

PATTERNS, MECHANISMS AND EVOLUTION OF AVIAN FACULTATIVE
HYPOTHERMIC RESPONSES: A SOUTHERN AFRICAN PERSPECTIVE

by

ANDREW EDWARD MCKECHNIE

Submitted in fulfilment of the requirements for the degree of

Doctor of Philosophy

in the

School of Botany and Zoology

University of Natal

Pietermaritzburg

2001

PREFACE

The experimental work described in this thesis was carried out in the School of Botany and Zoology, University of Natal, Pietermaritzburg, from January 1999 to June 2001, under the supervision of Professor Barry G. Lovegrove.

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



Andrew E. McKechnie

Pietermaritzburg

June 2001

Abstract

Recent evidence suggests that avian facultative hypothermic responses are more common than previously thought. Traditionally, several categories of avian hypothermic responses have been recognized, and are frequently differentiated on the basis of minimum body temperature (T_b). The available data suggest that the capacity for shallow hypothermia (rest-phase hypothermia) occurs throughout the avian phylogeny, but that the capacity for pronounced hypothermia (torpor) is restricted to certain taxa. However, there are currently too few data to test hypotheses concerning the evolution of avian hypothermic responses. Facultative hypothermia occurs over most of the avian body mass (M_b) range, but is most common in small species. Minimum body temperature during hypothermia (T_{min}) is continuously distributed from 4.3°C to ca. 38°C. The continuous T_{min} distribution, as well as recent evidence that the T_b ranges of different avian physiological states may overlap, question the biological reality of specific T_b limits. Patterns of thermoregulation during avian hypothermic responses are relatively variable, and do not necessarily follow the entry-maintenance-arousal patterns that characterize mammalian responses. Avian hypothermic responses are determined by a suite of ecological and physiological determinants.

I investigated normothermic thermoregulation and hypothermic responses to restricted food in the speckled mousebird *Colius striatus* in the context of the distinction between normothermia, rest-phase hypothermia, and torpor. The lowest T_b recorded in a bird which was able to arouse spontaneously was 18.2°C. However, I was unable to clearly discern between normothermic, hypothermic and torpor T_b ranges. Furthermore, hypothermic responses did not accord with the patterns typically observed in birds and mammals. Metabolic suppression normally associated with entry into torpor and the defence of a torpor T_b setpoint was largely absent.

Laboratory data for *C. striatus*, as well as published data for *Colius colius* suggest that clustering behavior plays an important thermoregulatory role in mousebirds. Hence, I investigated thermoregulation under semi-natural conditions in *C. striatus*. In particular, I was interested in the interaction between clustering behavior and hypothermic responses during energy stress (restricted feeding). In contrast to clustering birds, rest-phase thermoregulation in single birds was characterised by linear decreases in T_b , and the birds did not appear to defend a specific T_b setpoint. During restricted feeding, both clustering and single birds exhibited significant decreases in rest-phase T_b . The extent of these facultative hypothermic responses was greater in single birds than in clustering birds, supporting the prediction that clustering behavior moderates the use of facultative hypothermia.

I also tested the prediction that in free-ranging *C. colius*, the use of heterothermy should be rare, even at the coldest time of the year. I recorded mid-winter rest-phase body temperatures (T_b) in a flock of free-ranging *C. colius* in an arid habitat in the Karoo, South Africa. The mousebirds' rest-phase T_b was fairly labile, but was maintained above 33°C, despite T_a s as low as -3.4°C. The mousebirds showed no evidence of torpor under natural conditions; a facultative hypothermic response, during which T_b was reduced to 29 - 33°C, was only observed on one occasion. The observed patterns of thermoregulation supported my predictions, and suggest that thermoregulation in clustering *C. colius* in the wild is significantly different to that of single birds under laboratory conditions. My results also suggest that the pronounced capacity for heterothermy usually associated with mousebirds is not necessarily representative of their patterns of thermoregulation under natural conditions.

The capacity for avian torpor appears to be dependent on phylogeny. To investigate phylogenetic constraints on the capacity for torpor, I measured metabolic responses to food deprivation in a small, arid-zone passerine, the red-headed finch (*Amadina erythrocephala*). I

observed significant reductions in rest-phase energy expenditure and body temperature (T_b) in response to restricted feeding. The maximum extent of T_b suppression (ca. 5°C) and energy savings (ca. 10%) were consistent with those reported for a number of other passerines. The lowest T_b I observed in a bird able to arouse spontaneously was 34.8°C . My data support the hypothesis that the capacity for heterothermy in passerines is phylogenetically constrained, and that the majority cannot employ torpor in response to energetic stress.

Selection for the capacity for torpor is presumably similar to the selection pressures acting on other avian energetic traits, such as basal metabolic rate (BMR). I tested the generality of a recent model linking the slow-fast mammalian metabolic continuum to global patterns of climatic predictability using BMR data for 219 non-migratory bird species. Avian BMR varied significantly between zoogeographical zones, with Afrotropical, Indomalayan and Australasian species generally exhibiting lower BMR than Holarctic species. In addition, the magnitude of differences between arid and mesic species varied between zones. In the Nearctic, these differences were pronounced, whereas no significant differences were evident for Afrotropical or Australasian species. A slow-fast metabolic continuum similar to that described in mammals appears to exist for birds, with higher BMR associated with predictable, seasonal environments and lower BMR with less predictable environments, in particular those affected by the El Niño Southern Oscillation.

I constructed a generalised, conceptual model which attempts to predict the occurrence of torpor using phylogeny, M_b constraints, a trade-off between energetic benefits and potential ecological costs, and specific ecological factors. A recent hypothesis suggests that endotherm heterothermy is monophyletic, and predicts that torpor should be more widespread in phylogenetically older taxa. Once phylogeny is considered, the most important determinant of avian torpor is M_b . I used an existing model of endotherm torpor to predict the relationship

between M_b and minimum T_b during torpor. The available data show that the lower limit of torpor T_b is determined by the M_b -dependent costs of rewarming following a torpor bout. Finally, I constructed a model based on the assumption that torpor is adaptive if the energetic benefits exceed the potential ecological costs. The model predicted that torpor should be more prevalent in species near the extremes of the avian metabolic continuum. The available data provide tentative support for this prediction. In addition to generalised factors such as phylogeny and M_b , specific aspects of a particular species' ecology need to be considered when predicting the occurrence of avian torpor.

Acknowledgements

My sincere thanks go to my supervisor, Professor Barry Lovegrove. Throughout my postgraduate career, Professor Lovegrove has provided excellent academic supervision. I believe that the time I have spent in his laboratory has provided me with a good training for an academic career. During the course of my M.Sc and Ph.D, Professor Lovegrove paid for me to attend four international conferences, of which three were in Europe. Attending these meetings was a valuable experience, for which I am grateful.

I thank Gerhard Körtner for his involvement in several aspects of my research. Gerhard designed and built the data logger used to record signals from FM body temperature transmitters used in Chapters 3 and 4. He also assisted with the experimental work described in Chapter 3, and provided valuable advice on several aspects of Chapter 2. Mark Brigham kindly read an earlier version of Chapter 4, and his comments greatly improved the quality of the manuscript.

Richard and Sue Dean once again allowed me to use Tierberg Research Station during my field work. Jaishree Raman, Kwezi Mzilikazi and Beka Nxele kindly fed mousebirds and red-headed finches during my frequent absences from Pietermaritzburg. Professor Mike Savage of the Department of Agrometeorology, University of Natal, provided site-specific sunrise and sunset times for Pietermaritzburg and Tierberg. The staff of the Computing Centre for Water Research, University of Natal, provided climatological data for Tierberg. I gratefully acknowledge the contribution made by De Beers Consolidated Mining, who granted permission for red-headed finches to be trapped on Benfontein. I also thank Rita Covas and her assistants for their hospitality while staying at Benfontein, and for help in trapping the

finches. I am grateful to Professor T. Clutton-Brock and the staff and volunteers at the Meerkat Research Project near Vanzylsrus, who provided accommodation on one of my field trips. Carlos Bosque, Esa Hohtola, Gerhard Körtner and Karl Schuchmann commented on species lists and the arid/mesic assignment of particular species in Chapter 6. Michael Patten kindly commented on the phylogeny I constructed for the BMR analysis. I thank Professor Mike Lawes for his academic advice during the course of this project.

I thank Ellery Worth, Sven Bourquin, and Luke Arnot for their regular assistance in trying to trap fiery-necked nightjars in Pietermaritzburg. Despite our combined efforts, patterns of body temperature in this species remain unknown. I also thank Rob Symons and Nora Choveaux for allowing to me to work on their property.

Finally, and most importantly, I thank my parents for their encouragement and support during the course of my studies.

Table of contents

Preface.....	ii
Abstract.....	iii
Acknowledgements.....	vii
Introduction.....	1
Terminology.....	3
Thesis structure.....	5
Literature cited.....	7
Chapter 1. Avian facultative hypothermic responses: a review.....	9
Introduction.....	9
Data selection.....	11
Analyses and interpretation.....	11
Phylogenetic distribution.....	11
Zoogeographical distribution.....	20
Body size.....	21
Body temperature.....	23
Metabolic suppression.....	25
Patterns of thermoregulation during facultative hypothermia.....	26
Proximate determinants of facultative hypothermia.....	28
Conclusions.....	31
Literature cited.....	33

Chapter 2. Facultative hypothermic responses in the speckled mousebird (<i>Colius striatus</i>).....	45
Introduction.....	45
Materials and methods.....	47
Measurement of T_b	48
Metabolic measurements.....	48
Experimental protocol.....	50
Data analysis.....	51
Results.....	51
Body mass and metabolic substrate.....	51
Body temperature.....	52
Cooling rates during ad libitum feeding.....	57
Oxygen consumption.....	58
Energy expenditure.....	59
Discussion.....	61
Normothermia.....	61
Basal metabolic rate.....	64
Responses to restricted food.....	64
Evolutionary implications.....	67
Literature cited.....	70

Chapter 3. Thermoregulation in speckled mousebirds (<i>Colius striatus</i>) under semi-natural conditions: the role of clustering behaviour.....	76
Introduction.....	76
Materials and methods.....	78
Body temperature measurement.....	78
Experimental protocol.....	79
Data analysis.....	80
Results.....	80
Ad libitum feeding.....	81
Restricted feeding.....	86
Active-phase T_b	86
Discussion.....	88
Thermoregulation in single birds under laboratory and semi-natural conditions.....	88
Role of clustering behaviour in normothermic thermoregulation.....	89
Clustering behaviour and facultative hypothermic responses....	90
Coevolution of mousebird sociality and thermoregulation?.....	91
Literature cited.....	94

Chapter 4. Rest-phase thermoregulation in free-ranging white-backed mousebirds (<i>Colius colius</i>).....	98
Introduction.....	98
Materials and methods.....	100
Study site.....	100
Body temperature measurement.....	100
Data analysis.....	101
Results.....	101
General behaviour.....	101
Ambient temperature.....	102
Normothermic ρT_b	102
Hypothermic response - 21 st June.....	105
Other observations.....	106
Discussion.....	108
Thermoregulatory role of clustering behaviour.....	108
Facultative hypothermic responses.....	109
Synchronised patterns of ρT_b	110
Literature cited.....	113

Chapter 5. Thermoregulation and metabolic responses to food deprivation in an Afrotropical arid-zone passerine, the red-headed finch (<i>Amadina erythrocephala</i>).....	116
Introduction.....	116
Materials and methods.....	118
Body temperature measurements.....	119
Metabolic measurements.....	119
Experimental protocol.....	120
Data analysis.....	120
Results.....	122
Body mass and metabolic substrate.....	122
Body temperature.....	123
Oxygen consumption and energy expenditure.....	123
Thermal conductance.....	126
Discussion.....	127
Basal metabolic rate.....	128
Normothermic thermoregulation.....	130
Responses to food deprivation.....	131
General.....	132
Literature cited.....	135

Chapter 6. Avian basal metabolic rate: a zoogeographical perspective.....	143
Introduction.....	143
Materials and methods.....	146
Results.....	148
Aridity effects.....	149
Zonal effects.....	150
Within-zone arid-mesic BMR convergence.....	150
Discussion.....	153
Implications for comparative studies.....	156
Literature cited.....	159
Appendix 1.....	166
Appendix 2.....	172
 Chapter 7. Evolutionary and ecological determinants of avian torpor:	
a conceptual model.....	179
Introduction.....	179
Phylogeny.....	180
Body size.....	182
Trade-off between energetic benefits and ecological costs.....	186
Ecological factors.....	191
Literature cited.....	195
Appendix 1.....	203

Conclusions.....	206
The distinction between rest-phase hypothermia and torpor.....	206
The interaction between facultative hypothermia and communal roosting.....	207
Evolutionary and ecological determinants of avian facultative hypothermia.....	208
Literature cited.....	210

Introduction

Endothermic homeothermy, the maintenance of relatively high body temperature (T_b) by means of endogenous metabolism, is found in a minority of vertebrates. A constant high T_b confers fundamental physiological advantages, notably an increased rate of enzymatic catalysis and an increased capacity to exploit thermally unfavourable environments (Withers 1992). The selection mechanisms responsible for the evolution of vertebrate endothermy remain controversial (Hayes and Garland 1995). Of the models proposed to explain the selection of endothermy, the aerobic capacity model (Bennett and Ruben 1979) has received the most attention. This model argues that selection for increased maximal aerobic capacity led to a correlated increase of resting metabolism.

Although the reasons for the evolution of endothermy remain unclear, it is generally accepted that avian and mammalian endothermy evolved independently (Ruben 1995). Moreover, current evidence points towards ectothermy in early birds such as *Archaeopteryx lithographica* and suggests that endothermy was not a ubiquitous avian trait until the Cretaceous (Feduccia 1996).

The high metabolic rates associated with endothermic homeothermy represent a substantial cost. The metabolic costs of maintaining a high T_b are particularly pronounced in small mammals and birds with large surface-area : volume ratios and associated high rates of mass-specific heat loss (Withers 1992). The metabolic costs of endothermic homeothermy can be reduced by a variety of behavioural and physiological mechanisms, such as microhabitat selection, communal roosting, and adaptive change in metabolic parameters. Perhaps the most dramatic avenue whereby mammals and birds reduce their metabolic costs is by means of facultative decreases in metabolic rate and T_b . Such periods of facultative hypometabolism

and hypothermia appear to be vital in the energy balance of many endotherms (Lyman et al. 1982; Reinertsen 1996).

Although a substantial volume of literature has accumulated on facultative hypothermic responses, the majority has focussed on mammals and studies of avian hypothermic responses are comparatively rare. For instance, several fundamental aspects of avian non-shivering thermogenesis remain unknown (Duchamp et al. 1999; Marjoniemi and Hohtola 1999). Furthermore, of the 56 papers published in the proceedings of the 10th International Hibernation Symposium held in Tasmania in 1996, only four dealt with birds. At the 11th meeting held in Austria in 2000, only two out of 55 papers dealt specifically with birds.

Despite the relative paucity of data, there is reason to suspect that avian hypothermic responses, and torpor in particular, are more common than previously thought. Evidence is also accumulating that in contrast to the views of earlier authors, many species use torpor routinely and not only during periods of severe energy shortage. Telemetric studies of thermoregulation in free-ranging birds have revealed that torpor is a major component of daily energy balance, and that the use of torpor on a particular day is determined by a complex suite of factors.

Several studies have identified specific ecological and physiological determinants of avian facultative hypothermia, but generalised evolutionary and ecological determinants have been largely ignored. The identification of such evolutionary correlates requires a knowledge of the phylogenetic distribution of hypothermic responses, a task hampered at present by a paucity of data. The best approach may be to construct conceptual models to test hypotheses on the evolution of avian hypothermia with the limited empirical data available. Facultative hypothermia is primarily an energy-saving response, and the identification of selection

pressures responsible for adaptive variance in metabolic traits associated with energy budgets may well reveal some of the determinants of hypothermia.

Terminology

The terminology used to describe avian hypothermic states is inconsistent and confusing. For instance, the term “heterothermy” is widely used to refer to torpor (daily heterothermy) and hibernation (seasonal heterothermy). However, Merola-Zwartjes and Ligon (2000) considered “heterothermy” in Puerto Rican toadies (*Todus mexicanus*) to be a non-torpid state characterized by relatively labile rest-phase T_b (range 27.9 - 42.9°C). The use of the term “heterothermy” in the latter study provides a good example of the inconsistency with which terminology is used.

The International Union for Physiological Sciences (IUPS) defines “heterothermy” as a pattern of thermoregulation in a tachymetabolic species in which the variation in core temperature exceeds that which defines homeothermy (Bligh and Johnson 1973). Homeothermy refers to a pattern of thermoregulation in a tachymetabolic species in which the variation in core temperature is maintained within arbitrarily defined limits despite much larger variation in ambient temperature (Bligh and Johnson 1973). Hence, the term “heterothermy” is problematic in two senses. Firstly, it does not exclusively refer to T_b below normothermy. Secondly, the distinction between normothermic and heterothermic T_b is based on an arbitrary division (Bligh and Johnson 1973). Despite these problems, heterothermy is the term most commonly used in current literature to describe hibernation, torpor and rest-phase hypothermia.

The IUPS definition of “hypothermia” is the condition of a temperature-regulating animal in which the core temperature is more than one standard deviation below the mean

core temperature of the species in resting conditions in a thermoneutral environment (Bligh and Johnson 1973). “Hypothermia” has the disadvantage that, whereas “heterothermy” refers exclusively to tachymetabolic species (mammals and birds), “hypothermia” is applicable to any animal that regulates T_b . In addition, some species of birds, such as mousebirds and todies, exhibit relatively labile normothermic T_b s, and the IUPS definition of hypothermia does not make allowance for such normothermic variation.

Given the above limitations, the term I have chosen to describe endotherm hibernation, torpor and rest-phase hypothermia is “facultative hypothermic responses”. This term unambiguously incorporates both the pattern of thermoregulation (T_b below the normothermic range) and the physiological mechanism (facultative, reversible T_b depression, as opposed to pathological, irreversible heat loss). In this sense, facultative hypothermic responses represent heterothermic thermoregulation. However, heterothermy does not necessarily comprise facultative hypothermia, since heterothermy refers to T_b variation both above and below the normothermic range.

My initial intention was to use the term “facultative hypothermic responses” throughout the thesis. However, the use of “heterothermy” is widespread in the literature, and is incorporated into terms such as “daily heterothermy”, “seasonal heterothermy” and “heterotherm”. In many instances, it was simply not possible to discuss data in the context of recent studies without referring to “heterothermy”. Hence, I use “facultative hypothermic responses” and “heterothermy” interchangeably. Where I use “heterothermy”, it refers exclusively to T_b variation below the normothermic range. For convenience, I frequently refer to “facultative hypothermic responses” simply as “hypothermia”.

Thesis structure

The broad objective of this thesis is provide a conceptual framework for the study of avian facultative hypothermia by investigating various evolutionary, ecological and physiological determinants of hypothermia in southern African species. Specifically, I investigate the following topics:

1) The distinction between rest-phase hypothermia and torpor

One of the central issues in the study of avian hypothermia is whether shallow hypothermic responses and pronounced hypothermia (torpor) represent discrete physiological states or components of an avian hypothermic response continuum. In Chapter 1, I review avian hypothermic responses, and assess the widely-accepted distinction between these categories of responses using several physiological parameters. In Chapter 2, I investigate the distinction between normothermy, rest-phase hypothermia and torpor in a well-known avian heterotherm, the speckled mousebird *Colius striatus*.

2) The interaction between facultative hypothermia and communal roosting

In addition to facultative hypothermic responses, one of the avenues whereby birds substantially reduce rest-phase energy expenditure is communal roosting. Communal roosting and sociality have profound implications for many aspects of a species' ecology, and understanding how communally-roosting species use hypothermia may provide insights into ecological and evolutionary determinants of hypothermia. In Chapters 3 and 4, I use two species of mousebird as models to investigate the interaction between hypothermic responses and communal roosting.

3) *Evolutionary and ecological determinants of avian facultative hypothermia*

In Chapter 5, I use the red-headed finch (*Amadina erythrocephala*) as a model species to investigate the hypothesis that in passerines, the capacity for pronounced hypothermia may be constrained by phylogeny. *A. erythrocephala* is a small species endemic to the arid regions of southern Africa, and may be expected *a priori* to experience strong selection for the ability to reduce energy expenditure by means of hypothermia. Hence, this species offers insights into the relative importance of phylogenetic determinants and ecological determinants of avian hypothermic responses.

