 30.5° ± 0.8°C in three individuals (Figure 2). Circadian fluctuations in T_{skin} (maximum T_{skin} − minimum T_{skin}) ranged from 5.8° to 12.0°C. Minimum daily T_{skin} was reached at approximately 08h30 and was maintained for 0.5 to 2 h before the onset of re-warming (Figure 2). There was no relationship between the minimum T_{skin} and minimum T_a recorded on the same day during the study period ($F_{1,38} = 0.036$, $P = 0.85$). Three African Scops-Owls reduced T_{skin} below 30°C (mean absolute lowest T_{skin} = 29.0° ± 0.1°C, n = 3) during the study period

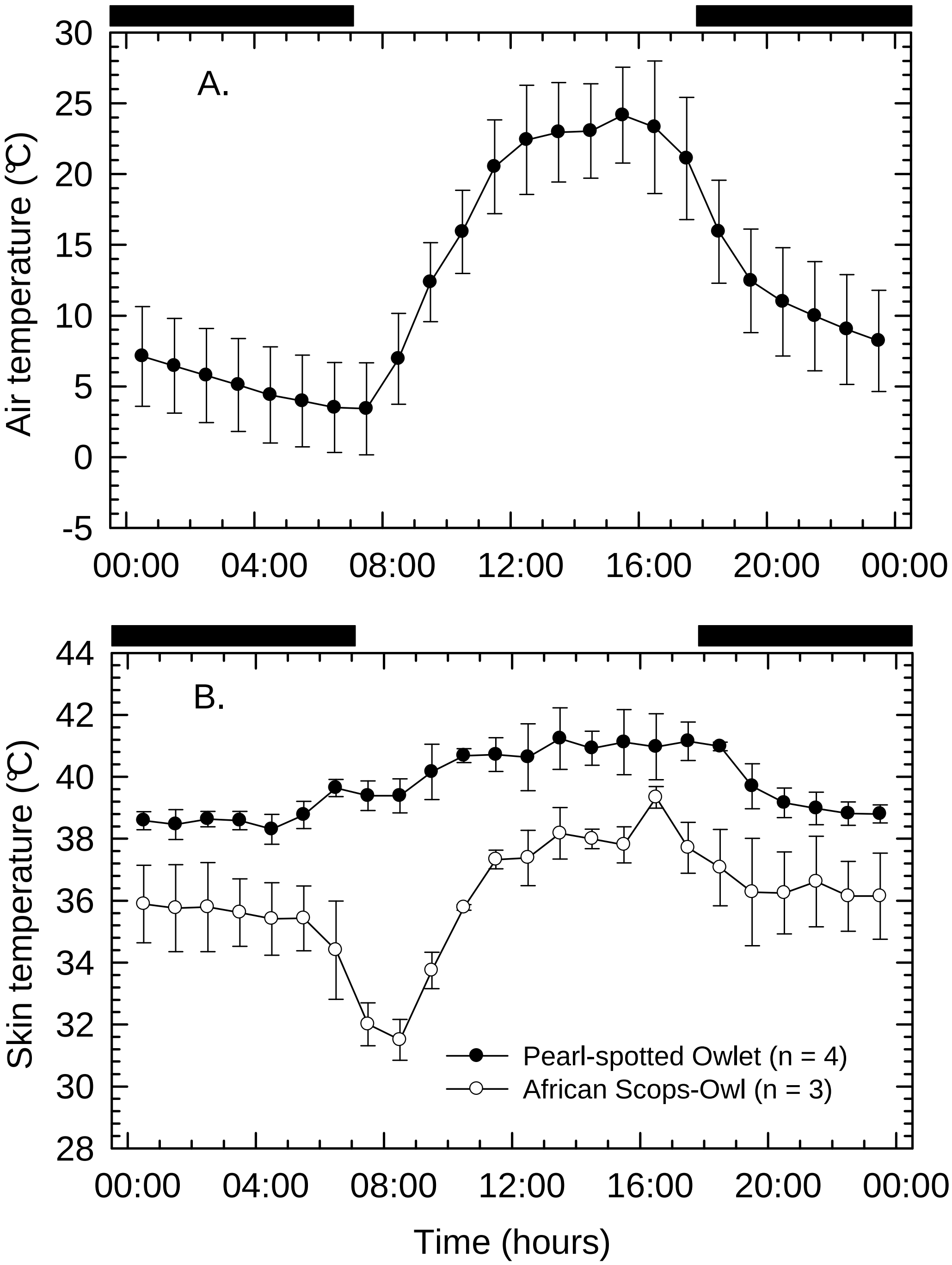

Figure 2: (A.) Mean ± SD hourly air temperature (T_{air}) and (B.) mean ± SD hourly T_{skin} for four Pearl-spotted Owlets and three African Scops-Owls recorded from 31 May to 9 August 2007 at Molopo Nature reserve. Each datum represents mean T_{air} or T_{skin} data for a species pooled to the nearest half an hour (e.g. 6:30 for 6:00 - 7:00). Black bars indicate night-time.

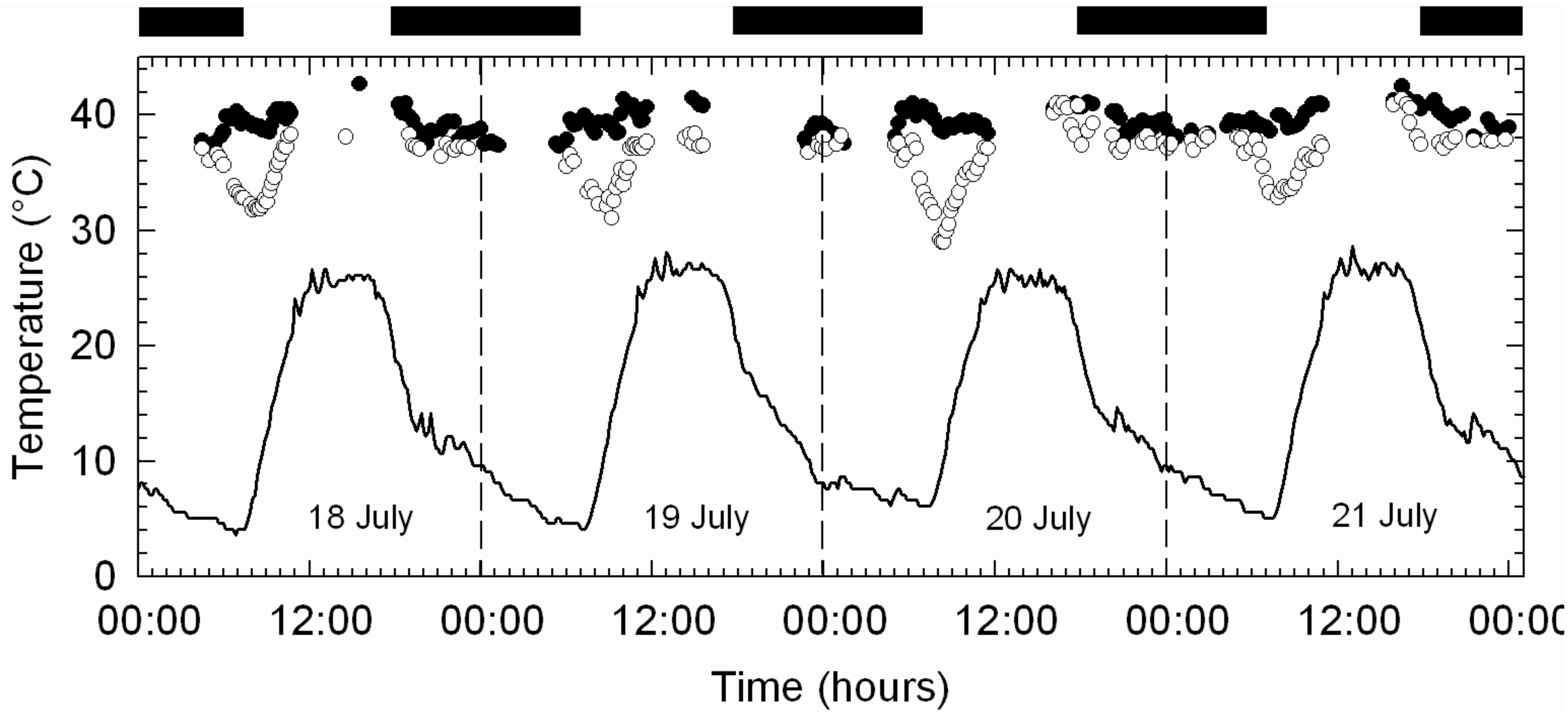

Figure 3: Skin temperature (T_{skin}) in a single Pearl-spotted Owlet (filled circles) and African Scops-Owl (clear circles) on four consecutive days during July 2007 at Molopo Nature Reserve. Air temperature (T_a) measured at the study site is represented by the solid line. The black bar at the top of the expanded figure indicates night-time. The Pearl-spotted Owlet typically remained homeothermic, whereas the African Scops-Owl showed shallow bouts of torpor every morning after sunrise. After sunrise on the morning of 20 July 2007 the African Scops-Owl reduced T_{skin} to 29.0°C.

(Figure 3, data from one bird). I recorded eight bouts where T_{skin} was reduced beolow 30°C and a further seven bouts where T_{skin} = 30°C. This minimum T_{skin} was usually maintained for less than 30 min.

The three African Scops-Owls from which I obtained reliable data showed multiple peaks in T_{skin} distributions and the range in T_{skin} was > 10°C (Figure 4). However, only two individuals showed T_{skin} distributions that were significantly non-normal ($p<0.05$; $p<0.01$; and $p<0.15$, respectively), despite the fact that all three these individuals showed similar ranges and patterns of T_{skin}. I therefore concluded that all three African Scops-Owls deviated from normothermy. The mean T_{skin} threshold for torpor was 33.7° ± 1.4°C (n = 3) and 31% of all T_{skin} measurements (n = 3, N = 358) fell below their respective thresholds, indicating frequent use of heterothermy by these individuals (Figure 4).

The mean re-warming rate of the African Scops-Owls was 0.05° ± 0.00°C.min^{-1} (n = 3, N = 22) and varied between 0.02° and 0.12°C.min^{-1}. These re-warming rates were equivalent to only 3 to 25% of the allometrically predicted endogenous re-warming rates for a 58 to 66 g bird (McKechnie and Wolf 2004a). Such low re-warming rates are usually the result of passive re-warming in the sun (McKechnie and Wolf 2004b), but I could not confirm whether the African Scops-Owls in this study were exposed to solar radiation during re-warming. One individual with T_{skin} = 31°C was approached at its roost site 2 h after sunrise. It was roosting in the shaded canopy of a *B. albitrunca* tree and responded to the disturbance by re-warming at 0.35°C.min^{-1}, i.e. three times faster than the maximum re-warming rate observed in undisturbed individuals.

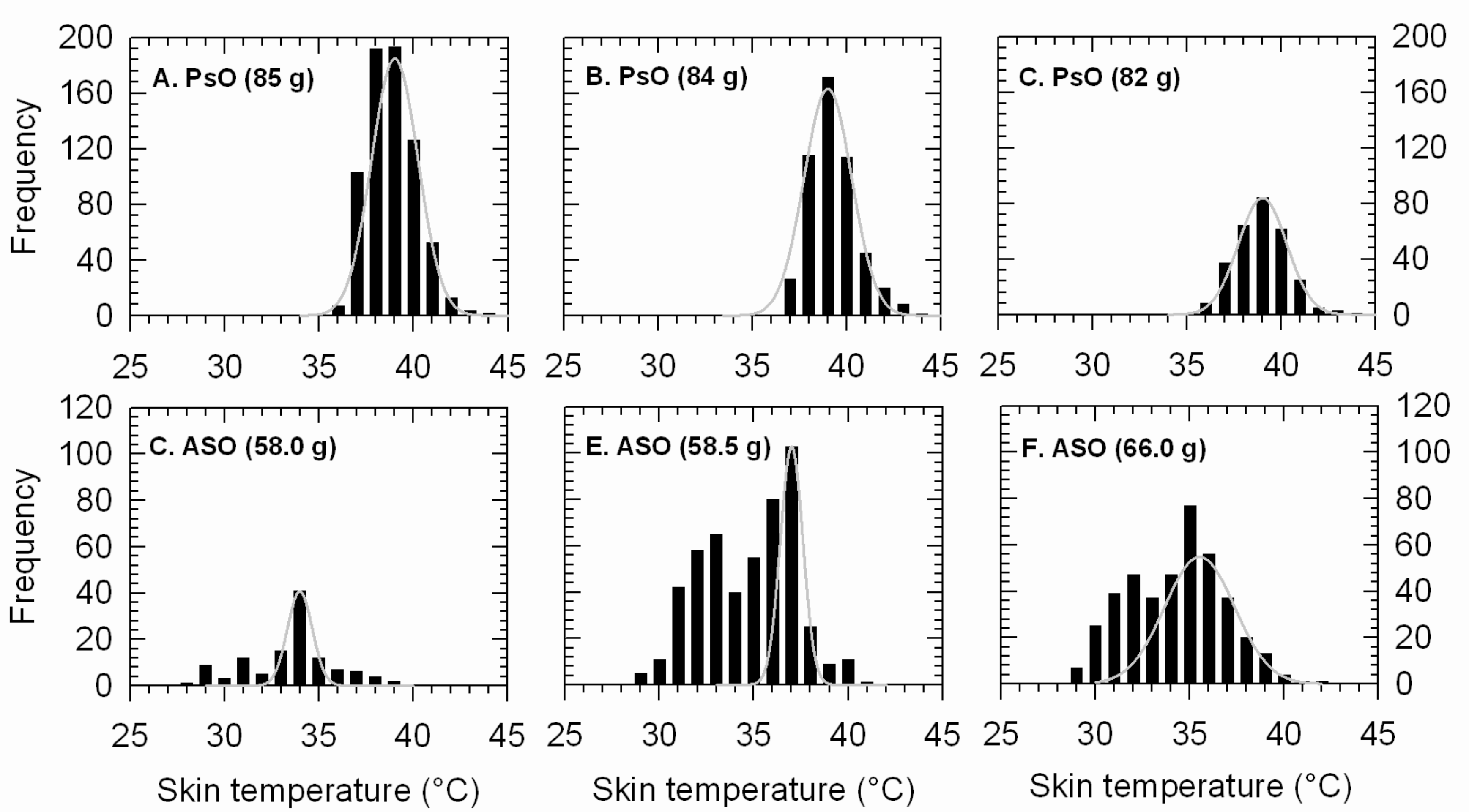

Figure 4: Frequency distributions of skin temperature (T_{skin}) in three Pearl-spotted Owlets (PsO: A − C) and three African Scops-Owls (ASO: D − F) monitored during June and July 2007. Each panel shows the T_{skin} data and M_b for an individual. The grey line represents a normal distribution of T_{skin} in a Pearl-spotted Owlet (Komolgorov Smirnoff, $p > 0.05$), or the calculated normothermic T_{skin} distribution for African Scops-Owls.