Chapter 6 is an analysis of zoogeographical variance in avian basal metabolic rate (BMR). While this chapter does not deal directly with avian hypothermic responses, it links broad-scale patterns of climatic variability to selection for reduced energy expenditure. Habitat characteristics which select for low maintenance energy requirements (i.e. low BMR) are presumably also important ecological determinants of hypothermia. In addition, this chapter identifies an important selection process underlying the avian metabolic continuum. I argue in Chapter 7 that the notion of an avian metabolic continuum may be useful in predicting the occurrence of torpor.

Avian facultative hypothermia has been investigated in a small number of species from a limited range of taxa. This lack of information means that it is difficult to identify generalised ecological correlates of the capacity for hypothermic responses, in particular the capacity for torpor. In Chapter 7, I present a conceptual model for evolutionary and ecological determinants of avian torpor. I argue that the occurrence of torpor can be predicted using phylogeny, the M_b -dependent costs of re-warming following a hypothermic bout, relative energetic benefits and potential ecological costs, and specific ecological factors.

Literature cited

- Bennett, A. F. and Ruben, J. A. 1979. Endothermy and activity in vertebrates. *Science* 206: 649 - 654.
- Bligh, J. and Johnson, K. G. 1973. Glossary of terms for thermal physiology. *J. Appl. Physiol.* 35: 941 - 961.
- Duchamp, C., Marmonier, F., Denjean, F., Lachuer, J., Eldershaw, T. P. D., Rouanet, J. L., Morales, A., Meister, R., Bénistant, C., Roussel, D., and Barré, H. 1999. Regulatory, cellular and molecular aspects of avian muscle non-shivering thermogenesis. *Ornis Fennica* 76: 151 - 165.
- Feduccia, A. 1996. The origin and evolution of birds. Yale University Press, New Haven.
- Hayes, J. P. and Garland, T. 1995. The evolution of endothermy: testing the aerobic capacity model. *Evolution* 49: 836 - 847.
- Lyman, C. P., Willis, J. S., Malan, A., and Wang, L. C. H. (Eds.) 1982. Hibernation and torpor in mammals and birds. Academic Press, New York.
- Marjoniemi, K. and Hohtola, E. 1999. Shivering thermogenesis in leg and breast muscles of Galliform chicks and nestlings of the domestic pigeon. *Physiol. Biochem. Zool.* 72: 484 - 492.
- Merola-Zwartjes, M. and Ligon, J. D. 2000. Ecological energetics of the Puerto Rican tody: heterothermy, torpor and intra-island variation. *Ecology* 81: 990 - 1002.

Reinertsen, R. E. 1996. Physiological and ecological aspects of hypothermia. In: Carey, C. (Ed.) *Avian energetics and nutritional ecology*. Chapman & Hall, New York.

Ruben, J. 1995. The evolution of endothermy in mammals and birds: from physiology to fossils. *Ann. Rev. Physiol.* 57: 69 - 95.

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

Chapter 1. Avian facultative hypothermic responses: a review.

Introduction

Circadian avian body temperature (T_b) cycles follow typical endotherm circadian rhythms (Aschoff 1982; Prinzinger et al. 1991). Body temperature (T_b) during the rest-phase (ρ) is regulated at a T_b setpoint a few degrees lower than that defended during the active phase (α) (Prinzinger et al. 1991). The amplitude of normothermic circadian T_b rhythms is inversely related to body mass (M_b) (Aschoff 1982). Facultative increases in the circadian amplitude of T_b rhythms, during which ρT_b is depressed below normothermic levels, have been observed in several species (Prinzinger et al. 1991; Reinertsen 1996). Periods of facultative hypothermia appear to be important proximate responses to increased thermoregulatory demands and/or reduced energy availability, particularly in small species with high mass-specific energy requirements (Lyman et al. 1982; Prinzinger et al. 1991; Reinertsen 1996).

Recent studies suggest that facultative hypothermic responses may be widespread among birds, and may play a more important role in avian physiological ecology than was previously thought. For instance, telemetric studies of thermoregulation in free-ranging Caprimulgids indicate that hypothermic responses are used routinely by common poorwills (*Phalaenoptilus nuttallii*), Australian owlet-nightjars (*Aegotheles cristatus*) and tawny frogmouths (*Podargus strigoides*) (Brigham 1992; Brigham et al. 2000; Körtner et al. 2000). Moreover, avian hypothermic responses occur over a larger range of body mass (M_b) than previously suspected (Körtner et al. 2000; Butler and Woakes 2001; Schleucher in press).

The hypothermic responses exhibited by endotherms are commonly categorized by physiological parameters such as bout length, minimum T_b , and the extent of metabolic suppression (Geiser and Ruf 1995). The physiological parameters of avian hypothermic

responses are in many cases consistent with those of mammalian daily torpor (Geiser and Ruf 1995). In addition, the common poorwill exhibits multi-day torpor bouts similar to mammalian hibernation (Jaeger 1948;1949; Brigham 1992). However, several bird species exhibit relatively shallow hypothermia during which T_b is depressed by less than 10°C below normothermic levels (Prinzinger et al. 1991; Reinertsen 1996). This hypothermic response does not appear to occur in mammals and is referred to as rest-phase hypothermia (Reinertsen 1996) or controlled rest-phase hypothermia (Prinzinger et al. 1991).

The distinction between rest-phase hypothermia and torpor remains controversial. Prinzinger et al. (1991) and Reinertsen (1996) have argued that the criteria for torpor, namely a state of inactivity and reduced responsiveness to external stimuli (Bligh and Johnson 1973), are met below specific T_b s. Whereas Prinzinger et al. (1991) argued that $T_b < 25^\circ\text{C}$ indicate torpor, Reinertsen (1996) suggested that the criteria for torpor are usually met at $T_b < 30^\circ\text{C}$. However, it is unclear whether avian rest-phase hypothermia and daily torpor represent discrete physiological phenomena or components of a hypothermic response continuum (Prinzinger et al. 1991; Reinertsen 1996). Moreover, little effort has been made to differentiate between these responses using physiological parameters, such as those used by Geiser and Ruf (1995) to distinguish between daily torpor and hibernation.

In this paper, I use the term “facultative hypothermic responses” to include hibernation, torpor and rest-phase/controlled hypothermia. This term describes both the pattern (T_b below normothermic levels) and the mechanism involved (facultative T_b depression, as opposed to unavoidable, pathological hypothermia) involved. For convenience, I frequently refer to “facultative hypothermic responses” simply as “hypothermia”.

The objectives of this study are to a) review the occurrence, patterns and proximate determinants of avian hypothermic responses, and b) assess the validity of the widely-

accepted distinction between avian daily torpor and rest-phase hypothermia using physiological parameters such as body mass (M_b) and minimum hypothermic T_b .

Data selection

Records of facultative hypothermic responses are available for approximately 95 avian species (Table 1). From these sources, I obtained as many of the following data as possible: body mass (M_b), normothermic T_b (T_{norm}), minimum T_b during hypothermia (T_{min}), minimum oxygen consumption ($VO_{2\text{min}}$) during hypothermia, as well as information regarding the apparent proximate determinant(s) of hypothermia. In cases where M_b was not provided, I obtained M_b from Dunning (1993). Initially, I attempted to obtain mean values for T_{min} for each species. However, in many studies a mean T_{min} value was not calculated, and I hence used the lowest T_{min} observed in each study in birds that were able to arouse spontaneously without any apparent adverse effects. I used Sibley and Ahlquist's (1990) average linkage (UPGMA) phylogeny for avian orders and families, and obtained taxonomic, phylogenetic and distribution data from Sibley and Ahlquist (1990) and Sibley and Monroe (1990), as well as regional field guides.

Analyses and interpretation

Phylogenetic distribution

Facultative hypothermic responses have been reported in species from 29 families representing 11 orders (Figure 1). However, the capacity for hypothermia in the majority of the 138 avian families remains unknown. In the infraclass Eoaves, shallow hypothermia has been reported in two species (*Coturnix coturnix* and *Branta leucopsis*) (Table 1, Figure 1). However, many species in the Eoaves are relatively large and their capacity for hypothermia

Table 1. Avian species known to use facultative hypothermia. Where possible, data include body mass (M_b), normothermic body temperature (T_{norm}), minimum hypothermic body temperature (T_{min}), $T_{norm}-T_{min}$, minimum metabolic rate during hypothermia (VO_{2min}), the extent of metabolic suppression (VO_{2min} as percentage of BMR) and the zoogeographical zone in which the species occurs.

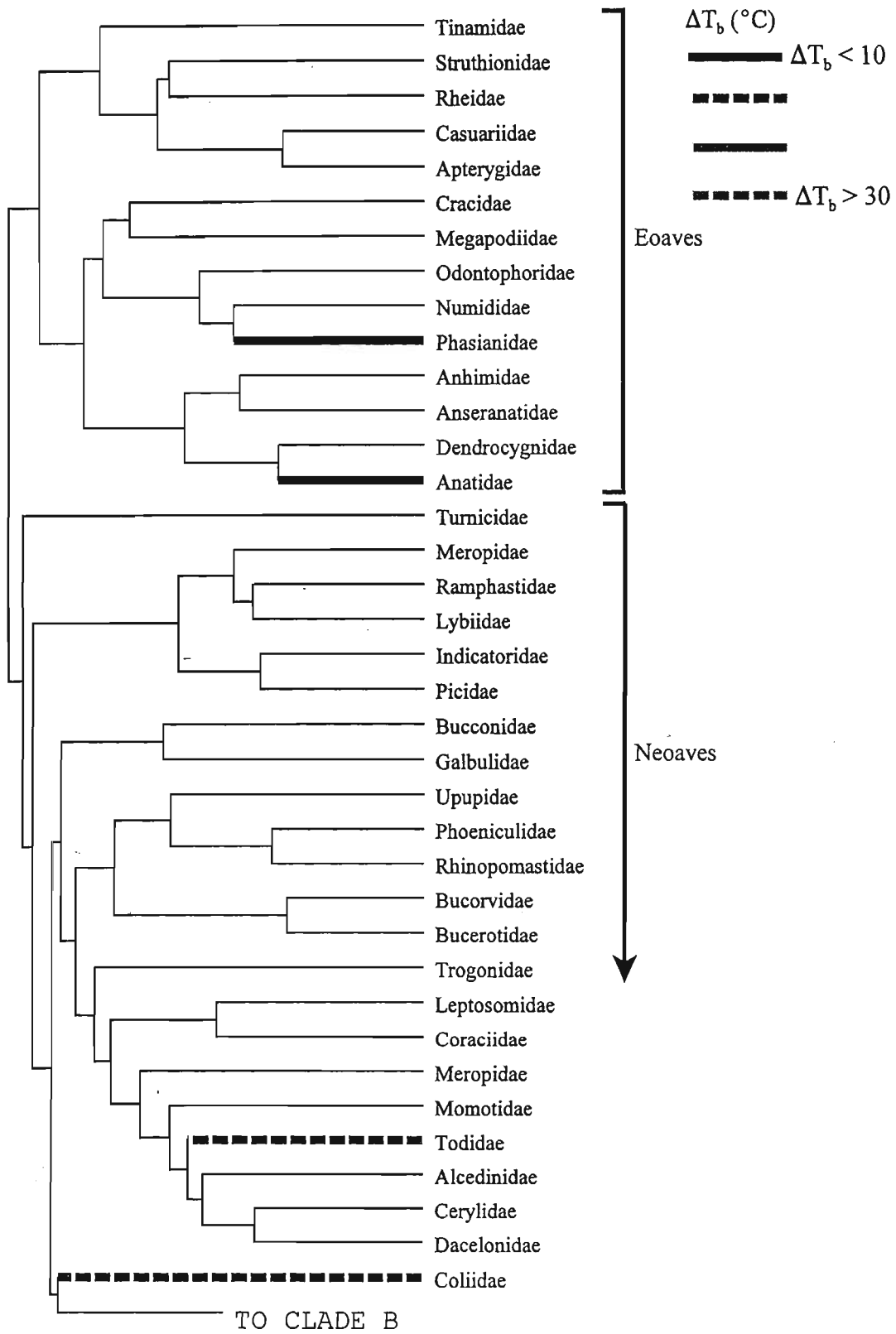
	Species	M_b (g)	T_{norm} (°C)	T_{min} (°C)	$T_{norm}-T_{min}$ (°C)	BMR ml O ₂ ·g ⁻¹ ·h ⁻¹	VO_{2min}	Reduction %	Zone	References	
Galliformes											
Phasianidae											
	Japanese quail	<i>Coturnix coturnix</i>	156	40.5	36.5	5			Pal	Hohtola et al. (1991)	
Anseriformes											
Anatidae											
	Barnacle goose	<i>Branta leucopsis</i>	1890	40.1	35.1	5			Pal	Butler and Woakes (2001)	
Coraciiformes											
Todidae											
	Puerto Rican tody	<i>Todus mexicanus</i>	6.2	36.3	26	10.3	3.24	3.10	4.3	Neo	Merola-Zwartjies and Ligon (2000)
Coliiformes											
Coliidae											
	Speckled mousebird	<i>Colius striatus</i>	51	36	18.2	17.8	0.83	0.11	86.8	Afro	Chapter 2
	Red-backed mousebird	<i>Colius castonotus</i>	58	38.5	20	18.5	1.20	0.09	92.5	Afro	Prinzinger et al. (1981)
	White-backed mousebird	<i>Colius colius</i>	35.1	35	26	9				Afro	McKechnie and Lovegrove (2001)
	Red-faced mousebird	<i>Urocolius indicus</i>	53	38.6				0.67		Afro	Hoffmann and Prinzinger (1984)
	Blue-naped mousebird	<i>Urocolius macrourus</i>	49	37.9	22	15.9	0.79	0.65	17.4	Afro	Schaub et al. (1999); Hoffmann and Prinzinger (1984)
Cuculiformes											
Neomorphidae											
	Roadrunner	<i>Geococcyx californianus</i>	295	38.4	34.3	4.1				Nearc	Ohmart & Lasiewski (1971)
Crotophagidae											
	Smooth-billed ani	<i>Crotophaga ani</i>	113		32.6					Neo	Warren (1960)
Apodiformes											
Apodidae											
	Common swift	<i>Apus apus</i>	42		20.1					Pal	Koskimies (1948)
	White-throated swift	<i>Aeronautes saxatilis</i>	31	38.6	17	21.6				Nearc	Bartholomew et al. (1957)
Trochiliformes											
Trochilidae											
	White-bellied woodstar	<i>Acestrura mulsant</i>	3.3							Neo	Krueger et al. (1982)
	Shining sunbeam	<i>Agleactis cupripennis</i>	7.2		18					Neo	Krueger et al. (1982)
	Plain-tailed emerald	<i>Amazilia leucogaster</i>	4	39.4	32	7.4				Neo	Morrison (1962)
	Versicolored emerald	<i>Amazilia versicolor</i>	4.1	36.8	23.8	13				Neo	Bech et al. (1997)
	Black-throated mango	<i>Anthracoceros nigricollis</i>	7.7		18					Neo	Krueger et al. (1982)
	Black-chinned hummingbird	<i>Archilochus alexandri</i>	3.2	38.8			3.53	0.20	94.3	Nearc	Lasiewski (1963)
	Chestnut-breasted coronet	<i>Boissonneaua matthewsii</i>	7.2							Neo	Krueger et al. (1982)
	Anna's hummingbird	<i>Calypte anna</i>	3.4	38	8.8		3.85	0.17	95.6	Nearc	Lasiewski (1963)
	Costa's hummingbird	<i>Calypte costae</i>	3.2				3.03	0.38	87.4	Nearc	Lasiewski (1963)
	Blue-tailed emerald	<i>Chlorostilbon mellisugus</i>	2.9		18					Neo	Krueger et al. (1982)
	Golden-tailed sapphire	<i>Chrysoronia oenone</i>	5	35	18	17		2.05		Neo	Krueger et al. (1982)
	Blue-chinned sapphire	<i>Clorestes notatus</i>	3	38.8	31	7.8				Neo	Morrison (1962)

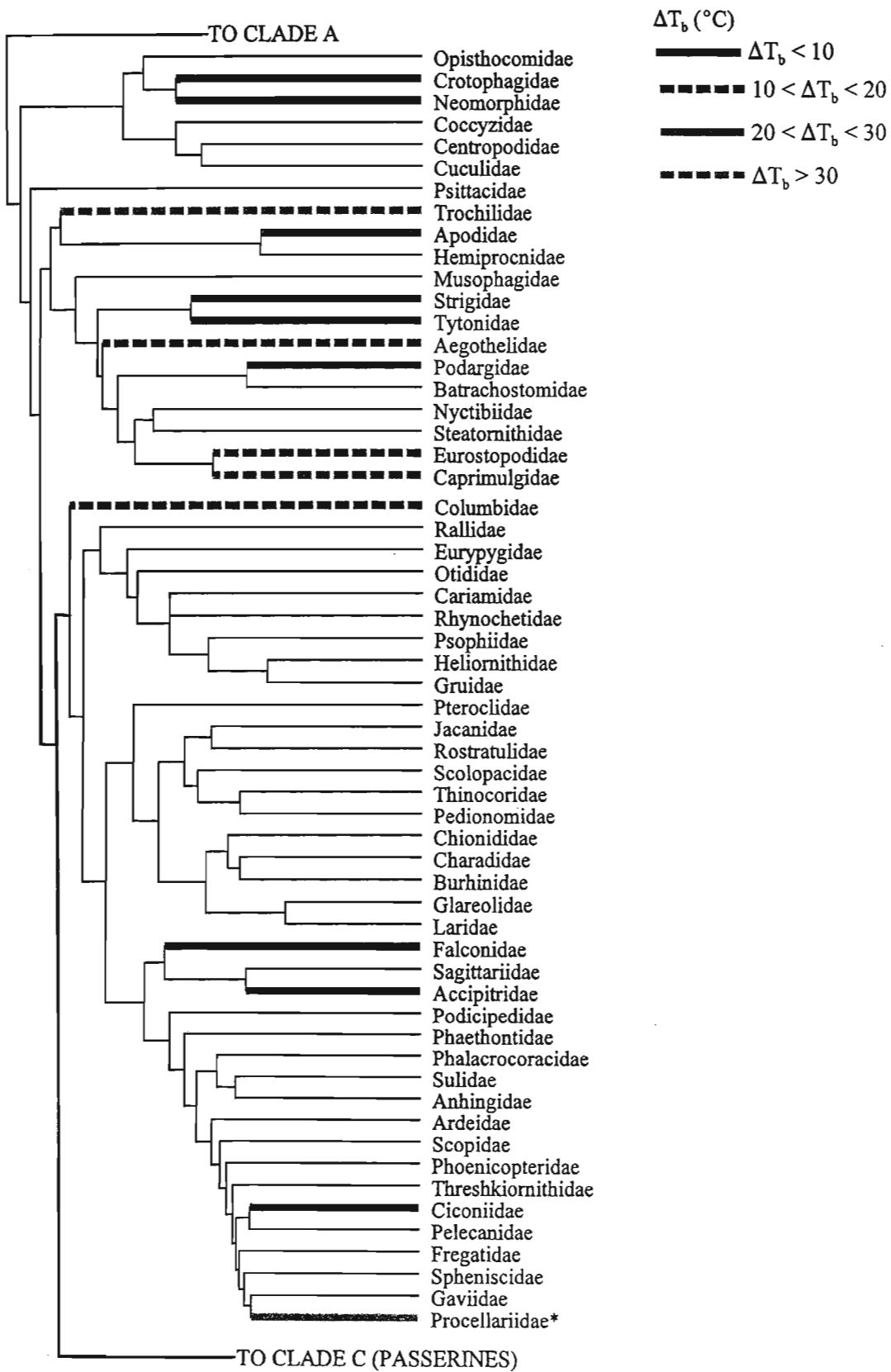
Rivoli's hummingbird	<i>Eugenes fulgens</i>	8		10					0.50	Neo	Wolf and Hainsworth (1972)	
Purple-throated carib	<i>Eulampis jugularis</i>	8		18					1.00	Neo	Hainsworth and Wolf (1970)	
Swallow-tailed hummingbird	<i>Eupetomena macroura</i>	8.6	37.1	23.2	13.9					Neo	Bech et al. (1997)	
White-necked jacobin	<i>Florisuga mellivora</i>	6.9		18						Neo	Krueger et al. (1982)	
White-chinned sapphire	<i>Hylocharis cyanus</i>	3		31						Neo	Morrison (1962)	
Blue-throated hummingbird	<i>Lampornis clemenciae</i>	8	35.7	19.6	16.1				0.45	Neo	Krueger et al. (1982)	
Black jacobin	<i>Melanotrochilus fuscus</i>	7.7	37.3	24.7	12.6					Neo	Bech et al. 1997	
Booted racket-tail	<i>Ocreatus underwoodii</i>	2.7	39	18	21					Neo	Krueger et al. (1982)	
Ecuadorian hillstar	<i>Oreotrochilus chimborazo</i>	8.1								Neo	French and Hodges (1959)	
Andean hillstar	<i>Oreotrochilus estella</i>	8.5	35.7	6.5	29.2				0.75	Neo	Carpenter (1974); Krueger et al. (1982)	
Antillean crested hummingbird	<i>Orthorhynchus cristatus</i>	2.9	39	20.8	18.2	6.01			1.25	79.2	Neo	Krueger et al. (1982)
Fiery-throated hummingbird	<i>Panterpe insignis</i>	5		10					0.50	Neo	Wolf and Hainsworth (1972)	
Giant hummingbird	<i>Patagona gigas</i>	19		18						Neo	Krueger et al. (1982)	
Streamertail	<i>Trochilus scitulus</i>	4								Neo	Krueger et al. (1982)	
Broad-tailed hummingbird	<i>Selasphorus platycerus</i>	3.4	38.7	6.5	32.2					Nearc	Calder and Booser (1976)	
Rufous hummingbird	<i>Selasphorus rufus</i>	3.3	38.8	13	25.8	3.35	0.43	87.2		Nearc	Lasiewski (1963), Hiebert (1990)	
Allen's hummingbird	<i>Selasphorus sasin</i>	3		22		3.80	1.24	67.4		Nearc	Pearson (1953); Lasiewski (1963)	
Whitetip (Hybrid)	<i>Urostroke benjamini</i> <i>Thalaurania furcata</i> X <i>T. scitulus</i>	3.9	38	28	10					Neo	Krueger et al. (1982) Krueger et al. (1982)	
Strigiformes												
Strigidae												
Snowy owl	<i>Nyctea scandiaca</i>	2032	38.6	32.6	6					Pal, Nearc	Gessaman and Folk (1969)	
Tytonidae												
Barn owl	<i>Tyto alba</i>	316	39.6	35.5	4.1					All	Thouzeau et al. (1999)	
Caprimulgidae												
Common nighthawk	<i>Chordeiles minor</i>	72.5	37	18	19					Nearc	Lasiewski and Dawson (1964)	
Lesser nighthawk	<i>Chordeiles acutipennis</i>	49.9	39.5	15.7	23.8					Nearc, Neo	Marshall (1955)	
European nightjar	<i>Caprimulgus europaeus</i>	69	37.4	7	30.4					Pal	Peiponen (1966)	
Common poorwill	<i>Phalaenoptilus nuttallii</i>	35	39.1	4.3	34.8					Nearc	Brigham (1992); Withers (1977)	
Whip-poorwill	<i>Caprimulgus vociferous</i>	55		18.5						Nearc	R.M. Brigham pers. comm.	
Eurostropodidae												
Spotted nightjar	<i>Eurostropodus argus</i> (= <i>guttatus</i>)	88	40.5	29.6	10.9	0.83	0.40	51.8		Aus	Dawson and Fisher (1969)	
Podargidae												
Tawny frogmouth	<i>Podargus strigoides</i>	500	36	27.2	8.8					Aus	Koertner et al. (2000)	
Aegothelidae												
Australian owlet-nightjar	<i>Aegotheles cristatus</i>	40		22						Aus	Brigham et al. (2000)	
Columbiformes												
Columbidae												
Rock pigeon	<i>Columba livia</i>	375	39.9	35	4.9					Pal	Graf et al. (1989); Rashotte et al. (1995)	
African collared dove	<i>Streptopelia roseogrisea</i> (= <i>risoria</i>)	150	38.5	32	6.5					Afro	Walker et al. (1983)	
Inca dove	<i>Scardafella inca</i>	44	39	28.5	10.5					Nearc	MacMillen and Trost (1967)	
Diamond dove	<i>Geopelia cuneata</i>	38	38.6	35.3	3.3					Aus	Schleucher (1994)	
Namaqua dove	<i>Oena capensis</i>	36	38.4	34.4	4	1.21	0.95	22.0		Afro	Schleucher (in press)	
Cloven-feathered dove	<i>Drepanoptila holosericea</i>	200	37.7	24.8	12.9	0.72	0.27	62.2		Aus	Schleucher (in press)	
Ciconiiformes												
Falconidae												

American kestrel	<i>Falco sparverius</i>	117.7	39.3	38.3	1					Nearc	Shapiro and Weathers (1981)
Accipiteridae											
Griffon vulture	<i>Gyps fulvus</i>	6580	37.9	35.3	2.6					Pal	Bahat and Choshniak (1998)
Ciconiidae											
Black vulture	<i>Cathartes aura</i>	2230	38	34	4					Nearc,Neo	Heath (1962)
Procellariidae											
Fork-tailed storm-petrel*	<i>Oceanodroma furcata</i>	55.3		10.6						Pelagic	Boersma (1986)
Passeriformes											
Tyrannidae											
Golden-collared manakin	<i>Manacus vitellinus</i>	15.5	37.9	26.8	11.1	2.69	1.80	33.1		Neo	Bartholomew et al. (1983)
Red-capped manakin	<i>Pipra mentalis</i>	12.3	37.9	29	8.9	2.84	2.25	20.8		Neo	Bartholomew et al. (1983)
Meliphagidae											
Singing honeyeater	<i>Meliphaga virescens</i>	24.6			10.7					Aus	Collins and Briffa (1984)
Brown honeyeater	<i>Lichmera indistincta</i>	13								Aus	Collins and Briffa (1984)
Noisy miner	<i>Manorina melanocephala</i>				32					Aus	T.A. Maddocks (pers. comm.)
Corvidae											
Gray jay	<i>Perisoreus canadensis</i>	75.6	39	36.5	2.5					Nearc	Waite (1981)
Dusky woodswallow	<i>Artamus cyanopterus</i>			25						Aus	T.A. Maddocks (pers. comm.)
Muscicapidae											
Blackbird	<i>Turdus merula</i>	118.3	38.6	35	3.6					Pal	Biebach (1977)
Paridae											
Black-capped chickadee	<i>Parus atricapillus</i>	12.7	38.9	33.8	5.1					Nearc	Grossman and West (1977); Chaplin (1976)
Carolina chickadee	<i>Parus carolinensis</i>	10.1		30						Nearc	Mayer et al. (1982)
Siberian tit	<i>Parus cinctus</i>	12.4		32.1						Pal	Haftorn (1972)
Great tit	<i>Parus major</i>	16.75	39	29	10					Pal	Reinertsen (1985); Reinertsen and Haftorn (1986)
Willow tit	<i>Parus montanus</i>	11.13	38.35	32.5	5.85					Pal	Reinertsen and Haftorn (1986)
Hirundinidae											
House martin	<i>Delichon urbica</i>	22	38.9	25.7	13.2				20.0	Pal, Nearc	Prinzinger and Siedle (1988)
Barn swallow	<i>Hirundo rustica</i>	16								All	Keskaik (1976,1981a,b); Keskaik and Lyuleyeva (1968)
Sand martin	<i>Riparia riparia</i>	14.6								All	Keskaik (1976,1981a,b); Keskaik and Lyuleyeva (1968)
Violet-green swallow	<i>Tachycineta thalassina</i>	14.2	- Anecdotal -							Nearc	Lasiewski and Thompson (1966)
White-backed swallow	<i>Cheramoeca leucosternum</i>	14.8	- Anecdotal -							Aus	Serventy (1970)
Zosteropidae											
Australian silvereye	<i>Zosterops lateralis</i>	11		35.2						Aus	Maddocks and Geiser (1997)
Nectariniidae											
Eastern double-collared sunbird	<i>Nectarinia mediocris</i>	7.3	37.3	24	13.3					Afro	Cheke (1971)
Tacazze sunbird	<i>Nectarinia tacazze</i>	11		27						Afro	Cheke (1971)
Lesser double-collared sunbird	<i>Nectarinia chalybea</i>	7		23.3						Afro	B. Leon and J. R. B. Lighton (unpubl.)
Malachite sunbird	<i>Nectarinia famosa</i>	16.5	39.5	25.4	14.1					Afro	C. T. Downs and M. Brown (unpubl.)
Passeridae											
House sparrow	<i>Passer domesticus</i>	27.3		35						Pal	Steen (1958)
Tree sparrow	<i>Passer montanus</i>	22		30						Pal, Indo	Steen (1958)
Red-headed finch	<i>Amadina erythrocephala</i>	21.5	39.6	34.8	4.8					Afro	Chapter 5
Fringillidae											
Brambling	<i>Fringilla montifringilla</i>	27		38						Pal	Steen (1958)
White-crowned sparrow	<i>Zonotrichia leucophrys</i>	28	39	35.4	3.6					Nearc	Ketterson and King (1978)

Redpoll	<i>Carduelis flammea</i>	11.3	39.79	32	7.79	Pal	Steen (1958); Reinertsen and Haftom (1986)
Greenfinch	<i>Carduelis chloris</i>	31.3		33		Pal	Steen (1958)
Red crossbill	<i>Loxia curvirostra</i>	36.5	39.1	34	5.1	Pal	Prinzinger (unpubl.), cited in Prinzinger et al. (1991)
Rosy finch	<i>Leucosticte arctoa</i>	23.4	39	37.6	1.4	Pal	Clemens (1989)
Bananaquit	<i>Coereba flaveola</i>	10	38.1	35.4	2.7	Neo	Merola-Zwartjes (1998)

* Chicks only





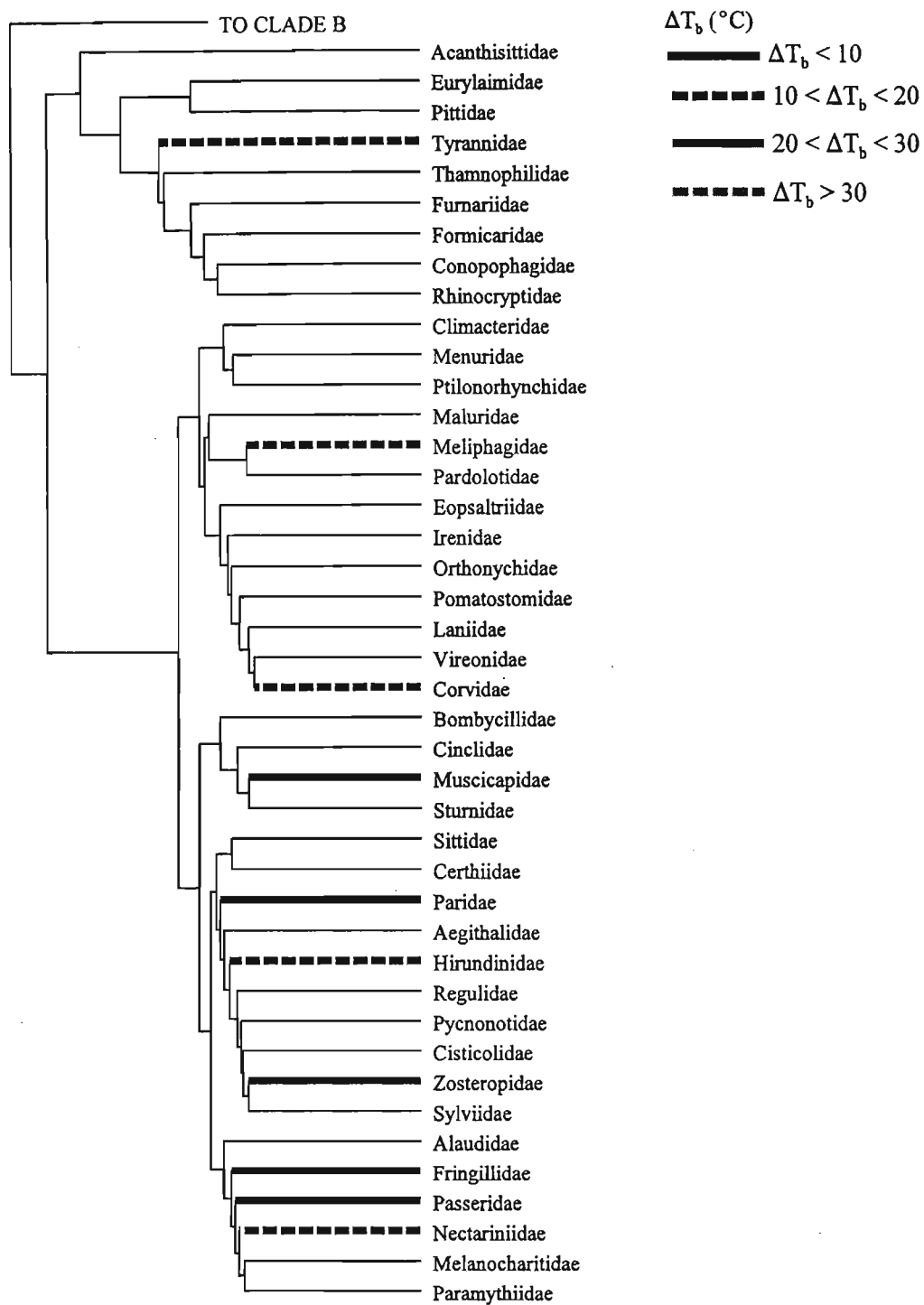


Figure 1. Phylogenetic distribution of avian facultative hypothermic responses. The phylogeny is that of Sibley and Ahlquist (1990). The extent of body temperature (T_b) depression is given as the difference between normothermic rest-phase T_b (T_{norm}) and minimum hypothermic T_b (T_{min}) i.e. $\Delta T_b = T_{norm} - T_{min}$. An asterisk indicates that T_{min} was recorded in chicks, not adult birds.

during a single circadian cycle is presumably constrained by large M_b (Prothero and Jürgens 1986). Within the infraclass Neoaves the capacity for moderate hypothermia, during which T_b is depressed by $< 20^\circ\text{C}$, occurs through-out the phylogeny (Table, Figure 1). On the other hand, more pronounced hypothermia during which T_b is depressed by 20°C or more, has been reported in only the Trochilidae, Apodidae and Caprimulgidae (Table 1, Figure 1).

The passerine capacity for hypothermia is limited, and T_b depression $>10^\circ\text{C}$ below normothermic levels has been reported in only 5 of 17 species for which measurements of T_{\min} exist (Table 1). The lowest passerine T_{\min} s were recorded in the Hirundinidae and Nectariniidae (Table 1, Figure 1). In addition, Bartholomew et al. (1983) calculated a T_b of 26.8°C from VO_2 measurements in a golden-collared mannikin (Tyrannidae: *Manacus vitellinus*). A T_b of ca. 25°C has been observed in a dusky woodswallow (Corvidae: *Artamus cyanopterus*) (T. A. Maddocks, pers. comm.).

The capacity for facultative hypothermia is not necessarily consistent within orders. For instance, infraordinal differences are marked in the Strigiformes. Body temperature depression of more than $6\text{--}8^\circ\text{C}$ has not been observed in owls (Strigidae and Tytonidae), and hypothermia may be absent altogether in *Aegolius funereus* (Hohtola et al. 1994). In contrast, T_b depression of more than 10°C appears to be widespread in the Caprimulgidae and allies (Podargidae, Eurostopodidae, and Aegithelidae). Moreover, the Caprimulgidae include the only known avian hibernator, the common poorwill (*Phalaenoptilus nuttalli*) (Jaeger 1948;1949; Brigham 1992).

The limited data (ca. 1% of extant species) are insufficient to objectively infer general patterns in the phylogenetic distribution of the avian capacity for hypothermia. Although the traits of hypothetical ancestors can be reconstructed using phylogenetic comparative methods (Garland and Ives 2000), there are presently too few data on avian hypothermic responses to

attempt this approach. At best, the available data suggest that the capacity for pronounced hypothermia increases with the relative age of taxa (Table 1, Figure 1). However, data on hypothermic responses in the older Neoaves, e.g. Piciformes and Upupiformes, are necessary to confirm this observation.

A pattern of more pronounced hypothermia in phylogenetically older taxa is consistent with current ideas regarding the evolution of heterothermy (daily torpor and hibernation). Malan (1996) has argued that heterothermy may be phylogenetically primitive, although it frequently constitutes a functionally advanced adaptation associated with small body size and unpredictable food supplies (Geiser 1998). A plesiomorphic, monophyletic origin of heterothermy, as proposed by (Malan 1996), predicts that heterothermy should be more widespread and pronounced in phylogenetically older taxa. Observations of daily torpor in the Macroscelidea (elephant shrews), a relatively old mammalian family, suggest a plesiomorphic origin of mammalian daily torpor (Lovegrove et al. 1999). Moreover, patterns of thermoregulation in two species of mousebird appear to represent an intermediate step in Malan's (1996) hypothesized origin of heterothermy, and provide circumstantial support for this hypothesis (McKechnie and Lovegrove 2000).

Zoogeographical distribution

Facultative hypothermic responses have been reported in species from all zoogeographic zones, except the Indomalayan zone (Table 2). Of the 95 species in the data set, 55 (58%) occur at latitudes $< 30^{\circ}\text{N/S}$. Fourteen species occur between $30 - 60^{\circ}\text{N/S}$, and only four species occur exclusively at latitudes $> 60^{\circ}\text{N/S}$. The available data set is clearly biased towards the Holarctic, in terms of both the number of species and taxonomic diversity (Table 2). Although the number of species in which hypothermia has been investigated is greatest in

the Neotropics (29 species), 25 of these are hummingbirds. Data on avian hypothermia are absent entirely for Indomalayan species.

Table 2. Summary of zoogeographic distribution of avian species and families in which facultative hypothermic responses have been reported.

Zone	No. species	No. families
Afrotropics	12	4
Australasia	11	8
Indomalaya	0	0
Nearctic	18	10
Neotropics	29	5
Palaeartic	16	10
Other (> 1 zone)	9	7

Body size

Facultative hypothermic responses have been recorded in species in the M_b range of 2.7g (*Ocreatus underwoodii*) to 6500g (*Gyps fulvus*). The M_b frequency distribution of species in which hypothermia has been reported is right-skewed (Figure 2). A comparison of this M_b distribution with a re-scaled distribution for of approximately 6200 avian species (dotted line in Figure 2), shows that hypothermia occurs across almost the entire avian M_b range, but the relative frequency is higher in small species.

To determine whether species that employ rest-phase hypothermia (sensu Prinzinger et al. 1991; Reinertsen 1996) and daily torpor (sensu Geiser and Ruf 1995) respectively are

distinguishable on the basis of M_b , I compared the M_b of species in which observed $T_{\min} > 27.5^\circ\text{C}$ with those in which $T_{\min} < 27.5^\circ\text{C}$. This body temperature is midway between the two T_b s previously proposed as the lower limit of rest-phase hypothermia - 25°C (Prinzinger et al. 1991) and 30°C (Reinertsen 1996). Moreover, $T_b = 27.5^\circ\text{C}$ represents a T_b depression of ca. 10°C below normothermic T_b for most species (Prinzinger et al. 1991).

The mean M_b of species in which $T_{\min} < 27.5^\circ\text{C}$ was significantly lower than species in which $T_{\min} > 27.5^\circ\text{C}$ (Kolmogorov-Smirnov test, $P < 0.05$). However, the respective frequency distributions of these two groups show a high degree of overlap (Figure 2 inset), and M_b is not a reliable criterion for distinguishing between rest-phase hypothermia and torpor.

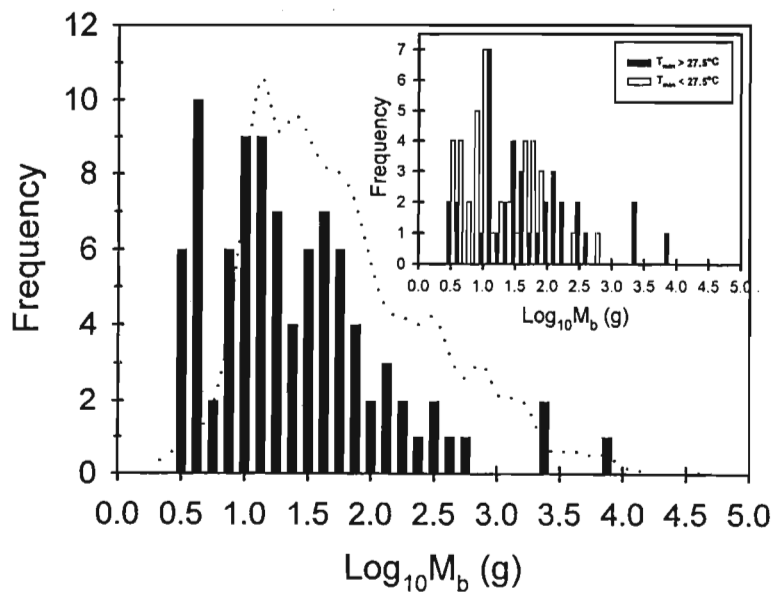


Figure 2. Frequency histogram of \log_{10} body mass (M_b) of avian species in which facultative hypothermic responses have been reported. The dotted line shows the $\log_{10} M_b$ frequency for approximately 6200 species (redrawn and rescaled from Blackburn and Gaston 1994). The inset graph shows the frequency histograms of \log_{10} body mass (M_b) of avian species for which minimum body temperature during facultative hypothermic responses (T_{\min}) is less than 27.5°C and greater than 27.5°C respectively.