Discussion

My data reveal divergent winter thermoregulation patterns in two small, sympatric owl species. Measurements of T_{skin} confirmed the use of short, shallow bouts of torpor in African Scops-Owls, whereas torpor was absent in Pearl-spotted Owlets during the study period.

I am confident that the reductions in T_{skin} in African Scops-Owls were not artefacts of loose transmitters, since (a) T_{skin} often remained constant despite rapid T_a cooling during the night, (b) decreases in T_{skin} often occurred during periods of steady or increasing T_a in the morning, and (c) the timing of T_{skin} reductions in individuals were predictable among days (Figure 3). If the T_{skin} fluctuations had been the result of loose harnesses, reductions in T_{skin} would have occurred in an unpredictable fashion during activity, as was seen in a few Pearl-spotted Owlets in this study on which harnesses were pulled loose (B. Smit, pers. obs.).

Although the limited laboratory data suggest that T_{skin} was a reliable predictor of T_b, the relationship between the latter two variables may well be modified by the more complex thermal environments experienced by free-ranging birds. The only data on T_b – T_{skin} gradients from small birds under natural conditions of which I am aware involved a single Australian Owlet-nightjar (*Aegotheles cristatus*) kept in an outdoor aviary, in which T_{skin} generally under-estimated T_b by 3.0° ± 0.8°C (Brigham et al. 2000). In addition, although the harnesses I used kept the transmitters in close contact with the owls' skin, I cannot rule out the possibility of variation in T_{skin} due to factors such as a thin layer of air between the transmitter and skin. Because of these potential sources of error, and the slight drift observed in two transmitters that were recovered, I used a threshold T_{skin} value for each bird equivalent to 3°C below the lower 99% C.L. for normothermic T_{skin}, and am confident that my conservative approach to identifying departures from normothermy minimized the effects of T_b-T_{skin} gradients. Moreover, the major conclusions of my study are based on changes in T_b, and are not dependent on the measurement of accurate absolute values.

The reductions in T_{skin} in African Scops-Owls are, to the best of my knowledge, the most pronounced T_{skin} reductions yet observed in owls, and are below the T_{skin} threshold for torpor of 30°C used in studies on caprimulgids (Brigham 1992; Brigham et al. 2000; Lane et al. 2004). However, the heterothermic bouts I observed in African Scops-Owls were not as pronounced as those recorded in caprimulgids of similar M_b (Brigham et al. 2000; Lane et al. 2004). I consider the T_{skin} reductions below normothermic limits in African Scops-Owls to represent shallow torpor, following Körtner et al. (2001). Although the depth of the heterothermic bouts in African Scops-Owls varied between 3° and 9°C, the patterns were highly consistent, suggesting that these bouts represented a common physiological response. Moreover, the shallow torpor bouts in African Scops-Owls were more similar to the torpor bouts recorded in caprimulgids (Brigham et al. 2000; Körtner et al. 2001; Fletcher et al. 2004) than patterns of nocturnal hypothermia (T_b reductions < 5°C) typically observed in passerines (Reinertsen 1996; McKechnie and Lovegrove 2003).

Skin temperature patterns in African Scops-Owls closely resembled the torpor bouts recorded around sunrise in Australian Owlet-nightjars, Common Nighthawks (*Chordeiles minor*) and Whip-poor-wills (*Caprimulgus vociferous*) (Brigham et al. 2000; Fletcher et al. 2004; Lane et al. 2004). Like many caprimulgids, African Scops-Owls are likely to undergo periods of energetic stress during cool winters when the availability of food resources (mainly arthropods) is reduced. African Scops-Owls at MNR were significantly heavier, by 13% on average, during summer ($n = 7$) compared to winter ($n = 7$) (Chapter 3). These winter reductions in body mass are consistent with the Dehnel Effect observed in small mammals which involves winter M_b and

BMR reductions that are mediated by seasonal endogenous leptin cycles (Mezhzherin 1964; Lovegrove 2005). However, it is noteworthy that the seasonal M_b changes in African Scops-Owls at MNR coincided with an 85% decrease in the abundance of nocturnal, terrestrial arthropods during winter (Chapter 3). Terrestrial arthropods are a primary source of food for African Scops-Owls (Kemp 2005a), and it is not surprising in the light of these large seasonal reductions in food availability that African Scops-Owls used torpor to reduce energy demands during winter in the Kalahari Desert.

Pearl-spotted Owlets, on the other hand, differ considerably from African Scops-Owls and caprimulgids in terms of their foraging behaviour and diet (Kemp 2005b). Whereas both African Scops-Owls and most caprimulgids are exclusively nocturnal, Pearl-spotted Owlets show considerable flexibility in their activity pattern and often hunt during the day (Kemp 2005b). Foraging opportunities of Pearl-spotted Owlets for arthropods are therefore not restricted to the night-time, as in African Scops-Owls. Moreover, Pearl-spotted Owlets are powerfully built with large, strong feet which enable them to include mammals, birds and reptiles of almost double their own M_b in their diet (Maclean 1993; Kemp 2005b). In contrast to the seasonal M_b changes recorded in African Scops-Owls, winter ($n = 6$) Pearl-spotted Owlets were 9.2% heavier than summer ($n = 5$) birds, although this difference was not significant (Chapter 3). Pearl-spotted Owlets are in all likelihood less energy-limited than African Scops-Owls during winter in the Kalahari Desert, potentially explaining why the former species did not display heterothermic responses during my study.

I have documented the occurrence of shallow torpor in African Scops-Owls, but cannot exclude the possibility that this species employs more pronounced torpor. Many studies on caprimulgids have reported considerable inter-individual variability in torpor use, with only small proportions of populations using pronounced torpor (Fletcher et al. 2004; Lane et al. 2004; McKechnie et al. 2007). I obtained sufficient data from only three individuals, all of which were males; whereas various studies have reported gender-specific variation of torpor use in birds and mammals. In both Puerto Rican Todies (Merola-Zwartjes and Ligon 2000), and Freckled Nightjars (*Caprimulgus tristigm*) (McKechnie et al. 2007), only females reduced T_b below 25°C. In mammals, testosterone inhibits torpor use in males (Hall and Goldman 1980; Lee et al. 1990; Barnes 1996; Mzilikazi and Lovegrove 2002), but this has not yet been established in birds (McKechnie and Lovegrove 2002). Another factor that possibly selects against the use of torpor is predation risk. During the study, I observed of a pair of Gabar Goshawks (*Melierax gabar*) flushing and attempting to kill a single African Scops-Owl at its roost early one morning. If such predation events are a common threat to African Scops-Owls in the Kalahari Desert, pronounced torpor with reduced responsiveness would presumably be selected against.

Owls are a globally widespread and diverse taxon with respect to body mass, diet and behaviour (Marks et al. 1991). My results suggest that the use of torpor as an energy conservation mechanism will be most prevalent in small, nocturnal owls that rely on temporally fluctuating or unpredictable food sources. The genus *Otus* represents such a group, and includes mainly small species that inhabit deserts or temperate regions (Marks et al. 1991). In this regard, it is noteworthy that, like caprimulgids, *Otus* owls are highly cryptic while roosting (Marks et al. 1991), a trait that presumably reduces the likelihood of detection when in torpor.

Summary

My study reiterates the importance of thermoregulatory data from wild, free-ranging populations when assessing the occurrence of torpor in birds (Brigham et al. 2000; Fletcher et al. 2004; Lane et al. 2004; Cooper et al. 2008). The fact that at least one owl species exhibits qualitatively similar patterns of heterothermy to caprimulgids provides further insight into the phylogenetic distribution of this phenomenon within the order Strigiformes. Prior to my study, the lack of evidence for torpor in owls led to the hypothesis that this trait evolved early in the suborder Caprimulgi (Lane et al. 2004). However, my data reveal that owls likely share a physiological capacity for heterothermic responses with the caprimulgids, providing further evidence that torpor represents a monophyletic, plesiomorphic trait in birds as hypothesized by Malan (1996). It should be noted that the above conclusions assume that owls and caprimulgids are closely related, as proposed by Sibley and Ahlquist (1990). However, Hackett et al. (2008) recently argued that owls and caprimulgids are in fact not sister taxa, and that the phylogenetic relationship of the owl taxon remains unclear. Irrespective of the true relationship between these two taxa, my findings reiterate that the capacity for torpor is phylogenetically widespread in birds.

Literature cited

Barclay R.M.R., C.L. Lausen, and L. Hollis. 2001. What's hot and what's not: defining torpor in free-ranging birds and mammals. Canadian Journal of Zoology 79:1885-1890.

Barnes B.M. 1996. Relationship between hibernation and reproduction in male ground squirrels. Pp. 71-79 in F. Geiser, A.J. Hulbert, and S.C. Nicol, eds. Adaptation to the Cold: Tenth International Hibernation Symposium. University of New England Press, Armidale.

Bligh J., and K.G. Johnson. 1973. Glossary of terms for thermal physiology. Journal of Applied Physiology 35:941-961.

Brigham R.M. 1992. Daily torpor in a free-ranging goatsucker, the common poorwill (*Phalaenoptilus nuttallii*). Physiological Zoology 65:457-472.

Brigham R.M., R.C.A. Gutsell, R.S. Wiacek, and F. Geiser. 1999. Foraging behavior in relation to the lunar cycle by Australian Owlet-nightjars (*Aegotheles cristatus*). Emu 99:253-261.

Brigham R.M., G. Körtner, T.A. Maddocks, and F. Geiser. 2000. Seasonal use of torpor by free-ranging Australian owlet-nightjars (*Aegotheles cristatus*). Physiological and Biochemical Zoology 73:613-620.

Choi I.-H., Y. Cho, Y.K. Oh, N.-P. Jung, and H.-C. Shin. 1998. Behavior and muscle performance in heterothermic bats. Physiological Zoology 71:257-266.

Cooper C.E., G. Kortner, M. Brigham, and F. Geiser. 2008. Body temperature and activity patterns of free-living Laughing Kookaburras: the largest kingfisher is heterothermic. The Condor 110(1):110-115.

Fletcher Q.E., R.J. Fisher, C.K.R. Willis, and R.M. Brigham. 2004. Free-ranging common nighthawks use torpor. Journal of Thermal Biology 29:9-14.

Geiser F. 2004. The role of torpor in the life of Australian arid-zone mammals. Australian Mammalogy 26:125-134.

Geiser F., N. Goodship, and C.R. Pavey. 2002. Was basking important in the evolution of mammalian endothermy? Naturwissenschaften 89:412-414.

Gessaman J.A., and C.E. Folk. 1969. Body temperature and thermal conductance of the snowy owl. Physiologist 12:234.

Hackett S.J., R.T. Kimball, S. Reddy, R.C.K. Bowie, E.L. Braun, J.L. Chojnowski, W.A. Cox, K.-L. Han, J. Harshman, C.J. Huddleston, B.D. Marks, K.J. Miglia, W.S. Moore, F.H. Sheldon, D.W. Steadman, C.C. Witt, and T. Yuri. 2008. A phylogenetic study of birds reveals their evolutionary history. Science 320:1763-1768.

Hall V., and B.D. Goldman. 1980. Effects of gonadal steroid hormones on hibernation in the Turkish hamster (*Mesocricetus brandti*). Journal of Comparative Physiology B 135:107-114.

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

Hohtola E., A. Pyörnilä, and H. Rintamäki. 1994. Fasting endurance and cold resistance without hypothermia in a small predatory bird: the metabolic strategy of Tengmalm's owl, *Aegolius funereus*. Journal of Comparative Physiology 164:130-437.

Hudson J.W. 1978. Shallow, daily torpor: a thermoregulatory adaptation. Pp. 67-108 in L.C.H. Wang, and J.W. Hudson, eds. Strategies in the cold: natural torpidity and thermogenesis. Academic Press, New York.

IUPS. 2003. Glossary of terms for thermal physiology Journal of Thermal Biology 28:77-106.

Kemp A.C. 2005a. African Scops-Owl *Otus senegalensis* Pp. in P.A.R. Hockey, W.R.J. Dean, and P.G. Ryan, eds. Roberts - Birds of Southern Africa, VIIth ed. The Trustees of the John Voelcker Book Fund, Cape Town.

Kemp A.C. 2005b. Pearl-spotted Owlet *Glaucidium perlatum* Pp. in P.A.R. Hockey, W.R.J. Dean, and P.G. Ryan, eds. Roberts - Birds of Southern Africa, VIIth ed. The Trustees of the John Voelcker Book Fund, Cape Town.

Kenward R.E. 2000. A manual of wildlife radio tagging. Academic Press, New York.

Körtner G., R.M. Brigham, and F. Geiser. 2000. Winter torpor in a large bird. Nature 407:318.