Body temperature

Minimum T_b recorded during avian facultative hypothermic responses ranges from 4.3°C (*Phalaenoptilus nuttallii*) to over 38°C (Table 1). Although the overall avian T_{min} frequency distribution is fairly continuous (Figure 3 inset), the distributions for specific taxa differ markedly from each other (Figure 4). For instance, T_{min} values observed in 8 species of nightjars and allies are continuously distributed between 4.3°C and 29.6°C (Figure 4). In contrast, the distribution of T_{min} in the Trochiliformes has a clear mode at 18 - 20°C (Figure 4). Hence, the overall avian T_{min} frequency distribution (Figure 3 inset) represents the sum of several taxon-specific subsets. The frequency distributions of $T_{norm} - T_{min}$ (Figure 3) and T_{min} (Figure 3 inset) are continuous, with no discernable gaps or obvious modality. These continuous distributions do not support the argument that avian hypothermic responses fall into physiologically discrete categories that are distinguishable on the basis of minimum T_b alone.

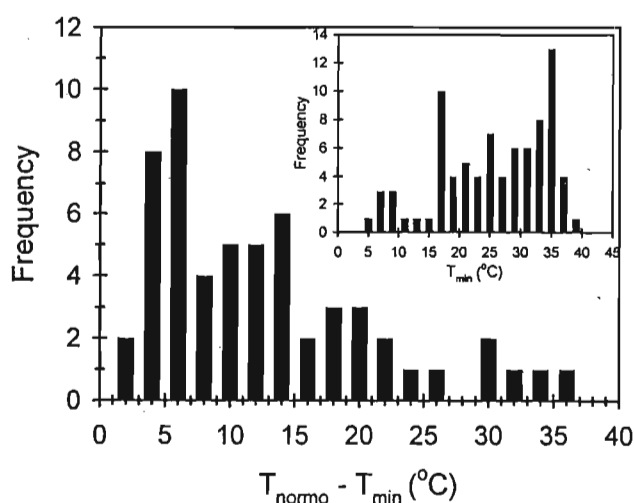


Figure 3. Frequency histogram of the difference between normothermic and minimum hypothermic body temperature ($T_{norm} - T_{min}$) in 57 avian species. The inset graph shows the frequency distribution of T_{min} in 82 species.

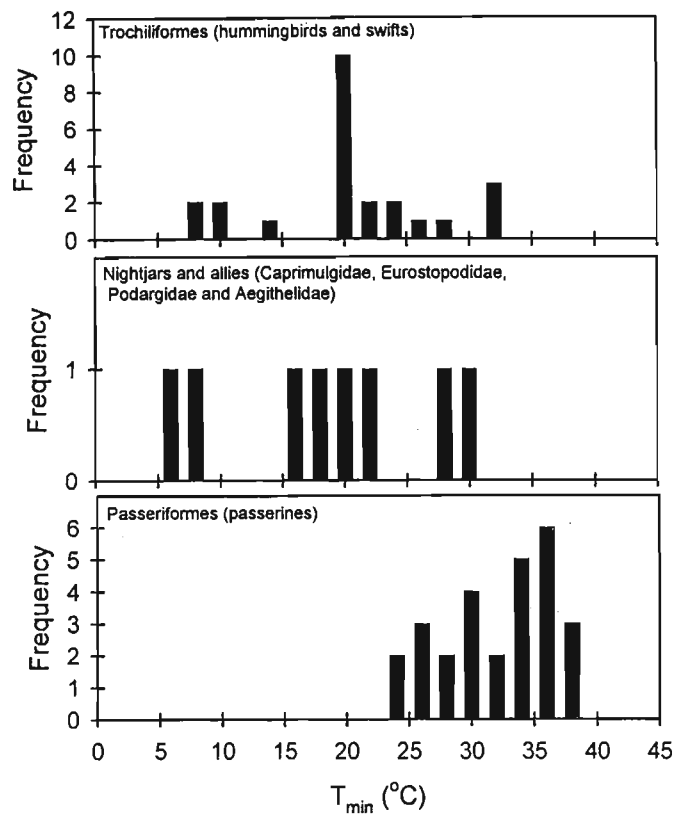


Figure 4. Frequency histograms of minimum hypothermic body temperature (T_{\min}) in three avian taxa.

Further evidence that T_b is not a reliable indicator of physiological state is provided by Merola-Zwartjes and Ligon (2000). These authors distinguished between “heterothermy” (apparently atypically labile normothermic T_b) and torpor in Puerto Rican todies (*Todus mexicanus*) by the degree to which the birds responded to external stimuli. Todies which did not respond to handling were considered to be torpid (Merola-Zwartjes and Ligon 2000). On the other hand, todies which remained alert, responsive to stimuli and capable of flight were considered to be in a state of “heterothermia” (Merola-Zwartjes and Ligon 2000). The minimum T_b observed in a non-torpid tody was 27.9°C, whereas the T_b of torpid birds ranged from 23.5°C to 29.3°C. The overlap of the torpid and non-torpid T_b ranges in *T. mexicanus* calls into question the notion of specific T_b limits for daily torpor and rest-phase hypothermia.

Although large differences in avian T_b (for instance $T_b = 35^\circ\text{C}$ and 15°C) undoubtedly reflect different physiological states, the biological reality of specific T_b limits, such as those proposed by Prinzinger et al. (1991) and Reinertsen (1996), is doubtful.

The question of whether avian rest-phase hypothermia and torpor represent discrete physiological states or components of a hypothermic response continuum is difficult to assess with the available data. The continuous distribution of avian T_{\min} (Figure 3 inset) supports Reinertsen's (1996) view that rest-phase hypothermia and torpor represent components of a continuum, rather than discrete physiological phenomena. However, the clear behavioural distinction between torpid and non-torpid birds (Merola-Zwartjes and Ligon 2000) supports Prinzinger et al.'s (1991) assertion that rest-phase hypothermia and torpor represent totally different physiological states.

Metabolic suppression

Whereas hypothermic T_b data are available for approximately 80 species, metabolic rates during hypothermia have been reported for relatively few species (Table 1). The lowest measured VO_2 was $0.09 \text{ ml O}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1}$ in the red-backed mousebird (*Colius castanotus*) (Table 1). The greatest extent of metabolic suppression (VO_2 equivalent to 4.4% of BMR) was observed in Anna's hummingbird (*Calypte anna*) (Table 1). Metabolic rates during hypothermia, expressed as a percentage of BMR, are available for 13 species which suppress T_b by 10°C or more, and range from 4.4% - 96% of BMR, similar to Geiser and Ruf's (1995) range of 4.4% - 67% for all daily heterotherms.

Body temperature during hypothermia depends on the degree of metabolic suppression as well as the M_b -dependent thermal conductance. Hence, a continuous frequency distribution of T_{\min} (Figure 4 inset) does not necessarily reflect a continuous underlying frequency

distribution of metabolic suppression. It may be possible to distinguish between avian hypothermic states using a metabolic parameter, such as metabolic rate during hypothermia expressed as a percentage of normothermic resting metabolic rate (RMR) at the same T_a . Geiser and Ruf (1995) used metabolic rate expressed as a percentage of basal metabolic rate (BMR) to distinguish between daily torpor and hibernation. However, many birds reduce T_b by only a few degrees below normothermic levels, and in such cases, expressing metabolic rate as a percentage of BMR is meaningless. At present, there are too few data to investigate the distinction between rest-phase hypothermia and torpor on the basis of metabolic suppression.

Patterns of thermoregulation during facultative hypothermia

In mammals, facultative hypothermic responses (daily torpor and hibernation) typically comprise three distinct phases. The entry phase is characterised by metabolic down-regulation and a concomitant decrease in T_b , and is followed by a maintenance phase during which T_b is regulated with respect to a reduced T_b setpoint (Lyman et al. 1982). The arousal phase involves an increase in metabolic heat production, which returns T_b to normothermic levels (Lyman et al. 1982).

Some traces of avian hypothermic T_b and/or VO_2 , such as those shown by a rufous hummingbird *Selasphorus rufus* (Figure 5a; Hiebert 1990) do fit the “entry-maintenance-arousal” pattern. However, in many cases avian hypothermic responses do not follow this pattern, and there may be substantial variation in the patterns of thermoregulation within species and individuals (Figure 5b-e). For instance, the patterns shown by three hummingbird species under semi-natural conditions (Figure 5b; Bech et al. 1997) were relatively variable. In addition to variability in the number of bouts exhibited during a single rest-phase, cooling rate

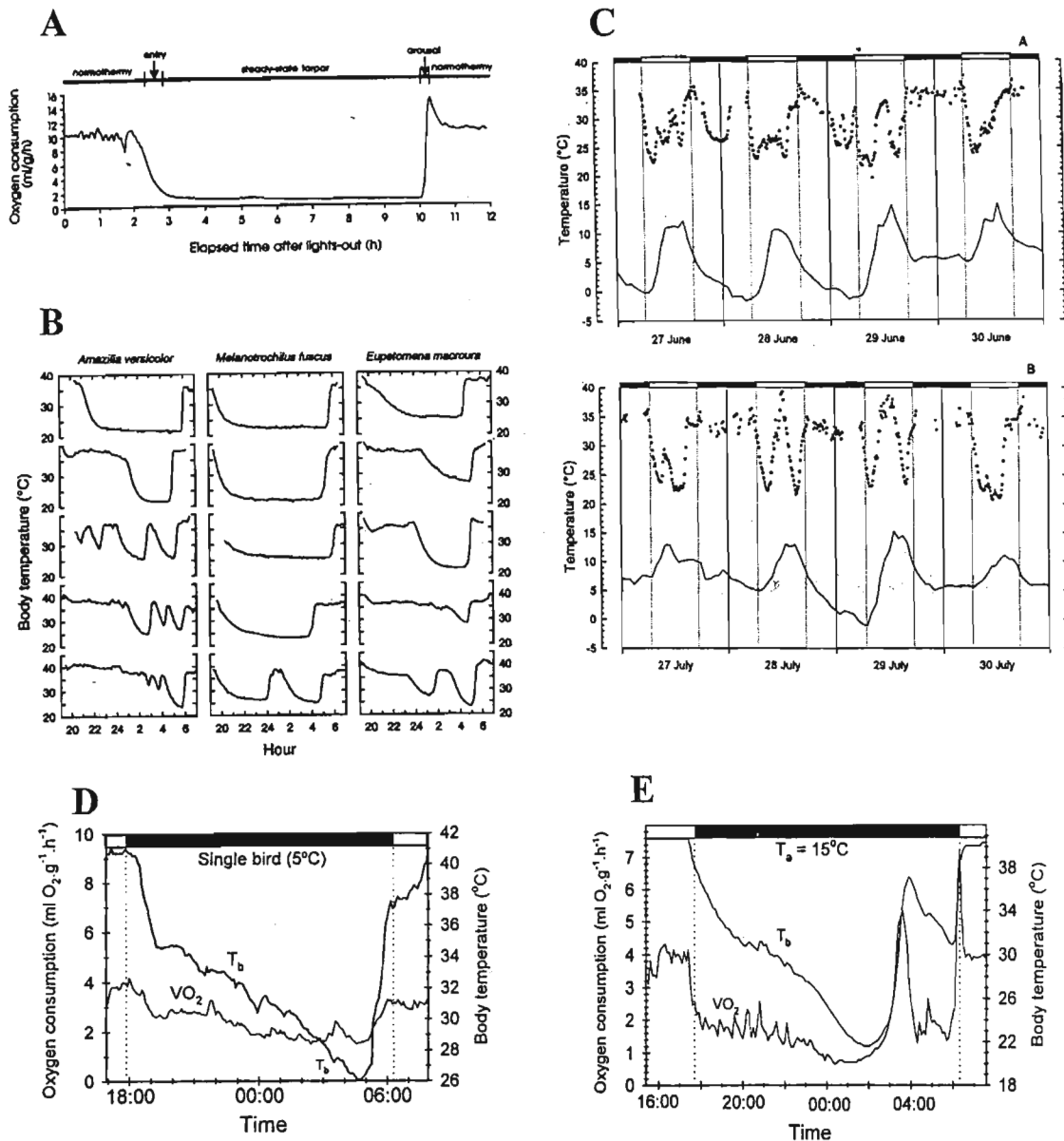


Figure 5. Traces of avian body temperature (T_b) and/or oxygen consumption (VO_2) during facultative hypothermic responses.

- A: VO_2 during torpor in rufous hummingbird *Selasphorus rufus* (Hiebert 1990). Note distinct entry, arousal and maintenance phases.
- B: multiple torpor bouts under semi-natural conditions in three species of hummingbird (Bech et al. 1997)
- C: Skin temperature (dotted line) and ambient temperature (T_a ; solid line) in a free-ranging Australian owlet-nightjar *Aegotheles cristatus* (Brigham et al. 2000)
- D: Rest-phase thermoregulation under laboratory conditions in single white-backed mousebird *Colius colius* at $T_a = 5^\circ\text{C}$ (McKechnie and Lovegrove 2001)
- E: Torpor bout under laboratory conditions in speckled mousebird *Colius striatus* (Chapter 2).

during the entry phase varied between individual bouts. Moreover, in some traces a maintenance phase was largely absent (Figure 5b). The reasons for the variability in cooling rate were unclear (C. Bech pers. comm.). Similarly, traces of skin temperature from an Australian owlet-nightjar (Figure 5c; Brigham et al. 2000) showed considerable variability. Whereas on some occasions a maintenance phase of several hours was apparent (e.g. night of 27-28 June), during other bouts the arousal phase followed the entry phase immediately (e.g. 28 July). A lack of initial metabolic suppression and concomitant rapid reduction in T_b was evident in two species of mousebirds, and approximately linear decreases in T_b preceded arousal (Figure 5d,e; McKechnie and Lovegrove 2001; Chapter 2). The unusual patterns of thermoregulation appear to be related to their distinctive communal roosting behaviour (McKechnie and Lovegrove 2001; Chapters 2-4).

Collectively, these data suggest that avian hypothermic thermoregulation is relatively variable compared to that observed during mammalian daily torpor and hibernation. The factors responsible for determining the pattern of thermoregulation during a particular hypothermic response have received little attention.

Proximate determinants of facultative hypothermia

Shallow hypothermic responses to food deprivation have been reported in several species, and have been particularly well-studied in pigeons (Graf et al. 1988;1989; Jensen and Bech 1992a,b; Phillips and Berger 1988; Rashotte et al. 1995;1988). Food deprivation also appears to be the proximate determinant of hypothermia in mousebirds (Bartholomew and Trost 1970; Hoffmann and Prinzinger 1984; Chapter 2). Whereas laboratory studies suggest that food scarcity is the proximate determinant of torpor in nightjars and allies, recent field data indicate that torpor is used routinely and that several factors other than food availability determine

whether or not a bird enters torpor (Brigham 1992; Csada and Brigham 1994; Geiser et al. 2000; Körtner et al. 2000).

In several species, hypothermia has been correlated with low T_a . Both shallow hypothermia (Merola-Zwartjes 1998) and torpor (Merola-Zwartjes and Ligon 2000) have been observed in tropical species in response to cold. Surprisingly, almost all facultative hypothermic responses to cold in Arctic and sub-Arctic species are fairly shallow, particularly those observed in the Paridae (Reinertsen 1983;1985; Reinertsen and Haftorn 1983;1986). However, hypothermic responses of Arctic species have only been investigated in passerines. Passerines in general do not exhibit the capacity for pronounced hypothermia (Table 1, Figure 1), and the absence of torpor in these species may be due to a phylogenetic limitation.

Early studies suggested that energy reserves were the sole proximate determinant of torpor in hummingbirds (Hainsworth et al. 1977). However, recent studies show that hummingbird torpor appears to be determined by a suite of factors that includes seasonal variation in the propensity for torpor (Carpenter 1974; Hiebert 1991), the perceived availability of food (Hiebert 1991) and temporal variation in assimilation efficiency (Hiebert 1991; McWhorter and Martinez del Rio 2000). A circannual cycle in the propensity for torpor has been observed in some species (Carpenter 1974; Hiebert 1991; Hiebert 1993). A possible mechanism for such circannual cycles involves seasonal physiological suppression of the stress response through variation in the sensitivity of the hypothalamic-pituitary-adrenal axis (Hiebert et al. 2000).

Testosterone levels appear to be responsible for gender-specific variation in the use of torpor and hibernation in several mammalian heterotherms (Barnes 1996; Lee et al. 1990; Hall and Goldman 1980; Mzilikazi 2000). Mzilikazi (2000) found that castrated Afrotropical pouched mice (*Saccostomus campestris*) readily entered torpor, whereas the application of

testosterone inhibited torpor. Potential endocrine determinants of avian torpor have received little attention. Merola-Zwartjes and Ligon (2000) found that torpor in the Puerto Rican tody *Todus mexicanus* was restricted to females, and suggested that gender-specific variation in the use of torpor was related to the effects of reproductive hormones, as well as the energetic stress of breeding experienced by the females. Elevated corticosterone levels increased the use of torpor in rufous hummingbirds (*Selasphorus rufus*), but the relationship between corticosterone concentration and torpor frequency varied between seasons (Hiebert et al. 2000).

Hypothermia appears to be avoided during incubation in some species, but not in others. Carpenter (1974) and Prinzinger and Siedle (1988) noted incidences of torpor in incubating broad-tailed hummingbirds (*Selasphorus platycercus*) and house martins (*Delichon urbica*) respectively, but torpidity adversely affected breeding success in the common poorwill (*Phalaenoptilus nuttallii*) and was avoided during incubation (Kissner and Brigham 1993; Csada and Brigham 1994; Brigham 1992). Incubating blue petrels (*Halobaena caerulea*) showed no evidence of hypothermia, even when experiencing severe energy stress (Ancel et al. 1998).

There is evidence that reductions in energy requirements by means of hypothermia may be important in migratory species. Carpenter and Hixon (1988) observed torpor in a rufous hummingbird (*Selasphorus rufus*) which was apparently in good condition, and argued that torpor may be used to conserve fat reserves prior to a migratory flight. More recently, Butler and Woakes (2001) showed that Barnacle geese used shallow hypothermia before and during their autumn migration. In the latter case, hypothermia was apparently used to reduce the rate at which fat reserves were depleted during migration (Butler and Woakes 2001).

Conclusions

The limited data on avian facultative hypothermic responses suggest that a) hypothermic responses occur through-out the avian phylogeny, b) hypothermic responses occur in species over most of the avian M_b range, c) the use of hypothermia is determined by suite of ecological and physiological determinants. Collectively, these observations support recent views that hypothermic responses are more widespread and play a more important role in avian energy balance than previously thought (Geiser et al. 2000; Körtner et al. 2000).

Several key questions regarding avian hypothermic responses remain unresolved. How did the avian capacity for facultative hypothermia evolve? The known phylogenetic distribution of pronounced hypothermia (torpor), as well as the patterns of thermoregulation in two species of mousebird (McKechnie and Lovegrove 2000) provide circumstantial evidence for a monophyletic, plesiomorphic origin of avian heterothermy, as proposed by Malan (1996). However, the absence of data of hypothermic responses in most avian families, and in particular the older Neoaves, precludes the rigorous testing of Malan's (1996) hypothesis.

The distinction between various avian hypothermic responses also remains controversial. Although T_b is widely used as the criterion for distinguishing between rest-phase hypothermia and torpor, the available data seriously question the notion of specific T_b limits. However, a more important issue, particularly in the context of the increasing number of studies on thermoregulation in free-ranging birds, is the relationship between physiological state and the ability of a bird to respond to external stimuli. The relative responsiveness of a hypothermic bird to external stimuli has far greater ecological significance than T_b per se, since reduced responsiveness presumably increases a bird's vulnerability to predation.

Finally, although the available data are limited, there is sufficient information to generate testable hypotheses concerning the evolutionary, ecological and physiological

determinants of avian hypothermia. Although telemetric studies on free-ranging birds are critical for understanding the energetic significance of hypothermic responses, experimental studies under controlled conditions remain necessary to understand the physiological determinants of avian hypothermia.