Körtner G., R.M. Brigham, and F. Geiser. 2001. Torpor in free-ranging tawny frogmouths (*Podargus strigoides*). Physiological and Biochemical Zoology 74:789-797.

Lane J.E., R.M. Brigham, and D.L. Swanson. 2004. Daily torpor in free-ranging whip-poor-wills (*Caprimulgus vociferus*). Physiological and Biochemical Zoology 77:297-304.

Lee T.M., K. Pelz, P. Licht, and I. Zucker. 1990. Testosterone influenences hibernation in golden-mantled ground squirrels. American Journal of Physiology 259:R760-R767.

Ligon J.D. 1969. Some aspects of temperature relations in small owls. Auk 86:458-472.

Lovegrove B.G. 1993. The living deserts of southern Africa. Fernwood Press, Vlaeberg.

Lovegrove B.G. 2005. Seasonal thermoregulatory responses in mammals. Journal of Comparative Physiology B 175:231-247.

Maclean G.L. 1993. Roberts' birds of southern Africa. John Voelcker Bird Book Fund, Cape Town.

Malan A. 1996. The origins of hibernation: a reappraisal. Pp. 1-6 in F. Geiser, A.J. Hulbert, and S.C. Nicol, eds. Adaptations to the cold: Tenth International Hibernation Symposium. University of New England Press, Armidale.

Marks J.S., R.J. Cannings, and H. Mikkola. 1991. Family Strigidae (typical owls). Pp. 76-241 in J. del Hoyo, A. Elliot, and J. Sargatal, eds. Handbook of the birds of the world. Vol. 5. Barn-owls to hummingbirds. Lynx Edicions, Barcelona.

McKechnie A.E., R.A.M. Ashdown, M.B. Christian, and R.M. Brigham. 2007. Torpor in an Afrotropical caprimulgid, the Freckled Nightjar (*Caprimulgus tristigma*). Journal of Avian Biology 38:261-266.

McKechnie A.E., and B.G. Lovegrove. 2002. Avian facultative hypothermic responses: a review. The Condor 104:705-724.

McKechnie A.E., and B.G. Lovegrove. 2003. Facultative hypothermic responses in an Afrotropical arid-zone passerine, the red-headed finch (*Amadina erythrocephala*). Journal of Comparative Physiology B 173:339-346.

McKechnie A.E., and B.O. Wolf. 2004a. The energetics of the rewarming phase of avian torpor. Pp. 265-273 in B.M. Barnes, and H.V. Carey, eds. Life in the cold: evolution, mechanisms, adaptation and application. 12th International Hibernation Symposium. Institute of Arctic Biology, University of Alaska Fairbanks, Alaska, U.S.A.

McKechnie A.E., and B.O. Wolf. 2004b. Solar radiation and the energetic cost of rewarming from torpor. Pp. 63-70 in B.M. Barnes, and H.V. Carey, eds. Life in the cold: evolution, mechanisms, adaptation and application. 12th International Hibernation Symposium. Institute of Arctic Biology, University of Alaska Fairbanks, Alaska, U.S.A.

Merola-Zwartjes M., and J.D. Ligon. 2000. Ecological energetics of the Puerto Rican tody: heterothermy, torpor and intra-island variation. Ecology 81:990-1002.

Meyer J., J. Steinhauser, F. Jeltsch, and R. Brandl. 2007. Large trees, acacia shrubs, and the density of *Thallomy nigricauda* in the thornveld savannah of South Africa Journal of Arid Environments 68:363-370.

Mezhzherin V.A. 1964. Dehnel's phenomenon and its possible explanation. Acta Theriologica 8:95-114.

Mzilikazi N., and B.G. Lovegrove. 2002. Reproductive activity influences thermoregulation and torpor in pouched mice, *Saccostomus campestris*. Journal of Comparative Physiology B 172:7-16.

Mzilikazi N., B.G. Lovegrove, and D.O. Ribble. 2002. Exogenous passive heating during torpor arousal in free-ranging rock elephant shrews, *Elephantulus myurus*. Oecologia 133:307-314.

Reinertsen R.E. 1996. Physiological and ecological aspects of hypothermia. Pp. 125-157 in C. Carey, ed. Avian energetics and nutritional ecology. Chapman & Hall, New York.

Rismiller P.D., and M.W. McKelvey. 1996. Sex, torpor and activity in temperate climate echidnas. Pp. 23-30 in F. Geiser, A.J. Hulbert, and S.C. Nicol, eds. Adaptations to the

Cold: Tenth International Hibernation Symposium. University of New England Press, Armidale.

Schleucher E. 2001. Heterothermia in pigeons and doves reduces energetic costs. Journal of Thermal Biology 26:287-293.

Schleucher E. 2004. Torpor in birds: taxonomy, energetics and ecology. Physiological and Biochemical Zoology 77:942-949.

Schleucher E., and R. Prinzinger. 2006. Heterothermia and torpor in birds: highly specialized physiological ability or just deep “nocturnal hypothermia”? — The limitations of terminology. Acta Zoologica Sinica 52 (suppl.):393-396.

Sibley C.G., and J.E. Ahlquist. 1990. Phylogeny and classification of birds. Yale University Press, New Haven.

Song X., G. Körtner, and F. Geiser. 1997. Thermal relations of metabolic rate reduction in a hibernating marsupial. American Journal of Physiology 273:R2097 - R2104.

Thouzeau C., C. Duchamp, and Y. Handrich. 1999. Energy metabolism and body temperature of barn owls fasting in the cold. Physiological and Biochemical Zoology 72:170-178.

Willis C.K.R. 2007. An energy-based body temperature threshold between torpor and normothermia for small mammals. Physiological and Biochemical Zoology 80:643-651.

Willis C.K.R., and R.M. Brigham. 2003. Defining torpor in free-ranging bats: experimental evaluation of external temperature-sensitive radio-transmitters and the concept of active temperature. Journal of Comparative Physiology B 173:379-389.

Withers P.C. 1992. Comparative animal physiology. Saunders College Publishing, Fort Worth.

CHAPTER 3:

AVIAN SEASONAL METABOLIC ADJUSTMENTS IN A SUBTROPICAL DESERT: WINTER DOWN-REGULATION OF BASAL METABOLISM

Introduction

Flexibility in phenotypic traits that determine maintenance metabolic requirements has been predicted to be very important in temporally heterogeneous environments where ecological conditions change frequently within an organism's life span (Pigliucci 2001; Piersma and Drent 2003). Seasonal adjustments in avian basal metabolic rate (BMR), summit metabolism (M_{sum}), and other thermoregulatory parameters are well documented (Dawson and Marsh 1989; Cooper and Swanson 1994; Maddocks and Geiser 2000; Liknes et al. 2002; Dawson 2003; Swanson and Liknes 2006). However, our current understanding of the functional significance of these adjustments in free-living birds is largely based on studies of small species inhabiting high northern latitudes [reviewed in Swanson (in press) and McKechnie (2008)].

In high-latitude Holarctic environments (i.e. North America and Eurasia), where seasonal weather changes are pronounced and winters are often extremely cold, many birds have elevated thermoregulatory demands during the coldest times of the year (Swanson and Liknes 2006). As a result, small birds become more cold tolerant in winter, through up-regulation of M_{sum} (the maximum resting thermogenic metabolic rate) and/or improved shivering endurance (Dawson and Marsh 1988; Liknes and Swanson 1996; Swanson and Liknes 2006). In most cases, seasonal metabolic adjustments related to cold tolerance also involve elevated winter BMR (i.e., the minimum metabolic rate of a resting, normothermic endotherm at thermoneutrality) (Swanson and Olmstead 1999; Liknes et al. 2002). Winter BMR elevations have been shown in ~ 80% of acclimatization studies, and increases in BMR have been observed in all studies involving short-term acclimation to low temperatures under laboratory conditions (Williams and Tieleman 2000; Tieleman et al. 2003b; Klaassen et al. 2004; Vezina et al. 2006; McKechnie et al. 2007; reviewed by McKechnie 2008).

BMR adjustments in response to cold temperatures seem to reflect changes in the maintenance costs of the metabolic machinery that are required to achieve peak metabolic performance (Swanson in press), such as elevated heat production or improved shivering thermogenesis, i.e. the energy demand hypothesis (Williams and Tieleman 2000). According to this view, an increased demand for shivering, for instance, requires elevated metabolic rates of pectoral muscles, larger organs associated with increased digestion rates and energy assimilation, and/or a higher metabolic intensity of such organs (Daan et al. 1990; Williams and Tieleman 2000; Tieleman et al. 2003a). The up-regulation of such metabolic machinery is thought to result in higher basal “idling” costs, which contributes to the BMR elevations after cold acclimation and winter acclimatization (Piersma 2002).

However, BMR is not always elevated during winter acclimatization, and a number of species show seasonally stable (Rising and Hudson 1974; Dawson et al. 1983; Ambrose and Bradshaw 1988; O'Connor 1996; Maldonado et al. 2009) or even reduced winter BMR (Maddocks and Geiser 2000). It has been proposed that climate and latitude are correlated with metabolic adjustments and that the direction and magnitude of seasonal BMR adjustments are different in regions where winter temperatures are milder (Swanson 1991; Maddocks and Geiser 2000). Most of the current data on the metabolic adjustments associated with seasonal acclimatization were obtained from the Holarctic region, above 40°N (West 1972; Swanson 1990, 1991; Cooper and Swanson 1994; Swanson and Weinacht 1997; Liknes et al. 2002). With the exception of a few studies from milder climates (Ambrose and Bradshaw 1988; Maddocks and Geiser 2000), seasonal metabolic adjustments in species from sub-tropical and tropical latitudes remain largely unknown. Although the latter regions do not experience the severe cold winters of the Holarctic regions, they can nonetheless be highly seasonal in terms of rainfall, and may experience unpredictable and variable precipitation patterns associated with phenomena such as the EL Niño Southern Oscillation (ENSO) (Stone et al. 1996). Since BMR has been shown to be correlated with variation in precipitation and temperature (White et al. 2007), it seems likely that phenotypic responses in BMR vary with climate and environmental conditions. It could be argued that if the maintenance costs associated with a high BMR exceed the benefits that it might provide, BMR should be reduced to the lowest affordable maintenance level (i.e. adaptive modulation hypothesis, see Karasov 1992).

The limited data on seasonal metabolic adjustments in Australasian and Afrotropical birds reveal that at least two species, the Rock Kestrel (*Falco rupicolis*) (Bush et al. 2008) and Australian Silver-eye (*Zosterops lateralis*) (Maddocks and Geiser 2000) show reduced winter BMR (12.3% and 20.1% compared to summer values, respectively). Although both these studies involved captive birds held in outdoor aviaries, these data suggest that winter reductions in maintenance energy requirements may be important components of seasonal acclimatization in some species inhabiting milder environments. Winter reductions in BMR may facilitate decreased energy demands when scarce and/or unpredictable food resources coincide with mild to cool temperatures in natural habitats. It is therefore possible that seasonal metabolic adjustments in species inhabiting tropical and subtropical regions reflect the requirement for energy conservation in winter, rather than improved cold tolerance. However, the fact that the above mentioned species showed winter reductions in BMR under captive conditions where they received food *ad libitum* (Maddocks and Geiser 2000; Bush et al. 2008), suggests that these adjustments are not the result of food shortages, but rather an adaptive response to reduce overall energy demands to the lowest affordable level when the metabolic requirements for reproduction outside the breeding season, are not needed (i.e. the adaptive modulation hypothesis). Several avian feeding guilds, such as nocturnal insectivores, may benefit from winter reductions BMR since they are more likely to experience energetic bottlenecks during winter associated with reduce prey activity levels.

The objective of this study was to investigate the magnitude and direction of seasonal BMR adjustments in five bird species resident year-round in the Kalahari Desert of southern Africa: the nocturnal African Scops-Owl (*Otus senegalensis senegalensis*), crepuscular/nocturnal Pearl-spotted Owlet (*Glaucidium perlatum licua*), and diurnal Fork-tailed Drongo (*Dicrurus adsimilis apivorus*), Crimson-breasted Shrike (*Laniarius atrococcineus*) and White-browed Sparrow-Weaver (*Plocepasser mahali mahali*). The Kalahari Desert is located within the sub-tropics and experiences seasonal changes in night-time air temperature and rainfall (Lovegrove 1993). I predicted that the magnitude of seasonal adjustment should vary between species depending on activity period; whereas diurnal species rely on resting thermogenic metabolic heat production during the night, nocturnal species such as the African Scops-Owl are active at this time and can at least partly thermoregulate using heat generated as a by-product of activity. Thus, I expected differences between diurnal and nocturnal species in the extent to which BMR is adjusted across seasons. In this chapter I also present an analysis of global variation in patterns of avian seasonal BMR adjustments.

Materials and methods

Study site

This study took place in Molopo Nature Reserve (MNR; 25° 47’ S, 22° 56’ E) at an elevation of 1000 m.a.s.l. in the Northwest Province of South Africa, during June - August 2007 (austral winter) and January - mid-March 2008 (austral summer). This reserve falls within the Kalahari Desert region, where the climate varies seasonally between cool and dry winters (mean daily range = 3.2°C to 27.6°C), and summers with high daytime air temperature maxima (mean daily range = 18.6°C to 32.5°C) and unpredictable rainfall patterns (Lovegrove 1993). The mean ± SD annual rainfall recorded at Molopo Nature Reserve over a 50-year period was 332 ± 105 mm, falling mainly between December and April (Meyer et al. 2007).

Air temperature measurements

Air temperature (T_a) was measured in the study area using two temperature-sensitive data loggers (iButton Thermochron, Dallas Semiconductor, Dallas, U.S.A.). The iButtons were housed in ventilated polystyrene cups suspended in the shade ~ 2 m above the ground, at two sites ~ 6 km apart. Before the study the iButtons were calibrated in a temperature-controlled water bath (model ME, Julabo Labortechnik, Seelbach, Germany), using a mercury thermometer (resolution = 0.2°C) with an accuracy traceable to the US National Bureau of Standards, over the approximate T_a range experienced at the study site during winter.

Terrestrial arthropod abundance

In the Kalahari desert a large proportion of the diets of the five study species consist of terrestrial arthropods (Hockey et al. 2005). It is generally considered that the availability of terrestrial arthropods is greatly reduced in winter, especially during cold nights. To verify that this was the case at MNR, I investigated the seasonal availability of terrestrial invertebrates during winter and summer, using pitfall traps. Two trapping grids (3 m x 3 m), consisting of 9 pitfall traps each were set ~ 1 km apart. To evaluate circadian variation in invertebrate abundance, I collected all invertebrates from the traps at sunrise and sunset. The traps were active for a period of 20 days and nights during both winter (July - August 2007) and summer (January - February 2008). All arthropods captured were identified to order, and their relative abundance compared between night and day, and among seasons.

Study birds

Seasonal metabolic measurements were obtained within 24 h after capture from wild-caught birds in a field laboratory at the study site. All the birds were captured during their active phases using mist nets or spring traps baited with Tenebroid beetle larvae (mealworms). Owls were typically lured into nets using vocalization playback. After the birds were captured they were weighed using a Pesola® scale (accurate to 0.5 g), and age and moult status were determined. Sexes of the study species could not be distinguished in a reliable manner, although sexes of owls were distinguished by the females’ softer and higher pitched calls (Hockey et al. 2005) when they responded to call playback before trapping. Juveniles and adults showing active brood patches were not used in laboratory experiments. Each bird was ringed with an aluminium band (SAFRING) for identification and kept individually in an indoor cages (0.125 m^3) constructed from shade cloth for a maximum of two days when not used in experiments. During this time they were fed mealworms *ad libitum*, but food was withheld for at least five hours prior to commencement of metabolic measurements to ensure post absorptive conditions. All birds were released within 1–2 days of capture.

Body temperature measurements

Body temperature (T_b) was measured during metabolic measurements using a lubricated fine-gauge Teflon-coated Cu-Cn thermocouple (IT-18, Physitemp, Clifton NJ) inserted into the cloaca to a depth at which a slight withdrawal did not result in a change in the temperature reading (i.e. ~ 2 cm). The thermocouple was secured by attaching the wire to the feathers immediately behind the cloaca, using adhesive tape and a wire paperclip. Body temperature data were discarded if there was any evidence that the thermocouple had become dislodged during measurements. Data from the thermocouples were digitized using a TC-1000 thermocouple meter (Sable Systems, Las Vegas, NV, USA).

Oxygen consumption and carbon dioxide production measurements

Oxygen consumption ($\dot{V}_{O_2}$) and carbon dioxide production ($\dot{V}_{CO_2}$) were measured using a portable respirometry system and temperature-controlled environmental chamber. Birds were placed in suitably-sized 1.69 – 1.9L plastic chambers within an insulated environmental chamber, constructed by lining the interior of a 66.2L cooler box with copper tubing, through which water was pumped by a temperature-controlled circulator (model ME, Julabo Labortechnik, Seelbach, Germany). Each bird perched above a stainless wire mesh screen placed at a height to allow normal perching postures. Only two respirometry chambers could be placed within the environmental chamber at a time. Air in the environmental chamber was mixed using a small electric fan. Ambient temperature within each respirometry chamber was measured using a 21-gauge CU-CN (IT-18, Physitemp, Clifton NJ) thermocouple and a TC-1000 thermocouple meter (Sable Systems, Las Vegas, NV, USA).

Atmospheric air from outside the building and drawn through a filter (model F3000-8G, CKD Corporation, China), was supplied to the respirometry chambers through Bev-A-Line tubing (Thermoplastic Processes Inc.,Warren, NJ) using an electrical air pump (D7 SE, Charles Austen Pumps, Surrey, UK). The flow rate through each respirometry chamber was regulated using one FMA-series mass flow controller (Omega, Bridgeport, NJ, USA) per chamber. The mass flow controllers were calibrated before the commencement of each season’s metabolic tests using a 1L soap bubble flow meter (Baker and Pouchot 1983). Flow rates of 1 – 2 $L.min^{-1}$ per minute were used throughout measurements, resulting in 99% equilibration times of 4 - 9 min, calculated using the equation of (Lasiewski et al. 1966).Excurrent air from each respirometry chamber and a control channel (atmospheric air subsampled downstream of the filter and pump) was sequentially subsampled using a TR-RM8 Respirometry Multiplexer (Sable Systems). Baseline O_2 and CO_2 concentrations were obtained from the control channel for 15 minutes at 1 h intervals. The CO_2 concentration of subsampled air was then measured using a LI-7000 CO_2/H_2O analyzer (Li-Cor, Lincoln, NE, USA). The latter analyzer was calibrated regularly using dry CO_2-free air and a certified span gas containing 1513.0 p.p.m. CO_2. (AFROX, South Africa). By adjusting the flow rate in each respirometry chamber, the dewpoint of excurrent air was maintained well below air temperature. The air samples then left the CO_2/H_2O analyzer, and water vapour and CO_2 were scrubbed using a silica gel/soda lime/silica gel column. The fractional O_2 concentration was then determined using a FC-10a oxygen analyzer (Sable Systems, Las Vegas, NV). Outputs from these two gas analyzers and the thermocouple meter were digitized using a Universal Interface II (Sable Systems) and recorded on a personal computer using EXPEDATA data acquisition software (Sable Systems), with a sampling interval of 15s.

Experimental protocol

All measurements of metabolic rate were obtained from post-absorptive birds, during the rest-phase of their circadian cycles in darkened chambers. The approximate sunrise to sunset times were approximately 07h15 to 17h45 during winter and 06h15to 19h15 during summer. Metabolic measurements for the two owl species were carried out during the day, since both are mainly nocturnal, although Pearl-spotted Owlets are sometimes active during the day in winter. Metabolic measurements from the three diurnal passerines were obtained at night. Each bird was placed in a respirometry chamber within the environmental chamber approximately one hour before sunrise (nocturnal species) and sunset (diurnal species), at which point the cloacal thermocouples were inserted and secured .We ensured that the birds settled down within the chambers and then started recording $\dot{V}_{O_2}$ and $\dot{V}_{CO_2}$ data at least an hour after sunset or sunrise. Measurements lasted at least six hours for each individual, and were terminated an hour before the next sunset or sunrise. Any drift in the baseline fractional [O2] or [CO2] was corrected for using the appropriate regression analyses in EXPEDATA (Sable Systems, Las Vegas, NV, USA). Resting metabolic rate (RMR) was calculated from steady state traces of $\dot{V}_{O_2}$ in EXPEDATA, with the lowest 10 min mean $\dot{V}_{O_2}$ over the test period considered to be RMR, following Liknes et al. (2002). All $\dot{V}_{O_2}$ and $\dot{V}_{CO_2}$ values were corrected to STPD.

To obtain a reliable estimate of BMR requires that RMR is measured within the thermal neutral zone (TNZ). Thus during each season, the first two or three individuals of each species caught were subjected to a ramped T_a profile during each test. An individual bird experienced at least three T_as, between 5° and 35°C, during a single measurement session, lasting no longer than 10 h. Least-squares linear regression models were fitted to RMR vs. T_a, and the lower limits of thermoneutrality (T_{lc}) were then estimated from the intercepts of the regression lines and the lowest observed RMR values. Because of the small sample sizes for my T_{lc} estimates, which were between 26° and 29°C for all five species, I measured metabolic rate at a T_a equivalent to 1° to 2°C higher than the estimated T_{lc} of each species, to ensure that all BMR measurements took place in the TNZ.

Data analyses

$\dot{V}_{O_2}$ was calculated using the relevant equation in Withers (1977) and $\dot{V}_{CO_2}$ using equation 3 in Walsberg and Wolf (1995). Respiratory exchange ratios were determined as $\dot{V}_{CO_2}/\dot{V}_{O_2}$ and averaged 0.88 ± 0.06 (mean ± SD) during the study. Gas exchange measurements were converted to metabolic rates (W) using the thermal equivalence data from table 4-2 in Withers (1992). This approach assumes that only carbohydrates and lipids are metabolized, and a maximum error of 6% is associated with protein metabolism (Walsberg and Wolf 1995).

Seasonal data were analyzed separately for each species. I used analyses of variance (ANOVA) to test for seasonal changes in body mass (M_b) and T_b and BMR. In the case of significant seasonal changes in M_b, I also performed an analysis of co-variance (ANCOVA) on total BMR, with M_b as a covariate. In this manner I could distinguish seasonal changes in BMR reflecting body mass changes, from adjustments in mass-specific BMR. In all species, a small number of individuals (one to four) were undergoing light-primary moult during summer, but I found no statistical difference between mass-specific BMR of moulting and non-moulting birds, and summer BMR data were thus pooled for tests against winter BMR. With the exception of two African Scops-Owls that were trapped during both seasons, all the seasonal metabolic measurements from the remaining species represent different individuals. All statistical procedures were carried out in STATISTICA version 7.0 (StatSoft, Inc. Tulsa, OK).

Currently, there are too few data to rigorously examine potential correlates of zoogeographical variation in seasonal BMR adjustments. Instead, I opted to compare the magnitude and direction of these adjustments among hemispheres, and used both conventional and phylogenetically-independent analysis of variance (PI-ANOVA) to test differences. I included winter/summer BMR ratios from the five species in this study and an additional 15 species from the literature (Table 1), and used only data that represented mass-specific BMR adjustments after acclimatization. All seasonal BMR ratios were arcsine-transformed before analyses. I constructed a phylogeny based on Sibley and Ahlquist's (1990) average linkage (UPGMA) phylogeny using PD TREE (Garland et al. 1993) (Figure 1). PI ANOVA was performed using the program PDANOVA on 1000 tip values simulated by PDSIMUL (Garland 1993). The significance of conventional *F*-statistics was tested against the critical *F*-values for $\alpha = 0.05$ (95% percentile) of the PI null *F*-distributions. I generated PI null *F*-distributions using four evolutionary models, following McKechnie and Wolf (2004): (1) gradual brownian with bounds, correlation set to that obtained from the regression of independent contrasts of the variables; (2) gradual brownian with bounds, correlation set to zero; (3) speciational brownian with bounds, correlation set to that obtained from the regression of independent contrasts of

Table 1: Avian species in which seasonal adjustments in mass-specific BMR have been investigated. Body mass (Mb), winter BMR/summer BMR (W/S) and hemisphere (H; N for northern and S for southern) of acclimatization are provided.

Species	**H**	**Mb (g)**	**W/S**	**Reference**
Long-eared Owl (*Asio otus*)	N	244	1.072	1
Monk Parakeet (*Myiopsitta monachus*)	N	83.1	0.756	2
Common Redpoll (*Acanthis flammea*)	N	14.6	1.308	3
Black-capped Chickadee (*Parus atricapillus*)	N	11.9	1.000	4
Black-capped Chickadee (*Parus atricapillus*)	N	13.1	1.144	5
White-crowned Sparrow (*Zonotrichia leucophrys*)	N	26.3	1.326	6
Downy Woodpecker (*Picoides pubescens*)	N	24.1	1.398	7
Dark-eyed Junco (*Junco hyemalis*)	N	18.6	1.092	8
White-breasted Nuthatch (*Sitta carolinensis*)	N	19.4	1.333	7
House Finch (*Carpodacus mexicanus*)	N	20.1	0.957	9
American Goldfinch (*Carduelis tristis*)	N	13.7	1.097	10
Chinese Bulbul (*Pyconotus sinensis*)	N	29.4	1.174*	11
Brambling (*Fringilla montifringilla*)	N	24.1	0.982	12
Rock Kestrel (*Falco rupicolis*)	S	214	0.877	13
Superb Fairy-wren (*Malurus cyaneus*)	S	9.05	1.117	14
Australian Silver-eye (*Zosterops lateralis*)	S	11.1	0.799	15

* = significant variation in body mass between upper and lower BMR values.
References: 1. Wijnandts (1984), 2. Weathers and Caccamise (1978), 3. Pohl and West (1973), 4. Rising and Hudson (1974), 5. Cooper and Swanson (1994), 6. Southwick (1980), 7. Liknes and Swanson (1996), 8. Swanson (1991), 9. O'Connor (1995), 10. Dawson and Carey (1976), 11. Zheng et al. (2008), 12. Pohl (1971), 13. Bush et al. (2008), 14. Lill et al. (2006), 15. Maddocks and Geiser (2000).