Literature cited

- Ancel, A., Petter, L., and Groscolas, R. 1998. Changes in egg and body temperature indicate triggering of egg desertion at a body mass threshold in fasting incubating blue petrels (*Halobaena caerulea*). *J. Comp. Physiol.* 168: 533 - 539.
- Aschoff, J. 1982. The circadian rhythm of body temperature as a function of body size. In: Taylor, C. R., Johansen, R., and Bolis, L. (Eds.) *A companion to animal physiology*. Cambridge University Press, Cambridge.
- Bahat, O., Choshniak, I., and Houston, D. C. 1998. Nocturnal variation in body temperature of Griffon vultures. *Condor* 100: 168 - 171.
- Barnes, B. M. 1996. Relationship between hibernation and reproduction in male ground squirrels. In: Geiser, F., Hulbert, A. J., and Nicol, S. C. (Eds.) *Adaptation to the cold: Tenth International Hibernation Symposium*. University of New England Press, Armidale.
- Bartholomew, G. A. and Trost, C. H. 1970. Temperature regulation in the speckled mousebird, *Colius striatus*. *Condor* 72: 141 - 146.
- Bartholomew, G. A., Vleck, C. M., and Bucher, T. L. 1983. Energy metabolism and nocturnal hypothermia in two tropical passerine frugivores, *Manacus vitellinus* and *Pipra mentalis*. *Physiol. Zool.* 56: 370 - 379.
- Bech, C., Abe, A. S., Steffensen, J. F., Berger, M., and Bicudo, J. E. P. W. 1997. Torpor in three species of Brazilian hummingbirds under semi-natural conditions. *Condor* 99:

780 - 788.

- Biebach, H. 1977. Reduktion des Energiestoffwechsels und der Körpertemperatur hungernder Amseln (*Turdus merula*). *J. Ornithol.* 118: 294 - 300.
- Blackburn, T. M. and Gaston, K. J. 1994. The distribution of body sizes of the world's bird species. *Oikos* 70: 127 - 130.
- Bligh, J. and Johnson, K. G. 1973. Glossary of terms for thermal physiology. *J. Appl. Physiol.* 35: 941 - 961.
- Boersma, P. D. 1986. Body temperatures, torpor, and growth in chicks of fork-tailed storm-petrels (*Oceanodroma furcata*). *Physiol. Zool.* 59: 10 - 19.
- Brigham, R. M. 1992. Daily torpor in a free-ranging goatsucker, the common poorwill (*Phalaenoptilus nuttallii*). *Physiol. Zool.* 65: 457 - 472.
- Brigham, R. M., Körtner, G., Maddocks, T. A., and Geiser, F. 2000. Seasonal use of torpor by free-ranging Australian owlet-nightjars (*Aegotheles cristatus*). *Physiol. Biochem. Zool.* 73: 613 - 620.
- Butler, P. J. and Woakes, A. J. 2001. Seasonal hypothermia in a large migrating bird: saving energy or fat deposition? *J. Exp. Biol.* 204: 1361 - 1367.
- Calder, W. A. and Booser, J. 1973. Hypothermia of broad-tailed hummingbirds during incubation in nature with ecological correlations. *Science* 180: 751 - 753.
- Carpenter, F. L. 1974. Torpor in an Andean hummingbird: its ecological significance. *Science* 183: 545 - 547.

- Carpenter, F. L. and Hixon, M. A. 1988. A new function for torpor: fat conservation in a wild migrant hummingbird. *Condor* 90: 373 - 378.
- Chaplin, S. A. 1976. The physiology of hypothermia in the black-capped chickadee (*Parus atricapillus*). *J. Comp. Physiol. B* 112: 335 - 344.
- Cheke, R. A. 1971. Temperature rhythms in African montane sunbirds. *Ibis* 113: 500 - 506.
- Clemens, D. T. 1989. Nocturnal hypothermia in rosy finches. *Condor* 91: 739 - 741.
- Collins, B. G. and Briffa, P. 1984. Nocturnal energy expenditure by honeyeaters experiencing food shortage and low environmental temperatures. *Comp. Biochem. Physiol.* 78A: 77 - 81.
- Csada, R. D. and Brigham, R. M. 1994. Reproduction constrains the use of daily torpor by free-ranging common poorwills (*Phalaenoptilus nuttallii*) (Aves: Caprimulgidae). *J. Zool., Lond.* 234: 209 - 216.
- Dawson, W. R. and Fisher, C. D. 1969. Responses to temperature by the spotted nightjar (*Eurostopus guttatus*). *Condor* 71: 49 - 53.
- Dunning, J. B. 1993. CRC handbook of avian body masses. CRC Press, London.
- Garland, T. and Ives, A. R. 2000. Using the past to predict the present: confidence intervals for regression equations in phylogenetic comparative methods. *Am. Nat.* 155: 346 - 364.
- Geiser, F. 1998. Evolution of daily torpor and hibernation in birds and mammals: importance of body size. *Clin. Exp. Pharmacol. Physiol.* 25: 736 - 740.

Geiser, F., Holloway, J. C., Körtner, G., Maddocks, T. A., Turbill, C., and Brigham, R. M.

2000. Do patterns of torpor differ between free-ranging and captive mammals and birds? In: Heldmaier, G. and Klingenspor, M. (Eds.) *Life in the cold*: 11th International Hibernation Symposium. Springer, Berlin.

Geiser, F. and Ruf, T. 1995. Hibernation versus daily torpor in mammals and birds:

physiological variables and classification of torpor patterns. *Physiol. Zool.* 68: 935 - 966.

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

Graf, R., Heller, H. C., Krishna, S., Rautenberg, W., and Misse, B. 1988. Adaptive capacity of the pigeon's daily body temperature rhythm. In: Bech, C. and Reinertsen, R. E. (Eds.) *Physiology of cold adaptation in birds*. Plenum Press, New York.

Graf, R., Krishna, S., and Heppner, F. 1989. Regulated nocturnal hypothermia induced in pigeons by food deprivation. *Am. J. Physiol.* 256: R733 - R738 -

Grossman, A. F. and West, G. C. 1977. Metabolic rate and temperature regulation in winter-acclimatized black-capped chickadees, *Parus atricapillus*, in interior Alaska. *Ornis Scand.* 8: 127 - 138.

Haftorn, S. 1972. Hypothermia of tits in the Arctic winter. *Ornis Scand.* 3: 153 - 166.

Hainsworth, F. R., Collins, B. G., and Wolf, L. F. 1977. The function of torpor in hummingbirds. *Physiol. Zool.* 50: 215 - 222.

- Hainsworth, F. R. and Wolf, L. L. 1970. Regulation of oxygen consumption and body temperature during torpor in a hummingbird, *Eulampis jugularis*. *Science* 168: 368 - 369.
- Hall, V. and Goldman, B. D. 1980. Effects of gonadal steroid hormones on hibernation in the Turkish hamster (*Mesocricetus brandti*). *J. Comp. Physiol. B* 135: 107 - 114.
- Heath, J. E. 1962. Temperature fluctuation in the turkey vulture. *Condor* 64: 234 - 235.
- Hiebert, S. M. 1990. Energy costs and temporal organization of torpor in the rufous hummingbird (*Selasphorus rufus*). *Physiol. Zool.* 63: 1082 - 1097.
- Hiebert, S. M. 1991. Seasonal differences in the response of rufous hummingbirds to food restriction: body mass and the use of torpor. *Condor* 93: 526 - 537.
- Hiebert, S. M. 1993. Seasonal changes in body mass and use of torpor in a migratory hummingbird. *Auk* 110: 787 - 797.
- Hiebert, S. M., Salvante, K. G., Ramenofsky, M., and Wingfield, J. C. 2000. Corticosterone and nocturnal torpor in the rufous hummingbird (*Selasphorus rufus*). *Gen. Comp. Endocrinol.* 120: 220 - 234.
- Hoffmann, R. and Prinzinger, R. 1984. Torpor und Nahrungsausnutzung bei 4 Mausvogelarten (Coliiformes). *J. Ornithol.* 125: 225 - 237.
- Hohtola, E., Hissa, R., Pyörnilä, A., Rintamäki, H., and Saarela, S. 1991. Nocturnal hypothermia in fasting Japanese quail: the effect of ambient temperature. *Physiol. Behav.* 49: 563 - 567.

- Hohtola, E., Pyörnilä, A., and Rintamäki, H. 1994. Fasting endurance and cold resistance without hypothermia in a small predatory bird: the metabolic strategy of Tengmalm's owl, *Aegolius funereus*. *J. Comp. Physiol.* 164: 130 - 437.
- Howell, T. S. and Bartholomew, G. A. 1959. Further experiments on torpidity in the poor-will. *Condor* 61: 180 - 185.
- Jaeger, E. C. 1948. Does the poor-will hibernate? *Condor* 50: 45 - 46.
- Jaeger, E. C. 1949. Further observations on the hibernation of the poor-will. *Condor* 51: 105 - 109.
- Jensen, C. and Bech, C. 1992a. Oxygen consumption and acid-base balance during shallow hypothermia in the pigeon. *Resp. Physiol.* 88: 193 - 204.
- Jensen, C. and Bech, C. 1992b. Ventilation and gas exchange during shallow hypothermia in pigeons. *J. Exp. Biol.* 165: 111 - 120.
- Keskaik, J. 1976. Ontogenetic development of torpidity in the swallows and martins (*Hirundo rustica*, *Delichon urbica*, *Riparia riparia*). *Commun. Baltic Comm. Bird Migr.* 10: 144 - 161.
- Keskaik, J. 1981. Ontogenetic formation of the homeothermic body temperature level in the house martin and the swift. *Commun. Baltic Comm. Bird Migr.* 13: 135 - 153.
- Keskaik, J. and Lyuleyeva, D. 1968. Temporary hypothermia in swallows. *Commun. Baltic Comm. Bird Migr.* 5: 122 - 145.
- Ketterson, E. D. and King, J. R. 1977. Metabolic rate and behavioral responses to fasting in

the white-crowned sparrow (*Zonotrichia leucophrys gambelli*). *Physiol. Zool.* 50: 115 - 129.

Kissner, K. J. and Brigham, R. M. 1993. Evidence for the use of torpor by incubating and brooding common poorwills. *Ornis Scand.* 42: 333 - 334.

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

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

Krüger, K., Prinzinger, R., and Schuchmann, K. L. 1982. Torpor and metabolism in hummingbirds. *Comp. Biochem. Physiol.* 73A: 679 - 689.

Lasiewski, R. C. 1963. Oxygen consumption of torpid, resting, and flying hummingbirds. *Physiol. Zool.* 36: 122 - 140.

Lasiewski, R. C. and Dawson, W. R. 1964. Physiological responses to temperature in the common nighthawk. *Condor* 66: 477 - 490.

Lasiewski, R. C. and Thompson, H. J. 1966. Field observations of torpidity in the violet-green swallow. *Condor* 68: 102 - 103.

Lee, T. M., Pelz, K., Licht, P., and Zucker, I. 1990. Testosterone influences hibernation in golden-mantled ground squirrels. *Am. J. Physiol.* 259: R760 - R767.

Lovegrove, B. G., Lawes, M. J., and Roxburgh, L. 1999. Confirmation of plesiomorphic daily torpor in mammals: the round-eared elephant shrew *Macroscelides proboscideus*

(Macroscelidea). *J. Comp. Physiol. B* 169: 453 - 460.

Lyman, C. P., Willis, J. S., Malan, A., and Wang, L. C. H. 1982. Hibernation and torpor in mammals and birds. Academic Press, New York.

MacMillen, R. E. and Trost, C. H. 1967. Nocturnal hypothermia in the inca dove *Scardafella inca*. *Comp. Biochem. Physiol.* 23: 243 - 253.

Maddocks, T. A. and Geiser, F. 1997. Energetics, thermoregulation and nocturnal hypothermia in Australian silvereyes. *Condor* 99: 104 - 112.

Malan, A. 1996. The origins of hibernation: a reappraisal. In: Geiser, F., Hulbert, A. J., and Nicol, S. C. (Eds.) *Adaptations to the cold: Tenth International Hibernation Symposium*. University of New England Press, Armidale.

Marshall, J. T. 1955. Hibernation in captive goat-suckers. *Condor* 57: 129 - 134.

Mayer, L., Lustick, C., and Battersby, B. 1982. The importance of cavity roosting and hypothermia in the energy balance of the winter acclimatized Carolina chickadee. *Int. Biometeor.* 26: 231 - 238.

McKechnie, A. E. and Lovegrove, B. G. 2000. Heterothermy in mousebirds: evidence of avian proto-torpor? In: Heldmaier, G. and Klingenspor, M. (Eds.) *Life in the cold: 11th International Hibernation Symposium*. Springer, Berlin.

McKechnie, A. E. and Lovegrove, B. G. 2001. Thermoregulation and the energetic significance of clustering behavior in the white-backed mousebird (*Colius colius*). *Physiol. Biochem. Zool.* 74: 238 - 249.

- McWhorter, T. J. and Martinez del Rio, C. 2000. Does gut function limit hummingbird food intake? *Physiol. Biochem. Zool.* 73: 313 - 324.
- Merola-Zwartjes, M. 1998. Metabolic rate, temperature regulation, and the energetic implications of roost nests in the bananaquit (*Coereba flaveola*). *Auk* 115: 780 - 786.
- Merola-Zwartjes, M. and Ligon, J. D. 2000. Ecological energetics of the Puerto Rican tody: heterothermy, torpor and intra-island variation. *Ecology* 81: 990 - 1002.
- Morrison, P. 1962. Modification of body temperature by activity in Brazilian hummingbirds. *Condor* 64: 315 - 323.
- Mzilikazi, N. 2000. The influence of gender on thermoregulation in pouched mice, *Saccostomus campestris*. M.Sc. Thesis, University of Natal.
- Ohmart, R. D. and Lasiewski, R. C. 1971. Roadrunners: energy conservation by hypothermia and absorption of sunlight. *Science* 172: 67 - 69.
- Pearson, O. P. 1953. Use of caves by hummingbirds and other species at high altitude in Peru. *Condor* 55: 17 - 20.
- Peiponen, V. A. 1966. The diurnal heterothermy of the nightjar (*Caprimulgus europaeus* L.). *Ann. Acad. Sci. Fennicae (A IV)* 101: 1 - 35.
- Phillips, N. H. and Berger, R. J. 1988. Metabolism and body temperature during circadian sleep and torpor in the fed and fasting pigeon. In: Bech, C. and Reinertsen, R. E. (Eds.) *Physiology of cold adaptation in birds*. Plenum Press, New York.
- Prinzinger, R., Göppel, R., Lorenz, A., and Kulzer, E. 1981. Body temperature and

metabolism in the red-backed mousebird (*Colius castanotus*) during fasting and torpor. *Comp. Biochem. Physiol.* 69A: 689 - 692.

Prinzinger, R., Preßmar, A., and Schleucher, E. 1991. Body temperature in birds. *Comp. Biochem. Physiol.* 99A: 499 - 506.

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

Prothero, J. and Jürgens, K. D. 1986. An energetic model of daily torpor in endotherms. *J. Theor. Biol.* 121: 403 - 415.

Rashotte, M. E., Basco, P. S., and Henderson, R. P. 1995. Daily cycles in body temperature, metabolic rate, and substrate utilisation in pigeons: influence of amount and timing of food consumption. *Physiol. Behav.* 57: 731 - 746.

Rashotte, M. E., Henderson, D., and Phillips, D. L. 1988. Thermal and feeding reactions of pigeons during food scarcity and cold. In: Bech, C. and Reinertsen, R. E. (Eds.) *Physiology of cold adaptation in birds*. Plenum Press, New York.

Reinertsen, R. E. 1983. Nocturnal hypothermia and its energetic significance for small birds living in the arctic and subarctic regions. A review. *Polar Res.* 1: 269 - 284.

Reinertsen, R. E. 1985. Hypothermia in northern passerine birds. In: Heller, H. C., Musacchia, X. J., and Wang, L. C. H. (Eds.) *Living in the cold: physiological and biochemical adaptations*. Elsevier, New York.

- Reinertsen, R. E. 1996. Physiological and ecological aspects of hypothermia. In: Carey, C. (Ed.) Avian energetics and nutritional ecology. Chapman & Hall, New York.
- Reinertsen, R. E. and Haftorn, S. 1983. Nocturnal hypothermia and metabolism in the Willow Tit *Parus montanus* at 63°N. *J. Comp. Physiol.* 151: 109 - 118.
- Reinertsen, R. E. and Haftorn, S. 1986. Different metabolic strategies of northern birds for nocturnal survival. *J. Comp. Physiol.* 156: 655 - 663.
- Schaub, R., Prinzinger, R., and Schleucher, E. 1999. Energy metabolism and body temperature in the Blue-naped mousebird (*Urocolius macrourus*) during torpor. *Ornis Fennica* 76: 211 - 219.
- Schleucher, E. 1994. Untersuchungen zur Ökophysiologie von Taubenarten aus extremen Biotopen am Beispiel des australischen Diamanttäubchens *Geopelia cuneata* und des afrikanischen Kaptäubchens *Oena capensis*. Ph.D. Thesis, University of Frankfurt.
- Schleucher, E. (in press). Heterothermia in pigeons and doves reduces energetic costs. *J. Therm. Biol.*
- Serventy, D. L. 1970. Torpidity in the white-backed swallow. *Emu* 70: 27 - 28.
- Shapiro, C. J. and Weathers, W. W. 1981. Metabolic and behavioural responses of American kestrels to food deprivation. *Comp. Biochem. Physiol.* 68A: 111 - 114.
- Sibley, C. G. and Ahlquist, J. E. 1990. Phylogeny and classification of birds. Yale University Press, New Haven.
- Sibley, C. G. and Monroe, B. L. 1990. Distribution and taxonomy of the birds of the world. Yale University Press, New Haven.
- Steen, J. 1958. Climatic adaptation in small northern birds. *Ecology* 39: 625 - 629.

- Thouzeau, C., Duchamp, C., and Handrich, Y. 1999. Energy metabolism and body temperature of barn owls fasting in the cold. *Physiol. Zool.* 72: 170 - 178.
- Waite, T. A. 1991. Nocturnal hypothermia in gray jays *Perisoreus canadensis* wintering in interior Alaska. *Ornis Scand.* 22: 107 - 110.
- Warren, J. W. 1960. Temperature fluctuation in the smooth-billed ani. *Condor* 62: 293 - 294.
- Withers, P. C. 1977. Respiration, metabolism and heat exchange of euthermic and torpid poorwills and hummingbirds. *Physiol. Zool.* 50: 43 - 52.
- Wolf, L. L. and Hainsworth, F. R. 1972. Environmental influence on regulated body temperature in torpid hummingbirds. *Comp. Biochem. Physiol.* 41A: 167 - 173.

Chapter 2. Facultative hypothermic responses in the speckled mousebird (*Colius striatus*).

Introduction

Normothermic metabolic rate and body temperature (T_b) cycles in endotherms are characterised by circadian fluctuations about a stable, long-term mean (Aschoff 1982).

Facultative hypothermic (heterothermic) responses are marked exaggerations of these cycles, and have been described in a variety of endotherms (Lyman et al. 1982; Boyer and Barnes 1999). These responses are usually divided into daily torpor (daily heterothermy) and hibernation (seasonal heterothermy) (Lyman et al. 1982; Geiser and Ruf 1995). Torpor and hibernation are distinguishable on the basis of several characteristics, including the extent of metabolic down-regulation, minimum T_b , and bout duration (Geiser and Ruf 1995).

Hibernation is typically a seasonal response, and is characterised by metabolic depression to ca. 5% of basal metabolic rate (BMR), long bout lengths (mean = 355 hrs) and a mean minimum T_b of 5.8°C (Geiser and Ruf 1995). Hibernation appears to be a predominantly mammalian phenomenon, and has been reported in only one bird species, the common poorwill *Phalaenoptilus nuttallii* (Jaeger 1948;1949).

Daily torpor is characterised by shorter bouts (mean = 11.2 hrs), metabolic depression to ca. 27% of BMR and a mean minimum T_b of 17.4°C (Geiser and Ruf 1995). Daily heterothermy has been described in several mammalian (e.g. Rodentia, Insectivora, Carnivora, Primates, Macroscelidea) and avian (e.g. Apodiformes, Caprimulgiformes, Coliiformes) orders (Geiser and Ruf 1995).

A third, supposedly independent response, rest-phase hypothermia, is also recognised in birds (Prinzinger et al. 1991; Reinertsen 1983;1996). During rest-phase hypothermia, T_b is

typically reduced by $< 10^{\circ}\text{C}$, and has been recorded in response to cold (e.g. Haftorn 1972; Reinertsen 1983; Reinertsen and Haftorn 1986) and food deprivation (e.g. Bartholomew et al. 1983; Graf et al. 1989).

Although the evolutionary link between daily torpor and hibernation is still the subject of debate (Malan 1996; Geiser 1998), similarities exist in the patterns of metabolic rate and T_b associated with these two hypothermic responses (Geiser and Ruf 1995). Both involve initial reductions of T_b associated with metabolic suppression, followed by a maintenance phase during which T_b is regulated with respect to a setpoint considerably lower than that during normothermia (Geiser and Ruf 1995). Body temperature returns to normothermic levels during the arousal phase, characterised by rapid increases in endogenous heat production which is usually entrained to the light-dark cycle (Geiser and Ruf 1995).