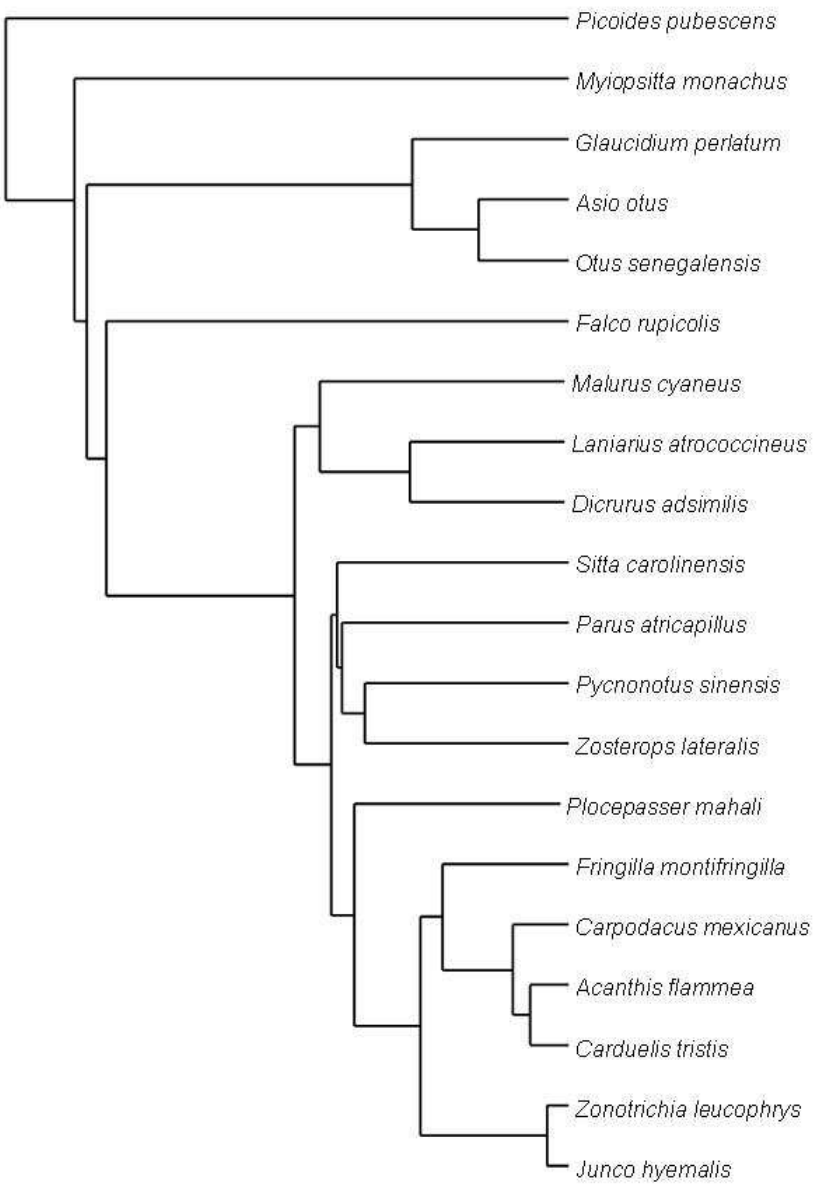

Figure 1: Phylogeny of 20 avian species in which seasonal adjustments in mass-specific basal metabolic rate have been investigated, constructed using the phylogenetic data from the five species in this study and an additional 15 species from the literature (Table 1). The total height of the phylogeny from the base node to the branch tips is 26.3 ΔT_{50}H units (Sibley and Ahlquist 1990).

the variables; and (4) speciational brownian with bounds, correlation set to zero. For bounds I used minimum and maximum winter/summer BMR ratios of 0.1 and 2.0, respectively

Results

Rainfall and temperature

From November 2007 to March 2008 (summer) more than 500 ml of rain was recorded at MNR, whereas in winter (2007) 15 mm of rain was recorded on 4 June 2007. The mean daily minimum T_a in winter was 3.2°C (lowest T_a = -7.6°C), compared to 18.6°C in summer (lowest T_a = 15.6°C) (Fig. 2A). The mean daily maximum T_a in winter was 27.6°C (highest T_a = 36.1°C), compared to 32.5°C in summer (highest T_a = 40.5°C) (Fig. 2A).

Terrestrial arthropod abundance

Insects comprised the majority of the terrestrial arthropods sampled in the pit-fall traps at MNR during both seasons (41% Coleoptera and 35% Hymemoptera), whereas the remaining orders were represented mainly by Scorpiones and Araneae and Isopoda. Both nocturnal and diurnal terrestrial arthropods were substantially more abundant during the summer 2008 than during winter 2007, although nocturnal arthropods underwent the greatest seasonal change in abundance, representing a reduction of ~ 82% (Fig. 2B).

Body mass

Significant changes in seasonal M_b were observed only in African Scops-Owls (Table 2), and the mean M_b of the winter sample was 12% lower than in summer (ANOVA, $F_{1,12} = 11.57$, $P < 0.01$).

Body temperature

All birds remained normothermic during metabolic measurements and none of the study species

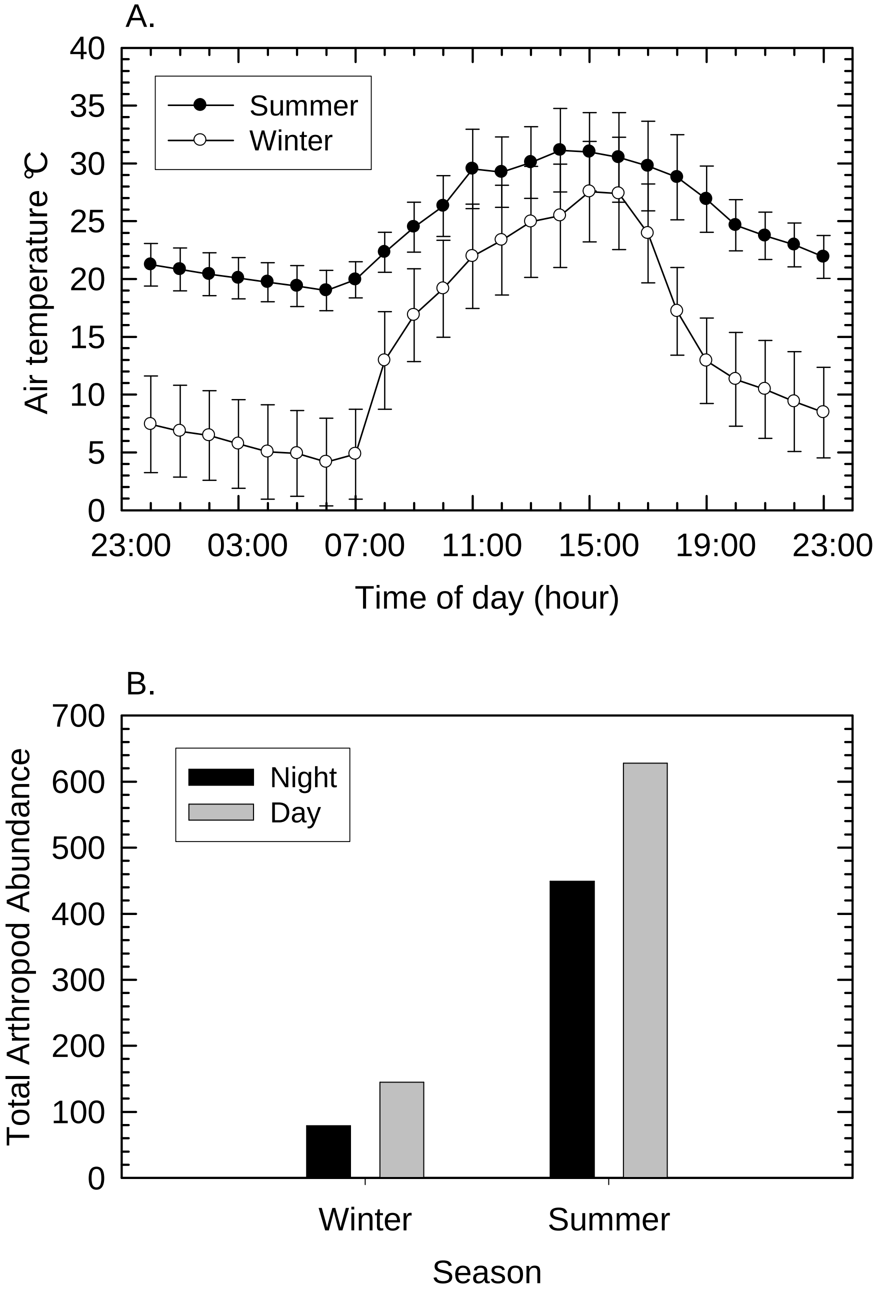

Figure 2: A.) Mean hourly (± SD) air temperature and B.) terrestrial arthropods captured in 18 pitfall traps over 20 days and nights, at Molopo Nature Reserve from July to late August 2007 (austral winter) and January to early March 2008 (austral summer).

showed any seasonal changes in their set point T_b (Table 2), although I did not obtain sufficient T_b-data from the two owl species during metabolic measurements to perform statistical analysis

Basal metabolic rate

In all five species BMR was lower in winter than in summer. Mass-specific BMR was significantly lower in winter in the African Scops-Owl (*Otus senegalensis*; 23%), Pearl-spotted Owlet (*Glaucidium perlatum*; 30%), Fork-tailed Drongo (*Dicrurus adsimilis*; 35%), Crimson-breasted Shrike (*Laniarius atrococcinneus*; 29%), and White-browed Sparrow-Weaver (*Plocepasser mahali*; 17%) (Table 2). The magnitude of seasonal adjustments in total BMR was generally consistent with mass-specific BMR adjustments (Table 2). In African Scops-Owls, however, the winter BMR reductions were largely explained by the 12% M_b reduction that occurred during winter (Figure 3), and total BMR was not significantly different after correcting for M_b (ANCOVA, $F_{1,11} = 2.100$, $P = 0.175$).

Global variation in seasonal BMR adjustments

Both conventional and PI analyses indicated that the direction of BMR adjustments differs significantly between northern and southern hemisphere species (Table 3). On average, southern Hemisphere species down-regulated BMR by 19% during winter, whereas northern Hemisphere species on average up-regulated BMR by 13% in winter. However, direct comparisons between Hemispheres are confounded by latitude and climate variables, since the majority of data from the southern Hemisphere are from mild to warm middle latitude regions, whereas data from the northern Hemisphere regions are from cold high latitude regions.

Table 2: Seasonal changes in body temperature, body mass, total basal metabolic rate (T BMR) and mass-specific basal metabolic rate (MS BMR) of African Scops-Owls (*Otus senegalensis*), Pearl-spotted Owlet (*Glaucidium perlatum*), Fork-tailed Drongo (*Dicrurus adsimilis apivorus*), Crimson-breasted Shrike (*Laniarius atrococcineus*) and White-browed Sparrow-Weaver (*Plocepasser mahali mahali*) in Molopo Nature Reserve, South Africa. Sample sizes are provided in parentheses. For each parameter, the *F*-ratio and probability estimated from an analysis of variance (ANOVA) is provided.

Species	**Summer**	**Winter**	***F***	***P***
African Scops-Owl				
Body temperature (°C)	39.3 (1)	38.7 ± 0.4 (2)	-	
Body mass (g)	62.2 ± 4.1 (7)	55.4 ± 3.7 (7)*	$F_{1,12}$ = 11.570	.005
T BMR (W)	0.411 ± 0.094 (7)	0.280 ± 0.042 (7)*,[a]	$F_{1,12}$ = 13.109	.004
MS BMR (mW g^{-1})	6.584 ± 1.330 (7)	5.045 ± 0.617 (7)*	$F_{1,12}$ = 8.228	.014
Pearl-spotted Owlet				
Body temperature (°C)	39.3 ± 0.3 (3)	39.6 (1)	-	
Body mass (g)	66.4 ± 4.8 (5)	70.3 ± 5.7 (3)	$F_{1,6}$ = 1.100	.335
T BMR (W)	0.526 ± 0.107 (5)	0.383 ± 0.059 (3)	$F_{1,6}$ = 5.505	.057
MS BMR (mW g^{-1})	7.881 ± 1.142 (5)	5.496 ± 1.132 (3)*	$F_{1,6}$ = 8.940	.024
Fork-tailed Drongo				
Body temperature (°C)	38.6 ± 0.4 (6)	38.6 ± 0.7 (6)	$F_{1,10}$ = 0.000	.989
Body mass (g)	44.8 ± 2.6 (8)	42.6 ± 4.0 (7)	$F_{1,13}$ = 1.670	.219
T BMR (W)	0.424 ± 0.107 (8)	0.266 ± 0.072 (7)*	$F_{1,13}$ = 17.075	.001
MS BMR (mW g^{-1})	9.425 ± 2.035 (8)	6.164 ± 1.215 (7)*	$F_{1,13}$ = 13.135	.003
Crimson-breasted Shrike				
Body temperature (°C)	38.6 ± 0.3 (5)	38.0 ± 0.8 (5)	$F_{1,8}$ = 3.380	.103
Body mass (g)	43.0 ± 2.8 (6)	41 ± 2.3 (5)	$F_{1,9}$ = 1.58	.240
T BMR (W)	0.398 ± 0.081 (6)	0.267 ± 0.050 (5)*	$F_{1,9}$ = 11.686	.008
MS BMR (mW g^{-1})	9.210 ± 1.444 (6)	6.520 ± 1.109 (5)*	$F_{1,9}$ = 12.793	.006

Table 2: continued

Species	**Summer**	**Winter**	***F***	***P***
White-browed Sparrow-Weaver				
Body temperature (°C)	38.8 ± 0.5 (4)	39.1 ± 1.2 (4)	$F_{1,6} = 0.310$	.601
Body mass (g)	40.6 ± 2.5 (7)	40.6 ± 3.4 (6)	$F_{1,11} = 0$	.950
T BMR (W)	0.346 ± 0.033 (7)	0.290 ± 0.049 (6)*	$F_{1,11} = 5.857$	.034
MS BMR (mW g^{-1})	8.573 ± 1.347 (7)	7.097 ± 0.636 (6)*	$F_{1,11} = 6.884$	.024

* = significant difference (ANOVA)

[a] = no significant difference after controlling for the effects of body mass using an ANCOVA.