In contrast, the distinction between rest-phase hypothermia and daily torpor in birds has not been rigorously examined. Prinzinger et al. (1991) suggested that $T_{b,s} < 25^{\circ}\text{C}$ are indicative of torpor, whereas Reinertsen (1996) proposed $T_{b,s} < 30^{\circ}\text{C}$. The distinction between rest-phase hypothermia and torpor on the basis of bout duration, extent of metabolic rate reduction, etc, remains similarly unresolved.

Torpor has been well-documented in the mousebirds (Coliiformes), which are endemic to sub-Saharan Africa (Fry et al. 1988). Torpor has been described in response to low body mass (M_b) in four species; the speckled mousebird *Colius striatus*, the red-backed mousebird *C. castanotus*, the blue-naped mousebird *Urocolius macrourus*, and the red-faced mousebird *U. indicus* (Bartholomew and Trost 1970; Prinzinger et al. 1981a,b; Hoffmann and Prinzinger 1984; Prinzinger 1988). Mousebirds are also known for their huddling behaviour (clustering) which has been shown to be important for reducing energy expenditure (Prinzinger et al. 1981b; Brown and Foster 1992; McKechnie and Lovegrove 2001). In the white-backed

mousebird (*C. colius*), clustering behaviour is essential for effective thermoregulation and the avoidance of pathological hypothermia at low ambient temperatures (T_a s) (McKechnie and Lovegrove 2001).

While investigating thermoregulation in the white-backed mousebird *Colius colius*, McKechnie and Lovegrove (2001) observed patterns of non-steady state metabolic rate and the apparent lack of a constant normothermic T_b setpoint in single birds during the rest-phase. These patterns did not accord with typical avian normothermia, hypothermia, or torpor, leading these authors to regard them as atypical normothermic cycles. However, McKechnie and Lovegrove (2001) did not investigate the effects of food deprivation, and were hence unable to rule out the possibility that at least some of the patterns represented facultative hypothermic responses.

These observations highlighted the lack of a clear distinction between the various avian hypothermic states. In this study, I investigated rest-phase thermoregulation in the speckled mousebird *Colius striatus* under ad libitum and restricted food treatments. The objective of the study was to assess the hypothermic responses of *C. striatus* in the context of the distinction between normothermia, rest-phase hypothermia and torpor.

Materials and methods

Twelve speckled mousebirds were trapped in Pietermaritzburg, South Africa, using a walk-in trap baited with fruit. They were housed in outdoor aviaries (3m long, 2m high, 1m wide) at the School of Botany and Zoology at the University of Natal. They were fed ad libitum on a variety of fruit, including pawpaws, bananas, grapes, apples and tomatoes. Each bird was marked with coloured celluloid rings for identification. All experiments were carried out during July and August 1999.

Measurement of T_b

Ten temperature-sensitive telemeters (Model XM, Mini-Mitter Co., Sunriver, Oregon) with an average mass of 1.2g were calibrated with a standard mercury thermometer (0.05°C) in a water bath at temperatures from $5^\circ - 45^\circ\text{C}$. These were implanted into the intra-peritoneal cavity under inhalation anaesthesia (Isoflurane in oxygen; induction and maintenance, 2%; flow rate, ca. $0.5 \text{ l}\cdot\text{min}^{-1}$). The birds were allowed 7 days to recover from surgery before any measurements were made. The Mini-Mitter signals were detected using dual antennae attached to Perspex sleeves surrounding the respirometers. Ambient temperatures in the cabinet and the respirometers were measured with thermistor probes, calibrated in a similar way.

Metabolic measurements

I measured oxygen consumption (VO_2) as an indirect measure of metabolic rate. All metabolic measurements were made in respirometers constructed from clear Perspex[®] under a light:dark cycle matched to the natural photoperiod prevailing at the time i.e. that in the aviaries (ca. 11L:13D). Measurements were made in 3.96- ℓ respirometers (22cm high, 12cm wide, 15cm long). The respirometers were placed in a 1 m^3 sound-proof temperature cabinet.

Measurements of VO_2 were made using an open flow-through system. Atmospheric air, acting as the control gas, was pumped from outside the building, partially dried using silica gel, and pumped into the cabinet, maintaining a relative humidity (RH) $< 50\%$ with the birds in the chambers. Air was drawn through the respirometers at flow rates chosen to maintain less than one percent oxygen depletion between the incurrent and excurrent air (ca. $0.8 \text{ l}\cdot\text{min}^{-1}$). Air was drawn into each respirometer at the base and removed at the top, maintaining a constant flow of air past the bird. The flow rate for each channel was measured

with a Brooks thermal mass flow meter (Model 5810) factory calibrated to STP. The use of solenoid valves and a pump for each respirometer allowed up to five respirometers, as well as a control channel, to be used simultaneously. The excurrent air from each respirometer was passed through a water condenser (consisting of copper pipes in which the air was cooled to approximately 3°C i.e. below dew point) and a CO₂ scrubber (soda lime) to remove water vapour and CO₂ gas respectively. After passing through pumps, solenoids, filters and the mass flow meters, the excurrent air was subsampled with an oxygen analyser (Model S-3A/1, Ametek) and a CO₂ analyzer (Model WA-445-MK3; Analytical Development Co.) to determine the fractional concentration of oxygen and carbon dioxide respectively in the dry air. The fractional concentrations in the control channel were measured every cycle (6 minutes or less, depending on number of respirometers being used) and O₂ and CO₂ measurements for the experimental channels were subtracted from this control value. In this way the inherent problem of long-term drift in the output of the O₂ and CO₂ analysers was limited to that which could occur over a maximum of 6 min, thus permitting long-term measurements of VO₂ and VCO₂. Analog signals from the thermistor probes, mini-mitters, mass flow meter and oxygen and carbon dioxide analysers were digitised using an A/D converter and recorded on a multi-channel WINDOWS-based recording program written by Barry Lovegrove. The sampling interval for each respirometer varied from 3 min to 6 min, depending on the number of respirometers used at any one time. Measurements of the various parameters for each channel (T_a, T_b, fractional O₂ and CO₂ concentration, etc) were recorded at the end of each 1 min measurement interval. The measurement of fractional O₂ and CO₂ concentrations was delayed until the last 5 s of this period, allowing sufficient time to flush air from the previous channel from ducting between the relay valves and the subsample tubing. Oxygen consumption was calculated using the equation $VO_2 = V_E(F_{I_{O_2}} - F_{E_{O_2}}) / (1 - F_{I_{O_2}})$ where VO₂ = metabolic rate

($\text{mlO}_2 \cdot \text{h}^{-1}$), V_E = flow rate ($\text{ml} \cdot \text{min}^{-1}$), $F_{I\text{O}_2}$ = incurrent fractional O_2 concentration and $F_{E\text{O}_2}$ = excurrent fractional O_2 concentration (Withers 1977). The birds were weighed before and after each experiment. Mass-specific VO_2 was calculated assuming a linear decrease in M_b during the measurements.

Experimental Protocol

For all experiments, birds were placed in the respirometers at ca. 15h30, to allow sufficient time to equilibrate before the onset of the rest-phase. Birds were removed from the respirometers at least two hours after lights-on the following morning, to ensure that T_b and VO_2 attained normothermic active-phase levels.

Measurements of T_b , VO_2 and VCO_2 were made in 8 - 10 birds at $T_a = 0, 5, 10, 15, 20, 25, 28, 31$ and 34°C in a randomly chosen sequence. The birds were maintained in the respirometers for the entire rest phase at each T_a .

I also investigated the birds' thermoregulatory responses to a decrease in T_a during the rest-phase. Measurements were made in nine birds which were exposed to $T_a = 15^\circ\text{C}$ for the first half of the rest-phase (ca. 6 hours), and then $T_a = 5^\circ\text{C}$ for the remainder of the rest-phase. The change in T_a occurred over a half-hour period.

The influence of food deprivation was investigated by starving nine birds for a day before measuring rest-phase VO_2 and T_b patterns. They were placed in the respirometers at ca. 15h00 and measurements were made until ca. 08h00 the next morning. Measurements were made at $T_a = 5^\circ, 10^\circ, 15^\circ$ and 20°C in a random sequence, with an entire rest-phase spent at each T_a . After each measurement, the birds were returned to the aviaries and fed ad libitum for a minimum of six days. Typically, M_b returned to levels characteristic of ad libitum feeding within two days.

Data analysis

Values are presented as mean \pm S.E (Zar 1999). Results were compared using repeated-measures analysis of variance (R-M ANOVA). VO_2 and T_b values during the first and final hours of the rest-phase were compared using analyses of covariance (R-M ANCOVA) with T_a as covariate. In addition, I used a T-test for dependent samples (Zar 1999) to compare energy expenditure. Minimum VO_2 ($\text{VO}_{2\text{min}}$) was calculated as the mean of the three lowest consecutive values i.e. over a 18 min period (sampling interval = 6 min). The regression model (linear, exponential or quadratic) which provided the best fit to a data set was determined by comparing the coefficient of determination (r^2) for the linear model with the r^2 values for regressions of predicted y-values vs. measured y-values for exponential and quadratic models, following Song et al. (1997). The coefficients of linear regressions were compared following Zar (1999).

To convert VO_2 to metabolic rates, I used a factor of $20.083 \text{ J.ml O}_2^{-1}$ (Schmidt-Nielsen 1990). To calculate rest-phase energy expenditure, I integrated mass-specific VO_2 data over 1 hour intervals during the experimental scotophase. I assessed energy savings arising from hypothermic responses by comparing the energy expenditures during the ad libitum and restricted food treatments respectively.

Results

Body mass and metabolic substrate

During the ad libitum food treatment, the mean body mass (M_b) of the mousebirds was $51.2 \pm 1.2\text{g}$ ($n = 11$), but decreased to ca. 10% below ad libitum levels ($45.9 \pm 1.1\text{g}$) after food restriction. The M_b did not vary significantly between the four T_a s at which measurements were made during the restricted food treatment (R-M ANOVA, $F_{3,32} = 0.079$, $P > 0.05$).

During the restricted food treatment, the mean M_b ($44.1 \pm 0.5\text{g}$) of birds in which minimum T_b decreased below 25°C was significantly lower than those that maintained minimum T_b above 25°C ($46.7 \pm 0.7\text{g}$) (R-M ANOVA; $F_{1,22} = 22.09$; $P < 0.05$).

During the ad libitum food treatment, RQs of ca. 1.0 indicated predominantly carbohydrate metabolism immediately following the commencement of data measurement at the onset of the scotophase. Thereafter, RQ decreased during the course of the rest-phase to ca. 0.7, indicating a shift from carbohydrate to fat metabolism.

In contrast, the RQ immediately following the commencement of data measurement in food restricted birds was ca. 0.7, confirming fat metabolism and a starved state. The RQ remained at this level for the duration of the scotophase. In most cases, heat production during arousal from hypothermia was associated with transient increases in the RQ to ca. 0.8.

Body temperature

During the ad libitum food treatment, rest-phase T_b s (ρT_b) ranged from 33.5°C to 38.5°C at $T_a = 28^\circ\text{C}$, the lower limit of thermoneutrality (T_{lc} ; see below) (Figure 1a). At $T_a < 28^\circ\text{C}$, the ρT_b range varied significantly with T_a (Friedman ANOVA, $\chi^2 = 534.63$, $P < 0.05$, $n = 923$, d.f. = 5), reaching a maximum lability at $T_a = 15^\circ\text{C}$ (Figure 1b-e). The frequency distribution of ρT_b at $T_a = 28^\circ\text{C}$ was skewed to the right, whereas at lower T_a s, the frequency distributions were either approximately normal (Figure 1b,e) or skewed to the left (Figure 1c,d). The variance of ρT_b increased at $T_a < 28^\circ\text{C}$, reaching an observed maximum at $T_a = 15^\circ\text{C}$, before decreasing at $T_a < 15^\circ\text{C}$ (Figure 1). These observations suggest that, at the T_{lc} , more precise regulation of the minimum ρT_b ($\rho T_{b,\text{min}}$) occurred than at $T_a < T_{lc}$.

During the restricted food treatment, a wider range of ρT_b (ca. 18°C to 38°C) was observed (Figure 1b-e). The frequency distributions of ρT_b were characterised by a a

downward modal shift relative to the ad libitum data (Figure 1b-e) and b) a marked increase in the left tail of the distributions. The distribution of ρT_b s exhibited during the restricted food treatment was similar to that of ρT_b during the ad libitum food treatment - the ρT_b range was widest at intermediate T_a s (Figure 1). The lowest observed T_b in a bird which was able to spontaneously arouse, was 18.2°C at $T_a = 15^\circ\text{C}$. I was unable to discern clear distinctions between normothermia, rest-phase hypothermia and torpor in these ρT_b frequency distributions. Had the birds exhibited typical avian patterns of torpor and/or rest-phase hypothermia, the expected T_b frequency distributions should indicate marked bimodality, reflecting the defence of lowered T_b setpoints. Instead, T_b s below ca. 30°C were uniformly distributed across a wide range with no obvious mode (Figure 1b-e).

On one occasion, a starved bird was unable to arouse spontaneously at $T_a = 5^\circ\text{C}$, but recovered after being reheated with an artificial heat source. The bird's T_b immediately prior to removal from the respirometer was 15.3°C . These data were not included in the analyses.

Rest-phase T_b patterns in *C. striatus* during both ad libitum and restricted food treatments were characterised by a lack of homeostasis. With few exceptions, the T_b of birds under both food treatments and at all $T_a < T_{lc}$ decreased during the course of the rest-phase (Figure 2,3). During the ad libitum treatment (Figure 2), the minimum ρT_b s during the final hour of the rest-phase ($\rho_2 T_b \text{min}$) at all $T_a < T_{lc}$ were significantly lower than the minimum ρT_b s during the first hour of the rest-phase ($\rho_1 T_b \text{min}$) (ANCOVA; $F_{1,117} = 126.138$, $P \ll 0.05$; Figure 4b inset). Whereas $\rho_1 T_b \text{min}$ was independent of T_a , $\rho_2 T_b \text{min}$ showed a curvilinear response to T_a (Figure 4b inset). The lowest values occurred at $T_a = 15^\circ\text{C}$ (Figure 4b, inset). The difference between $\rho_1 T_b \text{min}$ and $\rho_2 T_b \text{min}$ ($\Delta \rho T_b \text{min}$) was not correlated with T_a (ANOVA, $F_{1,58} = 2.544$, $P > 0.05$). The maximum $\Delta \rho T_b \text{min}$ was $5.02 \pm 0.98^\circ\text{C}$ ($n = 7$) at $T_a =$

15°C (Figure 4b, inset).

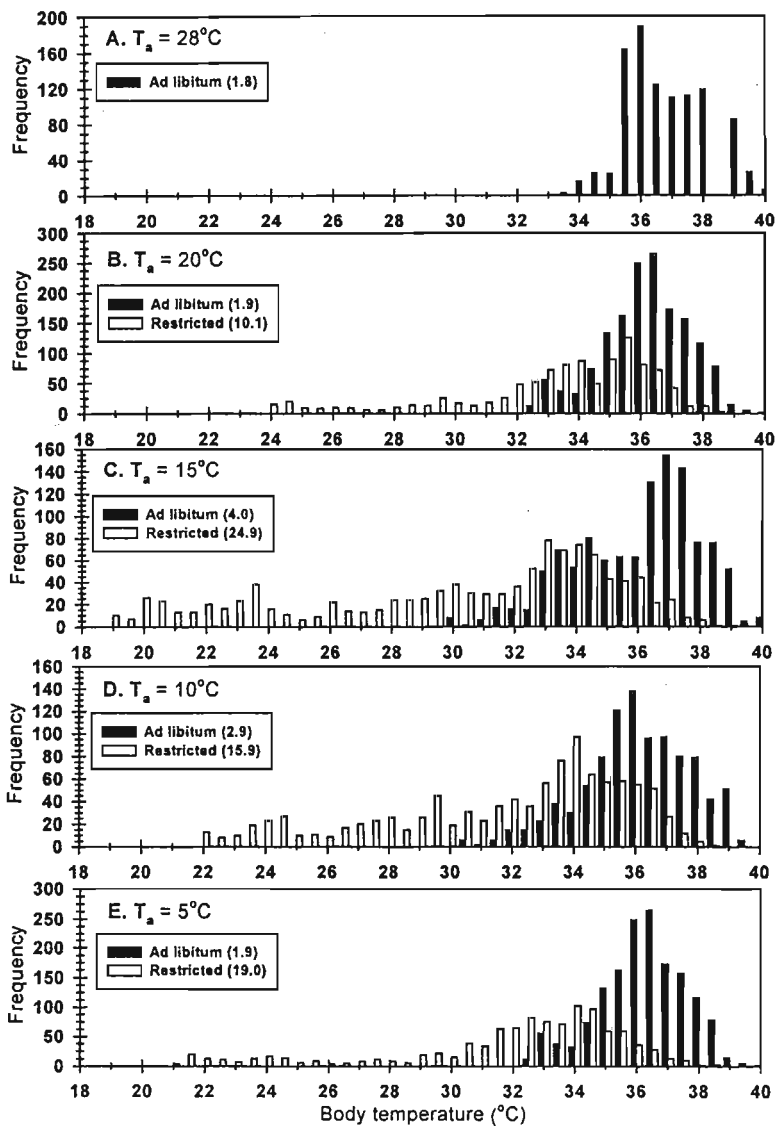


Figure 1. Frequency distributions of all rest-phase T_b measurements (recorded at 6-minute intervals) in speckled mousebirds (*Colius striatus*) at $T_a = 28^{\circ}\text{C}$, 20°C , 15°C , 10°C and 5°C respectively. Note the variation in the extent to which the minimum T_b was controlled during ad libitum food (black bars). The variances of pT_b are given in parentheses.

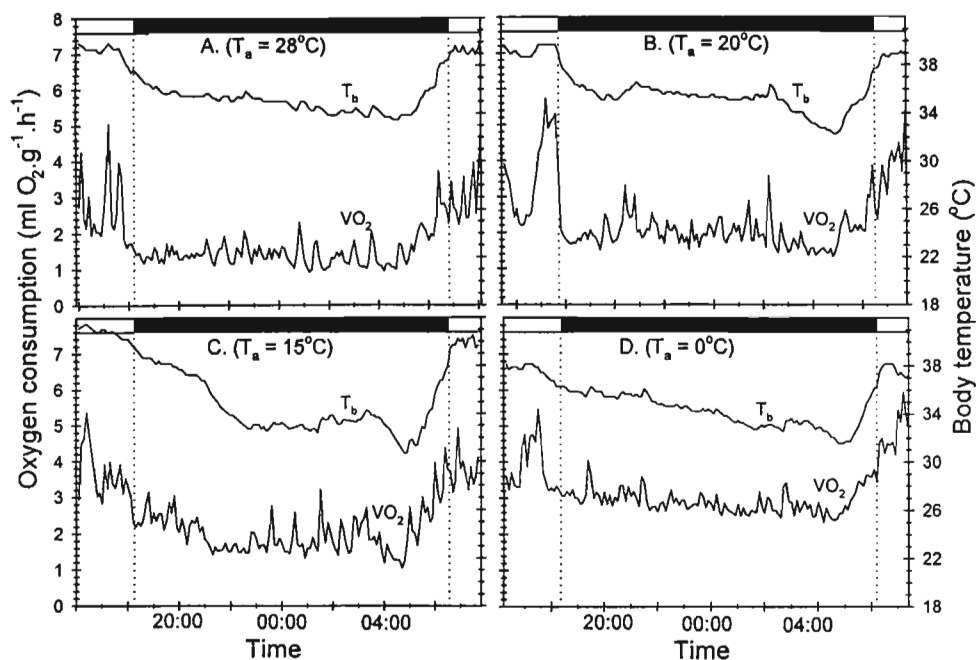


Figure 2. VO_2 and T_b traces in a speckled mousebird (*Colius striatus*) at four T_a s during the ad libitum food treatment. Note that at all four T_a s, VO_2 and T_b decreased during the course of the rest-phase. Also note the periods of more rapid cooling near the end of the rest-phase in (B) and (C).

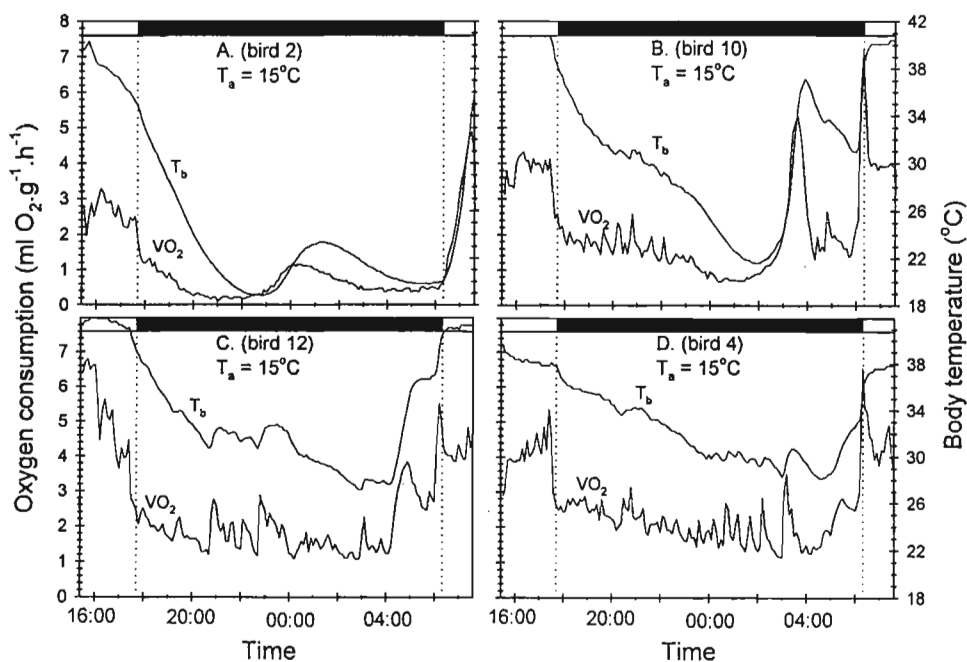


Figure 3. VO_2 and T_b traces in four speckled mousebirds (*Colius striatus*) at $T_a = 15^\circ\text{C}$, after being deprived of food for one day. Note variation in $\rho T_{b,\min}$, as well as the time taken to reach $\rho T_{b,\min}$.

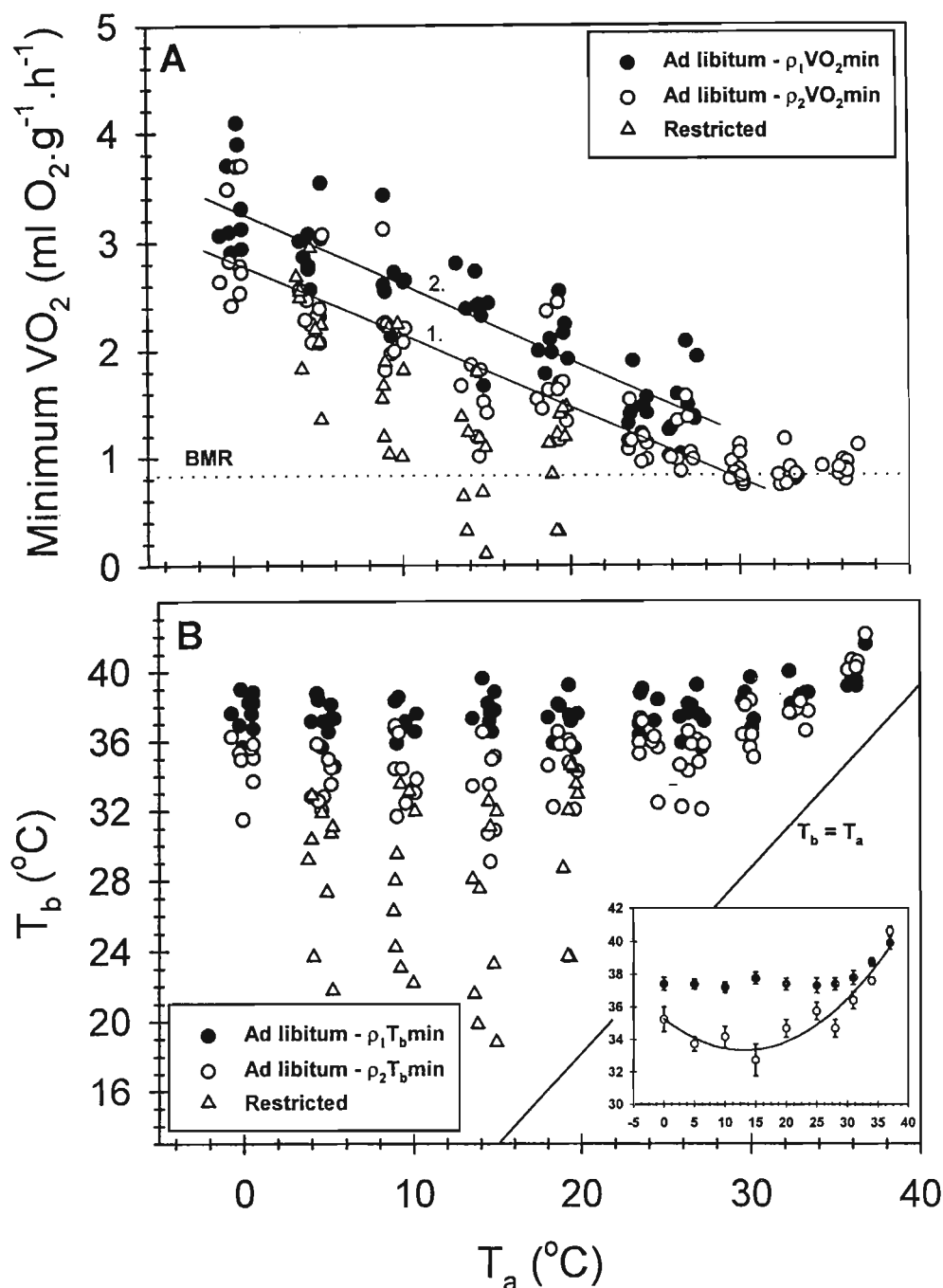


Figure 4. The relationship between $VO_2 \text{min}$ and T_a (A) and T_b and T_a (B) in speckled mousebirds (*Colius striatus*). The linear regressions in (A) indicate (1) relationship between $VO_2 \text{min}$ during the final hour of the rest-phase and T_a , $VO_2 \text{min} = -0.064T_a + 2.935$ ($r^2 = 0.631$) and (2) relationship between the $VO_2 \text{min}$ during the first hour of the rest-phase and T_a , $VO_2 \text{min} = -0.070T_a + 3.340$ ($r^2 = 0.791$). In (B), the inset graph shows the $\rho T_b \text{min}$ (mean \pm S.E.) during the first and final hours of the rest-phase ($\rho_1 T_b \text{min}$ and $\rho_2 T_b \text{min}$, respectively) during the ad libitum food treatment. Note that whereas $\rho T_b \text{min}$ during the first hour of the rest-phase ($\rho_1 T_b \text{min}$) was approximately constant, $\rho T_b \text{min}$ during the final hour ($\rho_2 T_b \text{min}$) was more variable, and showed a quadratic relationship with T_a .

Although the responses of individual birds during the ad libitum treatment were fairly consistent, there was considerable variation in T_b responses during the restricted food treatment (Figure 3). On six of the 11 occasions when $\rho T_{b,\min}$ was $< 25^\circ\text{C}$, $\rho T_{b,\min}$ occurred prior to midnight (Figure 3a), whereas in the remaining five, it occurred between midnight and the onset of the experimental photophase (Figure 3b). On the latter five occasions, bouts of endogenous heat production (characterised by rapid increases in $\dot{V}O_2$) occurred shortly after $\rho T_{b,\min}$ was attained. Thereafter, T_b was typically maintained at ca. 35°C . In one instance, T_b decreased to 23.6°C at 23h22, increased to 35.8°C at 02h22, and thereafter decreased to 27.7°C immediately prior to the onset of the photophase (Figure 3b).

Cooling rates during ad libitum feeding

Linear models fitted to time-dependent decreases in rest-phase T_b for each bird at each experimental $T_a < T_{lc}$ typically accounted for 70 - 95% of the T_b trend. Cooling rates (CR) were calculated from the onset of the rest-phase until the lowest T_b value was attained. I used the coefficients (slopes) of these regressions as estimates of cooling rates. These cooling rates should not be interpreted as accurate measurements of the rate of heat loss, since cooling rates during the course of any particular rest-phase showed a high degree of temporal variation (e.g. Figure 2b,c). Instead, these cooling rates were used as estimates of the degree to which thermoregulation during the course of the rest-phase differed from typical endotherm T_b homeostasis. These cooling rates showed a significant curvilinear relationship with T_a (ANOVA, $F_{2,57} = 5.741$, $P < 0.05$), best approximated with a quadratic equation, $CR = 0.2953 + 0.0082T_a - 0.005(T_a)^2$; $r^2 = 0.168$ (Figure 5).

When T_a was decreased from 15°C to 5°C in the middle of the rest-phase, the rate of

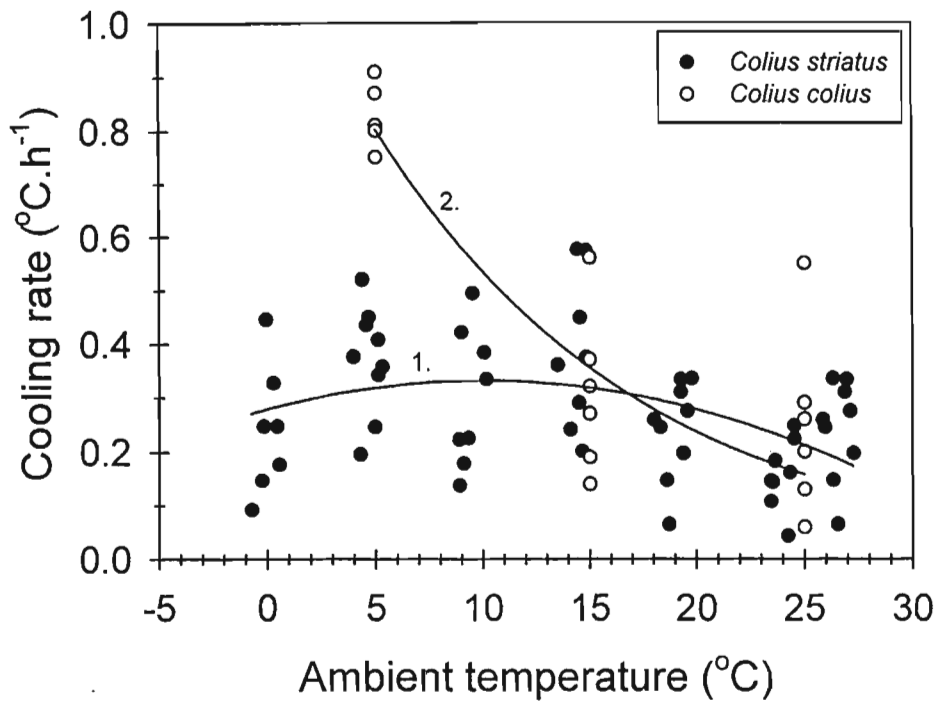


Figure 5. Relationship between linear cooling rates and T_a in speckled mousebirds (*Colius striatus*) and white-backed mousebirds (*Colius colius*). The lines indicate the best-fit regression models: (1) Cooling rate (CR) vs T_a in *C. striatus*, $CR = 0.279 + 0.010T_a - 0.001T_a^2$ ($r^2 = 0.167$); (2) CR vs T_a in *C. colius*, $CR = 1.206e^{0.082T_a}$ ($r^2 = 0.728$). The data for *C. colius* were obtained from McKechnie and Lovegrove (2001).

cooling increased significantly from $0.22 \pm 0.04^\circ\text{C}\cdot\text{h}^{-1}$ to $0.78 \pm 0.15^\circ\text{C}\cdot\text{h}^{-1}$ (R-M ANOVA, $F_{1,16} = 13.215$, $P < 0.05$; Figure 6). In some of the birds, these increased cooling rates were not maintained until the end of the rest-phase, but were followed either by the maintenance of a fairly stable T_b , or an increase in T_b (Figure 6b).

Oxygen consumption

The apparent lack of T_b homeostasis was reflected in the patterns of VO_2 (Figure 2,3). During the ad libitum treatment, the minimum VO_2 during the final hour of the rest-phase ($\rho_2\text{VO}_2\text{min}$) was significantly lower than that during the first hour ($\rho_1\text{VO}_2\text{min}$) at all $T_a < T_{lc}$

(ANCOVA, $F_{1,117} = 15.941$, $P < 0.05$, Figure 4a). The difference between $\rho_1\text{VO}_2\text{min}$ and $\rho_2\text{VO}_2\text{min}$ ($\Delta\rho\text{VO}_2\text{min}$) showed a significant relationship with T_a (ANOVA, $F_{2,57} = 3.179$, $P < 0.05$), again best described by a quadratic equation $\Delta\rho\text{VO}_2\text{min} = 0.226 + 0.034.T_a - 0.002.T_a^2$ ($r^2 = 0.100$).

Both $\rho_1\text{VO}_2\text{min}$ and $\rho_2\text{VO}_2\text{min}$ increased linearly with decreasing T_a at $T_a < T_{lc}$ (Figure 4a). The slopes of the linear regressions of $\rho_1\text{VO}_2\text{min}$ and $\rho_2\text{VO}_2\text{min}$ and $T_a < T_{lc}$ were not significantly different ($t = 0.04$, $P > 0.05$; Figure 4a).

Within the T_a range $29^\circ\text{C} < T_a < 35^\circ\text{C}$, $\rho\text{VO}_2\text{min}$ did not vary significantly with T_a (R-M ANOVA, $F_{1,15} = 1.391$, $P > 0.05$), and this was assumed to represent the zone of thermoneutrality of the birds (Figure 4a). The mean $\rho\text{VO}_2\text{min}$ within this T_a range was $0.831 \pm 0.117 \text{ ml O}_2\cdot\text{g}^{-1}\cdot\text{h}^{-1}$, and the BMR was hence calculated to be $16.69 \text{ J}\cdot\text{g}^{-1}\cdot\text{h}^{-1}$.

During the restricted food treatment, the $\rho\text{VO}_2\text{min}$ was significantly reduced, compared to ad libitum values (R-M ANCOVA, $F_{1,48} = 56.753$, $P < 0.05$). The lowest observed $\rho\text{VO}_2\text{min}$ was $0.110 \text{ ml O}_2\cdot\text{g}^{-1}\cdot\text{h}^{-1}$ in a starved bird at $T_a = 15^\circ\text{C}$. The $\rho\text{VO}_2\text{min}$ decreased below BMR on seven occasions, during which T_b was $< 24^\circ\text{C}$ (Figure 4). Despite the reductions in $\rho\text{VO}_2\text{min}$, the extent of metabolic suppression at the onset of the rest-phase (i.e. the difference between αVO_2 at the end of the α -phase and the initial level of ρVO_2) was not significantly greater than during the ad libitum treatment (R-M ANCOVA, $F_{1,65} = 1.988$, $P > 0.05$).

Energy expenditure

During the restricted food treatment, the mean rest-phase energy expenditure was significantly lower than during the ad libitum food treatment only at $T_a = 15^\circ\text{C}$ and $T_a = 20^\circ\text{C}$, but not at $T_a = 10^\circ\text{C}$ and $T_a = 5^\circ\text{C}$ (Table 1). The mousebirds reduced their energy expenditure by $23 \pm 5\%$

at $T_a = 20^\circ\text{C}$ and by $28 \pm 8\%$ at $T_a = 15^\circ\text{C}$.

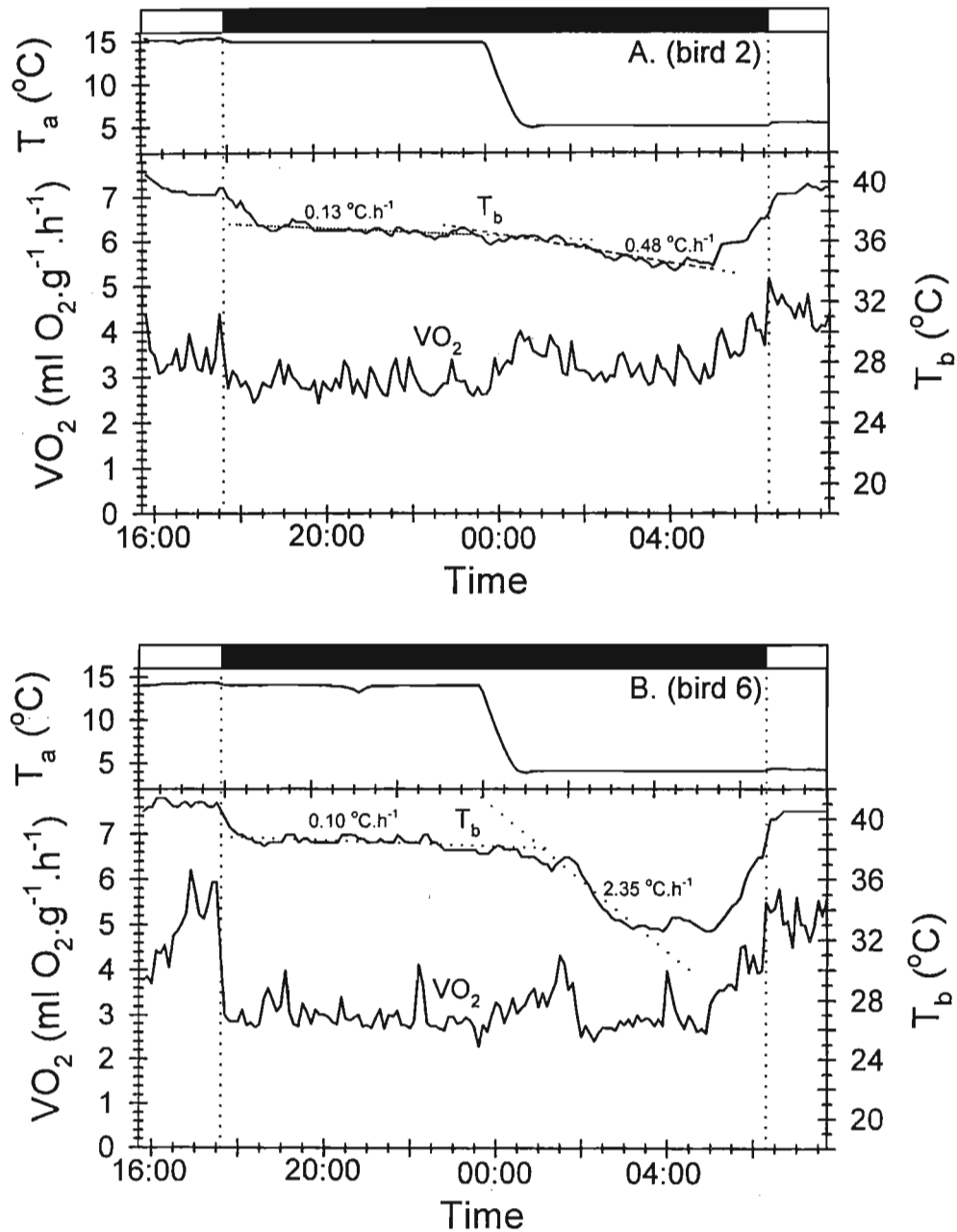


Figure 6. VO_2 and T_b in two speckled mousebirds (*Colius striatus*) exposed to two T_a s during the course of the rest-phase. The dotted lines indicate linear regressions of T_b as a function of time, and clearly indicate that a decrease in T_a was associated with increased cooling rates.

Table 1. Changes in rest-phase energy expenditure associated with restricted food in speckled mousebirds (*Colius striatus*).

T_a	n	Energy Expenditure ^a (J.g ⁻¹ .h ⁻¹)		Paired T-test	
		Ad libitum	Restricted	T	P
5	8 ^a	61.5 ± 1.9	67.1 ± 1.5	2.307	> 0.05
10	9	59.9 ± 2.5	51.3 ± 3.0	1.732	> 0.05
15	9	52.1 ± 3.2	35.9 ± 3.4	2.709	< 0.05
20	9	44.8 ± 1.4	34.5 ± 2.4	4.478	< 0.05

a. Excludes data for bird which was unable to arouse spontaneously.

Discussion

Hypothermic responses in *C. striatus* clearly did not accord with the widely accepted distinction between rest-phase hypothermia and torpor. Moreover, I observed several differences between rest-phase thermoregulation in *C. striatus* and typical avian thermoregulation. These differences involved an atypically labile ρT_b , as well as non-steady state metabolic rate and T_b during the rest-phase.

Normothermia

I was unable to clearly discern the normothermic ρT_b range in *C. striatus* (Figure 1). However, if I assume that all ρT_b s measured during the ad libitum food treatment were normothermic, then the normothermic ρT_b range in *C. striatus* apparently includes a wide (ca. 10°C) range of T_b s from ca. 30°C to ca. 40°C (Figure 1). Based on the frequency distributions of ρT_b (Figure 1), there is no reason to suspect that the mousebirds employed facultative hypothermia (sensu Prinzinger et al. 1991) in response to low temperatures. If the birds had exhibited rest-phase

hypothermia in response to cold, the lowest ρT_b s would presumably have been observed at $T_a = 0^\circ\text{C}$, whereas the lowest ρT_b s I observed were at $T_a = 15^\circ\text{C}$.