Table 3: Results of conventional and phylogenetically independent ANOVA comparing arcsine-transformed winter/summer ratios of BMR ratios between northern and southern Hemisphere species. Critical values for *F* were calculated as the ninety-fifth percentile of the null distribution of *F* generated using PDSIMUL module of PDAP (Garland et al. 1993). Conventional critical values for F were obtained from (Zar 1999)

						Conventional:		**Gradual (Correlation):**		**Gradual:**		**Speciational (Correlation):**		**Speciational:**	
Source of variation	**n**	**SS**	**df**	**MS**	***F***	**Critical Value**	***P***	**Critical Value**	***P***	**Critical Value**	***P***	**Critical Value**	***P***	**Critical Value**	***P***
Hemisphere	20	0.729	1	0.729	14.63	4.450	<.001	4.961	<.001	4.836	<.001	6.366	0.002	6.124	0.005

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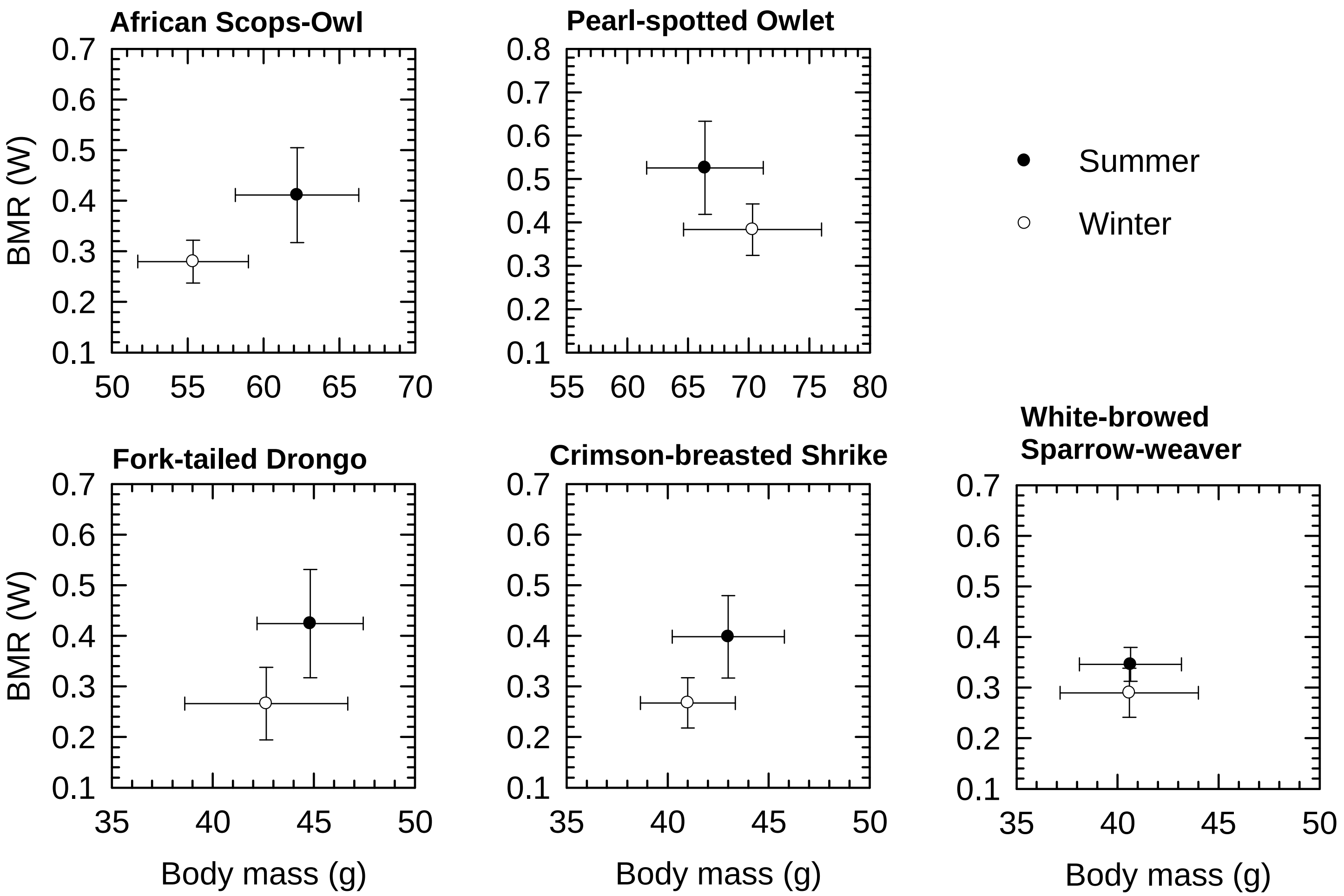

Figure 3: Mean ± SD total basal metabolic rate [BMR (W)] and body mass (g) measured in winter and summer in five bird species in Molopo Nature Reserve, South Africa.

Discussion

Winter BMR was substantially lower in all five species, providing further evidence that some birds reduce their maintenance metabolic requirements during colder months. Although winter BMR reductions have previously been reported in a small number of species, these studies involved individuals that were acclimatized under captive conditions. My data reveal that winter BMR reductions occur in wild populations of species from two orders and four families, suggesting that winter BMR down-regulation may be widespread in free-ranging birds in sub-tropical regions. The pattern observed contrasts with the winter metabolic up-regulation that typically occurs in northern hemisphere species, calling into question the functional significance of such seasonal adjustments.

I found no support for the idea that the magnitude or direction of seasonal BMR adjustments is related to the timing of activity; patterns were similar in diurnal and nocturnal species. Despite the fact that the diurnal species were periodically exposed to sub-zero temperatures while resting at night over the winter period, they also showed significant winter BMR reductions. These results indicate that the seasonal adjustments in BMR were not directly related to cold tolerance, suggesting that other factors must be involved in the winter BMR reductions. Overall, the thermoregulatory costs for species >40g are probably relatively low year round in the Kalahari Desert, since the seasonal change in average daily temperature was relatively small (~10°C), compared to regions in the Holarctic where seasonal temperature changes can exceed 30°C. The coldest temperatures that my study species experienced in MNR (−7°C) are significantly higher than the coldest temperatures birds experienced in the Holarctic (frequently below

−30°C). African Scops-Owls, for example, would expend between 2.5 and 3-times BMR at the minimum temperatures recorded in the Kalahari, which are below the metabolic rate elevations (3 to 8-times BMR) recorded for birds under cold exposure (Marsh and Dawson 1989; Saarela et al. 1995; Dutenhoffer and Swanson 1996), and much lower than the maximum metabolic rates that are usually achieved by birds during activity (Brackenbury 1984). Moreover, the study species at MNR only experienced the sub-zero temperatures for a few hours at night, which are normally followed by temperatures above 20°C during the day (Figure 2) that would require a low thermoregulatory input.

Avian resting metabolic rate is known to increase during moult, particularly in small species that undergo rapid moult (Lindström et al. 1993), and in such cases metabolic measurements may not reflective true minimum maintenance energy requirements. However, in other species the effects of feather synthesis on BMR are negligible (Brown and Bryant 1996; Buttemer et al. 2003), and similarly in the present study, BMR of individuals undergoing light moulting was not significantly different from non-moulting individuals. Only one out of eight Fork-tailed Drongos and two out of six Crimson-breasted Shrikes were undergoing moult. Since there was no statistical difference between the summer BMR of moulting and non-moulting individuals, I consider it unlikely that my results were affected by moult-associated metabolic costs.

In small mammals, seasonal changes in BMR are often explained by seasonal adjustments in M_b (Lovegrove 2005). In the present study, none of the three passerine species nor Pearl-spotted Owlets exhibited any significant seasonal changes in M_b, suggesting that their mass-specific BMR adjustments were largely the result of relative changes in body composition and/or the metabolic intensity of particular organs.

However, the winter sample size for Pearl-spotted Owlets was small (n = 3) and I could not control for possible sex differences of M_b in the three passerines. On the other hand, seasonal patterns of M_b in African Scops-Owls were consistent with the Dehnel effect observed in many small mammals, where M_b is reduced in winter to lower overall metabolic costs (Mezhzherin 1964; Lovegrove 2005). The African Scops-Owls used in the present study were mostly males (12 out of 14 individuals), since they responded to call play back giving low pitched calls before capture (see Chapter two).

All five of the study species breed mainly during summer in the Kalahari Desert when breeding activity is most likely to coincide with significant rainfall events (Maclean 1993). I excluded any individuals that showed signs of breeding activity, e.g. abdominal brood patch or smear marks around beak from feeding chicks. However, an overall increase in thyroid activity, stress hormone levels and/or increased energy demands of reproductive organs during the breeding seasons can result in increased metabolic rate (Siegel 1980; Wingfield and Farner 1993; Maddocks and Geiser 2000; Merola-Zwartjes and Ligon 2000). Such responses were especially likely to have occurred during the unusually wet conditions recorded at MNR during summer (rainfall from December 2007 to March 2008 was 150% of the mean annual rainfall for MNR).

A great deal of uncertainty exists as to the functional significance of BMR adjustments during seasonal acclimatization (Liknes et al. 2002). Moreover, when BMR flexibility in response to thermal acclimation, migration, intense exercise and starvation are also taken into account, it becomes clear that BMR adjustments are complex and diverse (see review by McKechnie 2008). Thus far, seasonal BMR adjustments have been associated most consistently with the “energy demand hypothesis”(Williams and

Tieleman 2000; Tieleman et al. 2003b), based on the notion that seasonal variation in support costs are needed to sustain the higher energy demand of nutritional organs and thermogenically active tissues during colder winter periods (Liknes et al. 2002). For instance, Swanson and Olmstead (1999) showed that over five consecutive winters, the magnitude of winter BMR elevations in three small species of passerine was best explained by the mean daily and minimum temperatures, 5 to 30 days preceding metabolic measurements. In the present study, however, the coldest period of the year did not elicit higher maintenance energy demands. My results suggest that BMR adjustments in the Kalahari are centred on increased demands for reproductive output during the breeding season, rather than thermostatic demands during winter (Swanson in press). Arguably, the need for large winter metabolic adjustments, such as the elevations in M_{sum} associated with enhanced cold tolerance (Liknes et al. 2002), are unnecessary for species resident in the Kalahari, and therefore reductions in BMR to the lowest affordable maintenance levels during winter are more feasible than in very cold environments. However, data on seasonal adjustments in M_{sum} and insulation, in addition to BMR, are necessary from future studies to more fully understand the functional significance of these flexible metabolic traits with respect to acclimatization.

All five species had lower BMR during both summer and winter than predicted by the allometric equation of McKechnie et al. (2006) for wild-caught birds (Table 4). However, the observed BMR values were consistent with the phylogenetically-independent predictions for desert birds (Tieleman and Williams 2000) (Table 4). Both mammals and birds that are resident in deserts show reduced maintenance metabolic requirements, believed to facilitate reduced energy requirements in resource-poor environments where primary production and precipitation are scarce and unpredictable (Lovegrove 2000; Tieleman and Williams 2000; Williams and Tieleman 2005); however, recent studies provided more consistent support for habitat temperature and annual range in temperature as predictors of BMR variation, and not primary production (White et al. 2007; Jetz et al. 2008). Furthermore, a reduced metabolic rate would also facilitate water savings in arid environments in terms of reducing water flux and total evaporative water loss (Tieleman and Williams 2000). The winter BMR reductions in my study were correlated with drier conditions and a reduction in terrestrial arthropod abundance, which comprise a major dietary component in all five species, although White-browed Sparrow-weavers are omnivorous and feed also on seeds (Hockey et al. 2005). It is not known to what extent these reductions in prey abundance affected the energetics of the five species.

Table 4: Mean (± SD) seasonal basal metabolic rate (BMR) of five species as percentages of the values predicted by allometric equations for wild-caught birds (McKechnie et al. 2006) and desert birds (Tieleman and Williams 2000) respectively. For all five species, summer and winter BMR was lower than the predicted values for wild-caught birds (McKechnie et al. 2006), but consistent with the predictions for desert birds (Tieleman and Williams 2000).

	McKechnie et al (2006) %		**Tieleman & Williams (2000) %**	
Species	**summer**	**winter**	**summer**	**winter**
African Scops-Owl	57 ± 12.5	40 ± 5.6	99 ± 5.7	90 ± 3.8
Pearl-spotted Owlet	72 ± 13.1	52 ± 8.6	104 ± 4.2	95 ± 5.2
Fork-tailed Drongo	66 ± 15.8	42 ± 10.2	106 ± 6.0	93 ± 6.8
Crimson-breasted Shrike	63 ± 11.8	43 ± 7.7	104 ± 4.1	95 ± 5.2
White-browed Sparrow-weaver	56 ± 6.3	46 ± 6.6	103 ± 4.1	97 ± 3.6

It could be argued that the species had a higher food intake rate during summer when arthropod food was more abundant, resulting in larger sizes of digestive organs and/or increased metabolic intensity of maintenance organs (Williams and Tieleman 2000). On the other hand, it is also possible that the absence of energy demands associated with reproduction during the dry period allowed BMR to decrease irrespective of food availability during winter months in the Kalahari Desert.

Global variation in seasonal BMR adjustments

The magnitude of seasonal BMR adjustments varies globally, with significantly lower winter/summer BMR ratios in southern Hemisphere species. The majority of southern Hemisphere species investigated so far reduced BMR in winter, whereas the opposite is true for northern Hemisphere. Currently, too few data are available to rigorously examine potential environmental correlates of inter-specific variation in the direction and magnitude of these adjustments. Nevertheless, there are at least three non-mutually exclusive potential explanations for the overall north-south differences I have documented here, namely: (1) genuine Hemispheric differences; (2) latitudinal and/or temperature differences; and M_b differences. Below, I outline key questions that need to be addressed.

All the southern Hemisphere species in my data set are from zoogeographical zones that experience spatially and temporally unpredictable patterns of precipitation, resulting from the ENSO phenomenon that causes temporal shifting and weakening of zonal circulation systems (Stone et al. 1996). Lovegrove (2000) hypothesized that the long term effect of these systems on environmental conditions is reflected in the conservative energy requirements (i.e., low BMR) of many Afrotropical and Australasian mammals. According to this possibility, it is likely that maintenance energy expenditure is regulated at minimum levels during winter and/or dry periods to reduce water and energy requirements, and only increases when environmental conditions are suitable for reproduction. In Holarctic regions, where winter temperatures are extremely cold, the demands for increased thermoregulatory output are higher and an up-regulated BMR might be more affordable since precipitation patterns are much more predictable and not influenced by the ENSO to the same extent (Stone et al. 1996; Lovegrove 2000) The winter BMR reductions presented by Weathers and Caccamise (1978) for Monk Parakeets (*Myiopsitta monachus*) (Table 1), provide an interesting exception since they represent individuals from a feral population that were acclimatized in New Jersey (43° N), although this species is actually native to South America. The current data set on northern and summer hemisphere species is, however, confounded by differences in latitude of acclimatization and body mass.

Seasonal variation in weather conditions generally increases with latitude, and the temperature of the coldest month of the year is negatively correlated with latitude (Lovegrove 2003). Thus, if minimum temperatures are a key determinant of the magnitude of seasonal metabolic adjustments, the magnitude of BMR adjustments is also likely to vary with latitude. Most of the southern Hemisphere species for which data exist occur at middle to low latitudes (< 30° S), whereas the majority of northern Hemisphere data are from much higher latitudes (> 40° N). The winter/summer BMR data currently available reveal significant relationships with both latitude and mid-winter temperatures (Figure 4B & C). Mid-winter temperatures, in particular, explained most of the variation

(57%) in seasonal BMR adjustments (Figure 4C). However, this analysis is confounded by the lack of data from lower latitudes in the northern Hemisphere and higher latitudes in the southern Hemisphere. More data on seasonal BMR adjustments from these regions are needed to draw any firm conclusions regarding the effects of climate and/or latitude. Moreover, there are very limited data from the true tropics (< 20°) where seasons vary more in terms of rainfall rather than temperature. For example, the Puerto Rican Tody (*Todus mexicanus*), endemic to a warm tropical island where seasonal changes in temperature are negligible, showed an elevated BMR during the breeding season (Merola-Zwartjes and Ligon 2000).

The third possible explanation involves the effects of M_b on BMR adjustments. Weathers and Caccamise (1978) argued that seasonal BMR adjustments are dependent on M_b, with birds < 200g generally elevating winter BMR, whereas larger birds typically showed winter BMR reductions. However, this conclusion was based in part on metabolic measurements that did not meet the criteria for BMR (McKechnie 2008). The current data set on winter/summer BMR ratios does not reveal a significant relationship with M_b (Figure 4A). However, a negative relationship is apparent since the northern Hemisphere species that up-regulated winter BMR are < 30g, whereas the majority of birds that down-regulated winter BMR (mostly my study species) are > 30g (Figure 4A). Nevertheless, the former relationship does not appear to be consistent; the small northern Hemisphere species show a wide range of winter/summer BMR ratios, with no apparent M_b correlation, and moreover, the Australian Silver-eye (one of the smallest species in the data set) show a winter BMR reduction of similar magnitude to larger species (Maddocks and Geiser 2000).

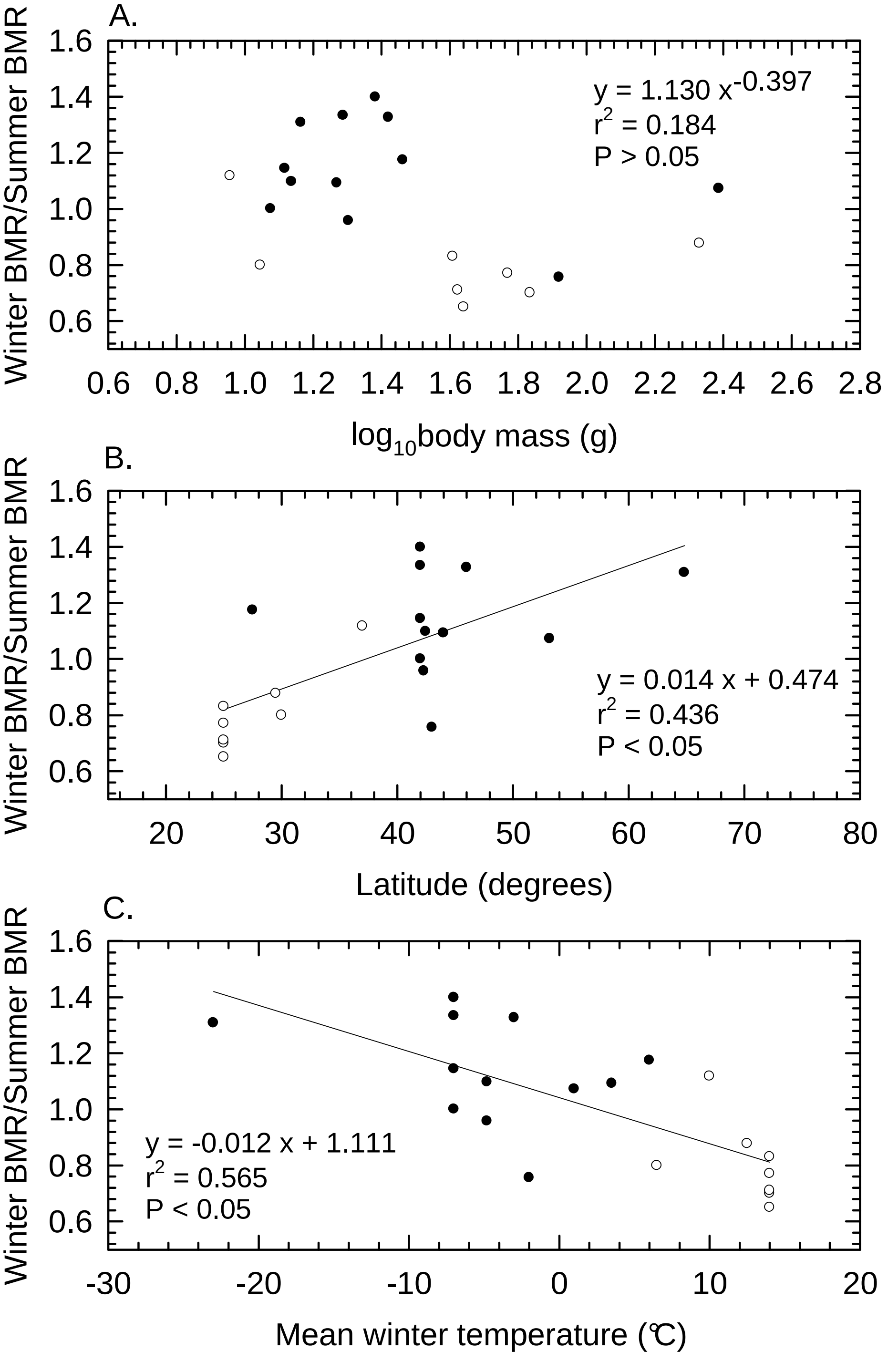

Figure 4: Relationships between avian winter/summer mass-specific basal metabolic rate (BMR) ratios and body mass (A.), latitude (B.) and mean daily temperatures for acclimatization sites during mid-winter (C.). Latitude and temperature values were obtained from either the original papers, or were downloaded online from http://www.worldclimate.com. The clear circles and black dots indicate southern and northern Hemisphere species, respectively. Linear regressions with significant fits are indicated with solid lines.

Summary

My findings are consistent with the hypothesis that phenotypic adjustments in maintenance energy requirements are important in temporally heterogeneous environments (Pigliucci 2001; Cavieres and Sabat 2008). Whereas seasonal variation in avian BMR is often associated with increased thermoregulatory capacity during winter, the down-regulation of BMR during winter that I observed in five species suggests that these adjustments did not reflect enhanced cold tolerance during winter. Instead, the seasonal BMR adjustments exhibited by five species resident in a seasonal arid environment in the Kalahari Desert suggest that these adjustments are related to energy and/or water savings, rather than increased thermoregulatory capacity. My results suggest that in regions with milder winter climates, winter reductions in avian BMR may reflect either (1) a modulation of maintenance energy requirements associated with thermoregulatory demands (resulting from the relatively warm day-time temperatures, and absence of breeding costs), or (2) a reduction in maintenance energy demands resulting from reduced food availability. On a global scale, the directions of seasonal BMR adjustments are correlated with winter climate and latitude, and possibly also seasonal aridity. A more thorough investigation of the functional significance of phenotypic adjustments in avian BMR is necessary, and there is an urgent need for further data from tropical and subtropical latitudes.

Literature cited

Ambrose S.J., and S.D. Bradshaw. 1988. Seasonal changes in standard metabolic rates in the white-browed scrubwren *Sericornis frontalis* (Acanthizidae) from arid, semi-arid and mesic environments. Comparative Biochemistry and Physiology 89A:79-83.

Baker W.C., and J.F. Pouchot. 1983. The measurement of gas flow. Part II. Journal of the Air Pollution Control Association 33:156-162.

Brackenbury J. 1984. Physiological responses of birds to flight and running. Biological Review 59:559-575.

Brown C.R., and D.M. Bryant. 1996. Energy expenditure during molt in dippers (*Cinclus cinclus*): No evidence of elevated costs. Physiological Zoology 69:1036-1056.

Bush N.G., M. Brown, and C.T. Downs. 2008. Seasonal effects on thermoregulatory responses of the Rock Kestrel, *Falco rupicolis*. Journal of Thermal Biology 33:404-412.

Buttemer W.A., S.C. Nicol, and A. Sharman. 2003. Thermoenergetics of pre-moulting and moulting kookaburras (*Dacelo novaeguineae*): they're laughing. Journal of Comparative Physiology B 173:223-230.

Cavieres G., and P. Sabat. 2008. Geographic variation in the response to thermal acclimation in rufous-collared sparrows: are physiological flexibilty and environmental heterogeneity correlated? Functional Ecology 22:509-515.

Cooper S.J., and D.L. Swanson. 1994. Seasonal acclimatization of thermoregulation in the black-capped chickadee. The Condor 96:638-646.

Daan S., D. Masman, and A. Groenewold. 1990. Avian basal metabolic rates: their association with body compostition and energy expenditure in nature. American Journal of Physiology 259:333-340.

Dawson W.R. 2003. Plasticity in avian responses to thermal challenges - an essay in honor of Jacob Marder. Israeli Journal of Zoology 49:95-109.

Dawson W.R., and C. Carey. 1976. Seasonal acclimation to temperature in Cardueline finches. Journal of Comparative Physiology 112:317-333.

Dawson W.R., and R.L. Marsh. 1988. Metabolic acclimatization to cold and season in birds. Pp. 83-94 in C. Bech, and R.E. Reinertsen, eds. Physiology of cold adaptation in birds. Plenum Press, New York

Dawson W.R., and R.L. Marsh. 1989. Metabolic acclimatization to cold and season in birds. Pp. 83-94 in C. Bech, and R.E. Reinertsen, eds. Physiology of cold adaptation in birds. Plenum Press, New York

Dawson W.R., R.L. Marsh, W.A. Buttermer, and C. Carey. 1983. Seasonal and geographic variation of cold resisitance in house finches. Physiological Zoology 56:353-369.

Dutenhoffer M.S., and D.L. Swanson. 1996. Relationship of basal to summit metabolic rate in passerine birds and the aerobic capacity model for the evolution on endothermy. Physiological Zoology 69:1232-1254.

Garland T., A.W. Dickerman, C.M. Janis, and J.A. Jones. 1993. Phylogenetic analysis of covariance by computer simulation. Systematic Biology 42:265-292.

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

Jetz W., R.P. Freckleton, and A.E. McKechnie. 2008. Environment, Migratory Tendency, Phylogeny and Basal Metabolic Rate in Birds. PLoS One 3:e3261.

Karasov W.H. 1992. Tests of adaptive modulation hypothesis for diet control of intestinal nutrient transport. American Journal of Physiology 263:R496-R502.

Klaassen M., M. Oltrogge, and L. Trost. 2004. Basal metabolic rate, food intake, and body mass in cold- and warm-acclimated Garden Warblers. Comparative Biochemistry and Physiology A 137:639-647.

Lasiewski R.C., A.L. Acosta, and M.H. Bernstein. 1966. Evaporative water loss in birds - I. Characteristics of the open flow method of determination, and their relation to estimates of thermoregulatory ability. Comparative Biochemistry and Physiology 19:445-457.

Liknes E.T., S.M. Scott, and D.L. Swanson. 2002. Seasonal acclimatization in the American Goldfinch revisited: to what extent do metabolic rates vary seasonally? The Condor 104:548-557.

Liknes E.T., and D.L. Swanson. 1996. Seasonal variation in cold tolerance, basal metabolic rate, and maximal capacity for thermogenesis in white-breasted nuthatches *Sitta carolinensis* and downy woodpeckers *Picoides pubescens*, two unrelated arboreal temperate residents. Journal of Avian Biology 27:279-288.

Lill A., J. Box, and J. Baldwin. 2006. Do metabolism and contour plumage insulation vary in response to seasonal energy bottlenecks in superb fairy-wrens? Australian Journal of Zoology 54:23-30.

Lindström Å., G.H. Visser, and S. Daan. 1993. The energetic cost of feather synthesis is proportional to basal metabolic rate. Physiological Zoology 66:490-510.

Lovegrove B.G. 1993. The living deserts of southern Africa. Fernwood Press, Vlaeberg.

Lovegrove B.G. 2000. The zoogeography of mammalian basal metabolic rate. American Naturalist 156:201-219.

Lovegrove B.G. 2003. The influence of climate on the basal metabolic rate of small mammals: a slow-fast metabolic continuum. Journal of Comparative Physiology B 173:87-112.

Lovegrove B.G. 2005. Seasonal thermoregulatory responses in mammals. Journal of Comparative Physiology B 175:231-247.

Maclean G.L. 1993. Roberts' birds of southern Africa. John Voelcker Bird Book Fund, Cape Town.

Maddocks T.A., and F. Geiser. 2000. Seasonal variations in thermal energetics of Australian silvereyes (*Zosterops lateralis*). Journal of Zoology, London 252:327-333.

Maldonado K.E., G. Cavieres, C. Veloso, M. Canals, and P. Sabat. 2009. Physiological responses in rufous-collared sparrows to thermal acclimation and seasonal acclimatization. Journal of Comparative Physiology B (in press).

Marsh R.L., and W.R. Dawson. 1989. Avian adjustments to cold Pp. 206-253 in L.C.H. Wang, eds. Advances in Comparative and Environmental Physiology 4: Animal Adaptation to the Cold. Springer-Verlag, Berlin

McKechnie A.E. 2008. Phenotypic flexibility in basal metabolic rate and the changing view of avian physiological diversity: a review. Journal of Comparative Physiology B 173:235-247.

McKechnie A.E., K. Chetty, and B.G. Lovegrove. 2007. Phenotypic flexibility in basal metabolic rate in Laughing Doves: responses to short-term thermal acclimation. Journal of Experimental Biology 210:97-106.

McKechnie A.E., R.P. Freckleton, and W. Jetz. 2006. Phenotypic plasticity in the scaling of avian basal metabolic rate. Proceedings of the Royal Society of London B 273:931-937.

McKechnie A.E., and B.O. Wolf. 2004. The allometry of avian basal metabolic rate: good predictions need good data. Physiological and Biochemical Zoology 77:502-521.

Merola-Zwartjes M., and J.D. Ligon. 2000. Ecological energetics of the Puerto Rican tody: heterothermy, torpor and intra-island variation. Ecology 81:990-1002.

Meyer J., J. Steinhauser, F. Jeltsch, and R. Brandl. 2007. Large trees, acacia shrubs, and the density of Thallomy nigricauda in the thornveld savannah of South Africa Journal of Arid Environments 68:363-370.

Mezhzherin V.A. 1964. Dehnel's phenomenon and its possible explanation. Acta Theriologica 8:95-114.

O'Conner T.P. 1995. Metabolic characteristics and body composition in house finches: effects of seasonal acclimatization. Journal of Comparative Physiology B 165:298-305.

O'Connor T.P. 1996. Geographic variation in metabolic seasonal acclimatization in house finches. The Condor 98:371-381.

Piersma T. 2002. Energetic bottlenecks and other design constraints in avian annual cycles. Integrative and Comparative Biology 42:51-67.

Piersma T., and J. Drent. 2003. Phenotypic flexibility and the evolution of organismal design. Trends in Ecology and Evolution 18:228-233.

Pigliucci M. 2001. Phenotypic Plasticity: Beyond Nature and Nurture. Johns Hopkins University Press, Balfimore.

Pohl H. 1971. Seasonal variation in metabolic functions of bramblings. Ibis 113:185-193.

Pohl H., and G.C. West. 1973. Daily and seasonal variation in metabolic response to cold during rest and exercise in the common redpoll. Comparative Biochemistry and Physiology 45A:851-867.

Rising J.D., and J.W. Hudson. 1974. Seasonal variation in the metabolism and thyroid activity of the black-capped chickadee (*Parus atricapillus*). The Condor 76:198-203.

Saarela S., B. Klapper, and G. Heldmaier. 1995. Daily rhythm of oxygen consumption and thermoregulatory responses in some European winter- or summer-acclimatized finches at different ambient temperatures. Journal of Comparative Physiology B 165:366-376.

Sibley C.G., and J.E. Ahlquist. 1990. Phylogeny and classification of birds. Yale University Press, New Haven.

Siegel H.S. 1980. Physiological stress in birds BioScience 30:529-534.

Southwick E.E. 1980. Seasonal thermoregulatory adjustments in white-crowned sparrows. Auk 97:76-85.

Stone R.C., G.L. Hammer, and T. Marcussen. 1996. Prediction of global rainfall probabilities using phases of the Southern Oscillation index. Nature 384:252-255.

Swanson D.L. 1990. Seasonal variation in cold hardiness and peak rates of cold-induced thermogenesis in the dark-eyed junco (*Junco hyemalis*). Auk 107:561-566.

Swanson D.L. 1991. Seasonal adjustments in metabolism and insulation in the Dark-eyed Junco. The Condor 93:538-545.

Swanson D.L. in press. Seasonal metabolic variation in birds: functional and mechanistic correlates. Pp. in Current Ornithology.

Swanson D.L., and E.T. Liknes. 2006. A comparative analysis of thermogenic capacity and cold tolerance in small birds. Journal of Experimental Biology 209:466-474.

Swanson D.L., and K.L. Olmstead. 1999. Evidence for a proximate influence of winter temperatures on metabolism in passerine birds. Physiological and Biochemical Zoology 72:566-575.

Swanson D.L., and D.P. Weinacht. 1997. Seasonal effects on metabolism and thermoregulation in northern bobwhite. The Condor 99:478-489.

Tieleman B.I., and J.B. Williams. 2000. The adjustment of avian metabolic rates and water fluxes to desert environments. Physiological and Biochemical Zoology 73:461-479.

Tieleman B.I., J.B. Williams, and P. Bloomer. 2003a. Adaptation of metabolic rate and evaporative water loss along an aridity gradient. Proceedings of the Royal Society of London 270:207-214.

Tieleman B.I., J.B. Williams, M.E. Buschur, and C.R. Brown. 2003b. Phenotypic variation of larks along an aridity gradient: are desert birds more flexible? Ecology 84:1800-1815.

Vezina F., K. Jalvingh, A. Dekinga, and T. Piersma. 2006. Acclimation to different thermal conditions in a northerly wintering shorebird is driven by body mass-related changes in organ size. Journal of Experimental Biology 209:3141-3154.

Walsberg G.E., and B.O. Wolf. 1995. Variation in the respirometry quotient of birds and implications for indirect calorimetry using measurements of carbon dioxide production. Journal of Experimental Biology 198:213-219.

Weathers W.W., and D.F. Caccamise. 1978. Seasonal acclimatization to temperature in monk parakeets. Oecologia 35:173-183.

West G.C. 1972. The effect of acclimation and acclimatization on the resting metabolic rate of the common redpoll. Comparative Biochemistry and Physiology 43A:293-310.

White C.R., T.M. Blackburn, G.R. Martin, and P.J. Butler. 2007. The basal metabolic rate of birds is associated with habitat temperature and precipitation, not productivity. Proceedings of the Royal Society B 274:287-293.

Wijnandts H. 1984. Ecological energetics of the long-eared owl (*Asio otus*). Ardea 72:1-92.

Williams J.B., and B.I. Tieleman. 2000. Flexibility in basal metabolic rate and evaporative water loss among hoopoe larks exposed to different environmental temperatures. Journal of Experimental Biology 203:3153-3159.

Williams J.B., and B.I. Tieleman. 2005. Physiological adaptation in desert birds. BioScience 55:416-425.

Wingfield J.C., and D.S. Farner. 1993. Endocrinology of reproduction in wild species. Pp. 163-327 in D.S. Farner, J.R. King, and K.C. Parkes, eds. Avian Biology, Volume IX. Academic Press, San Diego, Caifornia, USA.

Withers P.C. 1977. Measurement of VO2, VCO2, and evaporative water loss with a flow-through mask. Journal of Applied Physiology 42:120-123.

Withers P.C. 1992. Comparative animal physiology. Saunders College Publishing, Fort Worth.

Zar J.H. 1999. Biostatistical analysis. Prentice Hall, New Jersey.

Zheng W.-H., J.-S. Liu, X.-H. Jiang, Y.-Y. Fang, and G.-K. Zhang. 2008. Seasonal variation on metabolism and thermoregulation in Chinese bulbul. Journal of Thermal Biology 33:315-319.

CHAPTER 4:

CONCLUSIONS AND SUGGESTIONS FOR FUTURE RESEARCH

Heterothermy

Owls likely share a physiological capacity for heterothermic responses with their close relatives, the caprimulgids, providing further evidence that avian torpor represents a monophyletic, plesiomorphic trait as hypothesized by (Malan 1996). However, although a close phylogenetic relationship between owls and caprimulgids has been accepted for decades, there have been several counter-arguments and alternative classifications (Marks et al. 1991). For instance, the most recent assessment of the deep branches of the avian phylogeny, published while I was writing this dissertation, proposed that caprimulgids and owls are not closely related at all; caprimulgids are grouped with swifts and hummingbirds, whereas the phylogenetic relationship of owls remains unclear (Hackett et al. 2008). Presently therefore, conclusions on the evolution of heterothermy in birds are complicated by the debate surrounding the relationships between higher-order avian taxa.

The capacity for avian heterothermic responses appears to be phylogenetically widespread in small birds, particularly those that rely on unpredictable food sources such as aerial insects, nectar and fruit. However, the capacity for pronounced torpor, involving reductions in T_b by more than 30°C below normothermic values, appears to be limited to caprimulgids and hummingbirds (McKechnie and Lovegrove 2002). To establish whether the capacity for pronounced torpor represents a unique adaptation for particular avian taxa (e.g. hummingbirds and caprimulgids), more emphasis on other phylogenetically older taxa are necessary. Within the Neoaves, for instance, empirical data on thermoregulatory patterns from older taxa, e.g. Piciformes (honeyguides, barbets, woodpeckers and toucans), Galbuliformes (puffbirds and jacamars), Bucerotiformes (hornbills), Upupiformes (hoopoes, woodhoopoes and scimitarbills), Trogoniformes (trogons), and Musophagiformes (turacos) are necessary. On the other hand, the majority of avian taxa comprising the Paleognathae are large-bodied, and the use of torpor is probably constrained by M_b-related factors (Geiser 1998). However a limited number of species from the Neotropical order Tinamiformes, e.g. the 43-g Dwarf Tinamou (*Taoniscus nanus*) (Cabot 1992), are within the $\mathrm{M_b}$ range of birds that undergo torpor, and data from such species could provide valuable insights into the evolution of avian heterothermy.

Seasonal metabolic adjustments

My data on seasonal metabolic adjustments suggest that, in subtropical latitudes, the functional significance of such adjustments is related to winter reductions in maintenance metabolic requirements. However, seasonal metabolic adjustments can be the result of (1) photoperiod-mediated endocrinological cycles or (2) short-term phenotypic responses – and both these might be influenced by developmental plasticity (Piersma and Drent 2003; McKechnie et al. 2006). For future studies, more detailed assessments on the functional roles of specific environmental factors (e.g. food and water availability, temperature and photoperiod) on phenotypic metabolic adjustments are required from species that inhabit unpredictable environments. It could be argued that in environments where seasonal patterns of precipitation and primary productivity are unpredictable, photoperiod would play a relatively insignificant role, with short-term changes in food or water availability emerging as proximate factors acting on metabolic phenotypes. In this regard, it is noteworthy that my seasonal BMR measurements represent data from a dry winter (preceded by a year long drought during 2006/7), followed by a summer with above average rainfall, respectively (2005 – 2008, South African Weather Service). Summer droughts are frequent in the Kalahari Desert and are characterized by extremely hot daytime temperatures with very little or no primary production, as well as the absence of surface water (Lovegrove 1993). During summer droughts, a reduced BMR might also be favoured since both energy and water requirements would be reduced. Basal metabolic rate would then be elevated only during wetter seasons when conditions are suitable for reproduction. Longer-term studies in which BMR is measured over several years would shed light on this possibility.

Why then do so many small bird species from high latitudes in the northern Hemisphere up-regulate winter BMR, if it is energetically costly to do so? It is possible that the dichotomy observed in the global patterns of BMR adjustments represents an energy-saving/cold-tolerance trade-off, where extremely cold winter conditions result in up-regulated metabolic machinery associated with thermogenisis that requires greater support cost – i.e. BMR, at the expense of higher energy demands. The benefits associated with the latter response would presumably be highest in environments where birds have reliable access to food resources during extreme winters.

Literature cited

Cabot J. 1992. Family Tinamidae (Tinamous) Pp. 112-140 in J. del Hoyo, A. Elliot, and J. Sargatal, eds. Handbook of the birds of the world. Volume 1: Ostrich to Ducks. Lynx Edicions, Barcelona.

Geiser F. 1998. Evolution of daily torpor and hibernation in birds and mammals: importance of body size. Clinical and Experimental Pharmacology and Physiology 25:736-740.

Hackett S.J., R.T. Kimball, S. Reddy, R.C.K. Bowie, E.L. Braun, J.L. Chojnowski, W.A. Cox, K.-L. Han, J. Harshman, C.J. Huddleston, B.D. Marks, K.J. Miglia, W.S. Moore, F.H. Sheldon, D.W. Steadman, C.C. Witt, and T. Yuri. 2008. A phylogenetic study of birds reveals their evolutionary history. Science 320:1763-1768.

Lovegrove B.G. 1993. The living deserts of southern Africa. Fernwood Press, Vlaeberg.

Malan A. 1996. The origins of hibernation: a reappraisal. Pp. 1-6 in F. Geiser, A.J. Hulbert, and S.C. Nicol, eds. Adaptations to the cold: Tenth International Hibernation Symposium. University of New England Press, Armidale.

Marks J.S., R.J. Cannings, and H. Mikkola. 1991. Family Strigidae (typical owls). Pp. 76-241 in J. del Hoyo, A. Elliot, and J. Sargatal, eds. Handbook of the birds of the world. Vol. 5. Barn-owls to hummingbirds. Lynx Edicions, Barcelona.

McKechnie A.E., R.P. Freckleton, and W. Jetz. 2006. Phenotypic plasticity in the scaling of avian basal metabolic rate. Proceedings of the Royal Society of London B 273:931-937.

McKechnie A.E., and B.G. Lovegrove. 2002. Avian facultative hypothermic responses: a review. The Condor 104:705-724.

Piersma T., and J. Drent. 2003. Phenotypic flexibility and the evolution of organismal design. Trends in Ecology and Evolution 18:228-233.