In contrast to *C. striatus*, most birds regulate normothermic T_b within a relatively narrow range about a species-specific setpoint (see traces in Maddocks and Geiser 1997; Boix-Hinzen and Lovegrove 1998; McKechnie and Lovegrove 1999). Furthermore, T_b s of $< 35^\circ\text{C}$ are observed only during rest-phase hypothermia (Haftorn 1972; Bartholomew et al. 1983; Reinertsen 1983;1996). The normothermic ρT_b range of *C. striatus* hence appears to include T_b s which, in the majority of avian species, are associated only with facultative hypothermia.

Normothermic rest-phase thermoregulation in *C. striatus* was characterised by a lack of T_b homeostasis, arising from insufficient heat production to maintain a constant T_b . There were initial reductions in metabolic rate within the first 30 mins or so of the rest-phase scotophase. Thereafter, ρT_b was not maintained at a constant level, as typically occurs in endotherms. Instead, ρT_b gradually decreased in an apparently linear fashion until the onset of reheating prior to the α -phase. During ρT_b cooling, there was no evidence of additional thermoregulatory heat production to compensate for decreasing T_b . The observation that cooling rates showed a significant quadratic relationship with T_a , whereas $\Delta T_{b,\text{min}}$ did not, may be explained by the fact that in some cases, cooling was attenuated before the end of the rest-phase.

Whereas *C. striatus* did exhibit T_a -dependent cooling, it appeared that the birds were able to reduce cooling rates at lower T_a s, suggesting that such cooling may be facultative. This is in contrast to the obligatory nature of T_a -dependent cooling in *C. striatus*, which at $T_a = 5^\circ\text{C}$ resulted in $\rho T_b < 30^\circ\text{C}$ and several instances of pathological hypothermia (McKechnie and Lovegrove 2001). The apparently greater ability of *C. striatus* to thermoregulate at low T_a s

suggests that this species does not rely on behavioural thermoregulation to the same extent as *C. colius*. Nevertheless, the observation that a 10°C reduction in T_a during the rest-phase was associated with a significant increase in cooling rate, suggests that T_a may, under some circumstances, play a role in determining the cooling rate (Figure 6). At least one of the birds appeared to thermoregulate at a lower T_b setpoint following a decrease in T_a (Figure 6b).

Normothermic rest-phase thermoregulation in *Colius* mousebirds differs fundamentally from typical endothermic thermoregulation. Several well-documented characteristic features of endothermic thermoregulation are absent in both *C. striatus* and *C. colius*. Firstly, ρT_b does not appear to be defended with respect to a constant setpoint, as typically occurs in endotherms (Aschoff 1982; Prinzinger et al. 1991). Possible mechanisms for the observed decreases in ρT_b are discussed in McKechnie and Lovegrove (2001). Secondly, the minimum ρT_b , and hence the amplitude of circadian T_b fluctuation, is not constant, but is determined by ambient temperature, although this appears to be a partly facultative response in *C. striatus*.

The cooling patterns shown by *C. striatus* and *C. colius* have not been previously described in birds, but are suggested by previous measurements of VO_2 in *C. striatus* (Figure 8 in Bartholomew and Trost 1970). Furthermore, traces of VO_2 and T_b in torpid *U. macrourus* show a similar lack of homeostasis during the maintenance phase (Figure 3 in Schaub et al. 1999). However, such non-steady state thermoregulation may not be unique to the Coliidae. Waite (1991) recorded T_b cycles in three Gray Jays (*Perisoreus canadensis*), and observed that ρT_b gradually decreased during the rest-phase (see Figure 1 in Waite 1991). In addition, T_{bmin} was correlated with T_a . However, the extent of ρT_b cooling was much less than in *C. striatus* or *C. colius*. The jays reduced ρT_b from ca. 40°C to 36 - 37°C during the course of the rest-phase, at T_a s between -15°C and -25°C (Waite 1991).

Irrespective of whether the ρT_b patterns shown by *Colius* mousebirds and *P. canadensis* represent a common physiological phenomenon, such time-dependent variation in ρT_b represents an exception in avian thermoregulation. The majority of species defend a constant normothermic T_b setpoint during the rest-phase at $T_a < T_{lc}$ (e.g. Maddocks and Geiser 1997; Boix-Hinzen and Lovegrove 1998; McKechnie and Lovegrove 1999).

Basal metabolic rate

The BMR of $16.69 \text{ J.g}^{-1}.\text{h}^{-1}$ observed in this study was lower than the minimum metabolic rate previously reported for *C. striatus*. Bartholomew and Trost (1970) reported a minimal daytime metabolism of $24 \text{ J.g}^{-1}.\text{h}^{-1}$, and Hoffmann and Prinzinger (1984) reported a minimum rest-phase metabolic rate of $38.27 \text{ J.g}^{-1}.\text{h}^{-1}$ at $T_a = 23^\circ\text{C}$. Brown and Foster (1992) reported a BMR of $28.5 \text{ J.g}^{-1}.\text{h}^{-1}$, but since this value was measured during the day, i.e. the active-phase, it cannot be considered to represent basal metabolism (Schmidt-Nielsen 1990). My observed BMR is equivalent to 62% of the resting metabolic rate (RMR) predicted for a 51g bird by Bennett and Harvey (1987), and to 40% of the phylogenetically-corrected BMR predicted by Reynolds and Lee (1996).

Responses to restricted food

Restricted food in *C. striatus* was associated with considerable changes in the ρT_b range (Figure 1), but these changes did not accord with the generally accepted distinction between rest-phase hypothermia and torpor (Reinertsen 1983; 1996; Prinzinger et al. 1991; Wang and Wolowyk 1987). I was also unable to distinguish between these hypothermic responses using the characteristics employed by Geiser and Ruf (1995) i.e. minimum T_b (Figure 4b), minimum VO_2 (Figure 4a) or bout length. Hypothermic responses in *C. striatus* hence appear to

represent a continuum, rather than discrete proximate responses.

Prinzinger et al (1991) proposed that avian torpor is characterised by minimum T_b s < 25°C. Based on this definition, there were 11 instances of “torpor” in the present study. However, several characteristics of the thermoregulatory patterns shown during these instances were inconsistent with current definitions of torpor. Firstly, “torpor” in *C. striatus* was not characterised by the distinct entry, maintenance and arousal phases usually observed in endotherms (Lyman et al. 1982; Geiser and Ruf 1995). Such typical endothermic torpor bouts have been well described in hummingbirds (Hiebert 1990, Bucher and Chappell 1992). During these bouts, VO_2 rapidly decreased following the onset of the rest-phase and was maintained at an approximately constant level until the commencement of arousal. Although torpor VO_2 increased at low T_a s in hummingbirds, presumably in defence of a torpor T_b setpoint, at no stage was torpor VO_2 equal to, or greater than, BMR (Hiebert 1990). Body temperature during torpor showed similar entry, maintenance and arousal phases (Bech et al. 1997). These patterns are consistent with those reported in mammalian heterotherms (Geiser 1988).

“Torpor” in *C. striatus* was not consistent with these typical endothermic patterns. The initial reductions in VO_2 were similar to circadian fluctuations in normothermic birds, but were followed by gradual decreases in VO_2 , rather than regulation at a constant level (Figure 3). Body temperature was similarly not regulated at a torpor T_b setpoint, but decreased throughout the night. In approximately half of the “torpor” bouts, the birds reheated to ca. 35°C shortly after attaining the minimum T_b (e.g Figure 3b). Thereafter, T_b either remained fairly stable, or decreased again (Figure 3b). This pattern of partial arousal during the course of the rest-phase, followed by a second hypothermic bout, is similar to the multiple torpor bouts reported in some hummingbird species (Bech et al. 1997). In addition, metabolism

during “torpor” was higher than is typical during torpor - only in seven cases was torpor $VO_{2min} < BMR$ (Figure 4a).

My observed lowest $T_b = 18.2^\circ C$ in a bird able to spontaneously arouse is lower than previously measured in *C. striatus* (Bartholomew and Trost 1970). My data also suggest that the mousebirds were unable to arouse from $T_b < ca. 18^\circ C$. This is consistent with Prinzinger et al.’s (1981a,b) observations on *C. castanotus*. Prinzinger et al. (1991) suggested that for most birds the minimum critical T_b during torpor is around 18 - 20°C. Geiser and Ruf (1995) found that the mean minimum T_b of avian and mammalian daily heterotherms was 17.4°C. My observed minimum metabolic rate during torpor of 2.2 $J.g^{-1}.h^{-1}$ was higher than the minimum value of 1.26 $J.g^{-1}.h^{-1}$ recorded in *C. striatus* by Hoffmann and Prinzinger (1984).

“Torpor” in *C. striatus* appeared to be a response to low M_b . This observation is consistent with the those of Bartholomew and Trost (1970), who induced torpor in *C. striatus* by reducing M_b by 10 - 15%, and those of Prinzinger et al. (1981 a,b), Hoffmann and Prinzinger (1984) and Prinzinger (1988) who investigated torpor in *C. striatus*, *C. castanotus*, *U. macrourus* and *U. indicus*. Torpor in response to food deprivation has also been reported in other avian species, including members of the Caprimulgidae (Dawson and Fisher 1969; Lasiewski and Dawson 1964; Peiponen 1966;1970), and Apodidae (Bartholomew et al. 1957).

The physiological mechanism whereby endotherms determine fat reserves remains unknown (Boyer and Barnes 1999). However, experimental evidence suggests that the protein leptin may be the peripheral signalling component of a so-called “lipostat” (Zhang et al. 1994; Stephens and Caro 1998). It may be that in *C. striatus* and other avian species facultative hypothermia represents a proximate response to fat reserves falling below a threshold level determined by such a lipostat.

The energy savings that the mousebirds were able to make during the restricted food

were significant at $T_a = 15^\circ\text{C}$ and 20°C , but not at lower T_a s (Table 1). This was surprising, since the need for reductions in energy expenditure by means of hypothermic responses are presumably greater at low T_a s. Possible reasons for this observation are discussed below.

Evolutionary implications

The facultative hypothermic responses exhibited by *C. striatus* in response to restricted food clearly do not constitute typical endothermic torpor (sensu Lyman et al. 1982; Geiser and Ruf 1995). Although *C. striatus* has the physiological capacity to arouse from heterothermy, as long as T_b does not decrease to $< 18^\circ\text{C}$, the species apparently does not suppress metabolism during entry into torpor, nor does it maintain a constant level of metabolism or T_b during torpor. Hence, the patterns of “torpor” shown by *C. striatus* are apparently intermediate between normothermy and typical avian torpor. A similar observation can be made regarding the T_a -dependent cooling patterns exhibited by *C. colius* (McKechnie and Lovegrove 2001). The traces of metabolism shown in Figure 5 in Prinzinger et al. (1981b) suggest similar patterns to those I observed in *C. striatus* - moderate metabolic suppression followed by a gradual decrease through out the night, with the minimum T_b occurring shortly before arousal. It should be noted that I have not investigated the possibility that *C. striatus* does exhibit more typical torpor patterns under conditions of more severe starvation. However, gradual cooling is a considerably less effective energy-saving mechanism than typical torpor, and T_b s of 18°C appear to be near the lethal limit for mousebirds (Prinzinger et al. 1981;1991). If *C. striatus* does possess the capacity for pronounced metabolic downregulation, I would have expected the birds in my study to avoid the low T_b s I observed, while achieving comparable reductions in energy expenditure.

There are conflicting views as to whether torpor and hibernation represent

plesiomorphic patterns, or adaptive traits which have arisen independently in a polyphyletic assemblage of endotherms. Whereas Malan (1996) has proposed that the normothermic T_b patterns shown by endotherms represent an inhibition of the primitive tendency to wide-amplitude circadian T_b cycling, Geiser (1998) has pointed out that the polyphyletic distribution of avian heterothermy suggests that torpor has evolved independently in response to environmental factors. These two viewpoints provide a framework in which to examine the implications of the intermediate patterns of heterothermy exhibited by *C. striatus*, *C. colius*, and possibly other mousebird species.

The Coliiformes diverged from the Cuculiformes and Psittaciformes approximately 100 million years B.P. (Sibley & Ahlquist, 1990). Considered to be “living fossils”, the order has remained relatively unchanged since its divergence (Rich and Haarhof, 1985; Sibley and Ahlquist 1990). In contrast to most endotherms, neither *C. striatus* or *C. colius* appears to maintain normothermic rest-phase T_b with reference to a constant set-point T_b . Furthermore, although I observed hypothermic responses to restricted food in *C. striatus*, the thermoregulatory patterns during these responses appeared to be intermediate between the presumably normothermic patterns exhibited by birds fed ad libitum, and typical patterns of avian torpor.

I believe that the key to understanding the thermoregulatory patterns shown by mousebirds, is the clustering behaviour characteristic of all extant Coliiformes (Fry et al. 1988). Clustering behaviour is an important component of thermoregulation in both species, and is necessary for the defence of a constant rest-phase T_b in *C. colius* (McKechnie and Lovegrove 2001) and *C. striatus* (Chapter 3). Clustering behaviour also appears to be important in the avoidance of pathological hypothermia at low T_a s in *C. colius* (McKechnie and Lovegrove 2001). In addition, clustering behaviour is an important mechanism for

reducing rest-phase energy expenditure. Brown and Foster (1992) reported savings of 31% in a group of four *C. striatus* at $T_a = 16^\circ\text{C}$, whereas Prinzinger et al. (1981b) recorded a reduction in energy expenditure of 45.1% in a group of three *C. castanotus* at $T_a = 8^\circ\text{C}$. McKechnie and Lovegrove (2001) recorded energy savings of 50% in *C. colius* in a cluster of six at $T_a = 15^\circ\text{C}$. The energy savings that *C. striatus* are able to make by means of clustering behaviour are hence similar to, or greater than, the energy savings associated with any form of “adaptive” hypothermic responses.

If sociality and clustering behaviour are plesiomorphic traits in the Coliiformes, as is strongly suggested by its ubiquitous occurrence in the order, it suggests that typical avian torpor had not yet evolved in this phylogenetically ancient group. Presumably, the selective pressures leading to the evolution of torpor in other avian groups were partly obviated by the thermoregulatory role of clustering behaviour. This reduced selection for physiological energy-saving mechanisms has resulted in extant mousebirds exhibiting what may be termed avian “proto-torpor”. In terms of Malan’s (1996) argument, the ability to rapidly increase T_b by means of endogenous heat production would logically constitute a prerequisite to the evolution of the metabolic suppression associated with entry into typical endothermic torpor. Hence, I suggest that the “proto-torpor” shown by *C. striatus* represents an intermediate stage between Malan’s (1996) proposed ancestral high-amplitude T_b cycling, and modern patterns of endothermy, and furthermore argues for a plesiomorphic origin of torpor. Thermoregulatory patterns in *C. striatus*, *C. colius* and possibly other mousebirds may hence represent a “snapshot” in the development of avian torpor.

Literature cited

- Aschoff, J. 1982. The circadian rhythm of body temperature as a function of body size. In: Taylor, C. R., Johansen, R., and Bolis, L. (Eds.) A companion to animal physiology. Cambridge University Press, Cambridge.
- Bartholomew, G. A., Howell, T. R., and Cade, T. J. 1957. Torpidity in the white-throated swift, anna hummingbird, and poor-will. *Condor* 59: 145 - 155.
- Bartholomew, G. A. and Trost, C. H. 1970. Temperature regulation in the speckled mousebird, *Colius striatus*. *Condor* 72: 141 - 146.
- Bartholomew, G. A., Vleck, C. M., and Bucher, T. L. 1983. Energy metabolism and nocturnal hypothermia in two tropical passerine frugivores, *Manacus vitellinus* and *Pipra mentalis*. *Physiol. Zool.* 56: 370 - 379.
- Bech, C., Abe, A. S., Steffensen, J. F., Berger, M., and Bicudo, J. E. P. W. 1997. Torpor in three species of Brazilian hummingbirds under semi-natural conditions. *Condor* 99: 780 - 788.
- Bennett, P. M. and Harvey, P. H. 1987. Active and resting metabolism in birds: allometry, phylogeny and ecology. *J. Zool., Lond.* 213: 327 - 363.
- Boix-Hinzen, C. and Lovegrove, B. G. 1998. Circadian metabolic and thermoregulatory patterns of red-billed woodhoopoes (*Phoeniculus purpureus*): the influence of huddling. *J. Zool., Lond.* 244: 33 - 41.
- Boyer, B. B. and Barnes, B. M. 1999. Molecular and metabolic aspects of mammalian

hibernation. *BioScience* 49: 713 - 724.

Brown, C. R. and Foster, G. G. 1992. The thermal and energetic significance of clustering on the speckled mousebird, *Colius striatus*. *J. Comp. Physiol.* B162: 664 - 685.

Bucher, T. L. and Chappell, M. A. 1992. Ventilatory and metabolic dynamics during entry and arousal from torpor in *Selasphorus* hummingbirds. *Physiol. Zool.* 65: 978 - 993.

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

Fry, C. H., Keith, S., and Urban, E. K. 1988. The Birds of Africa Vol. 3. Academic Press, London.

Geiser, F. 1988. Reduction of metabolism during hibernation in mammals and birds: temperature effect or physiological inhibition? *J. Comp. Physiol.* 158: 25 - 37.

Geiser, F. 1998. Evolution of daily torpor and hibernation in birds and mammals: importance of body size. *Clin. Exp. Pharmacol. Physiol.* 25: 736 - 740.

Geiser, F. and Ruf, T. 1995. Hibernation versus daily torpor in mammals and birds: physiological variables and classification of torpor patterns. *Physiol. Zool.* 68: 935 - 966.

Graf, R., Krishna, S., and Heppner, F. 1989. Regulated nocturnal hypothermia induced in pigeons by food deprivation. *Am. J. Physiol.* 256: R733 - R738.

Haftorn, S. 1972. Hypothermia of tits in the Arctic winter. *Ornis Scand.* 3: 153 - 166.

Hiebert, S. M. 1990. Energy costs and temporal organization of torpor in the rufous

hummingbird (*Selasphorus rufus*). *Physiol. Zool.* 63: 1082 - 1097.

Hoffmann, R. and Prinzinger, R. 1984. Torpor und Nahrungsausnutzung bei 4
Mausvogelarten (Coliiformes). *J. Ornithol.* 125: 225 - 237.

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

Jaeger, E. C. 1949. Further observations on the hibernation of the poor-will. *Condor* 51: 105 -
109.

Lasiewski, R. C. and Dawson, W. R. 1964. Physiological responses to temperature in the
common nighthawk. *Condor* 66: 477 - 490.

Lyman, C. P., Willis, J. S., Malan, A., and Wang, L. C. H. (Eds.) 1982. Hibernation and
torpor in mammals and birds. Academic Press, New York.

Maddocks, T. A. and Geiser, F. 1997. Energetics, thermoregulation and nocturnal
hypothermia in Australian silvereyes. *Condor* 99: 104 - 112.

Malan, A. 1996. The origins of hibernation: a reappraisal. In: Geiser, F., Hulbert, A. J., and
Nicol, S. C. (Eds.) Adaptations to the cold: Tenth International Hibernation
Symposium. University of New England Press, Armidale.

McKechnie, A. E. and Lovegrove, B. G. 1999. Circadian metabolic responses to food
deprivation in black-shouldered kites. *Condor* 101: 426 - 432.

McKechnie, A. E. and Lovegrove, B. G. 2001. Thermoregulation and the energetic
significance of clustering behavior in the white-backed mousebird (*Colius colius*).
Physiol. Biochem. Zool. 74: 238 - 249.

- Peiponen, V. A. 1966. The diurnal heterothermy of the nightjar (*Caprimulgus europaeus* L.).
Ann. Acad. Sci. Fennicae (A IV) 101: 1 - 35.
- Peiponen, V. A. 1970. Body temperature fluctuations in the nightjar (*Caprimulgus e. europaeus* L.) in light conditions of southern Finland. *Ann. Zool. Fennici* 7: 239 - 250.
- Prinzinger, R. 1988. Energy metabolism, body-temperature and breathing parameters in non-torpid blue-naped mousebirds *Urocolius macrourus*. *J. Comp. Physiol.* B157: 801 - 806.
- Prinzinger, R., Göppel, R., and Lorenz, A. 1981a. Der torpor beim Rotrückenmausvogel, *Colius castanotus*. *J. Ornithol.* 122: 379 - 392.
- Prinzinger, R., Göppel, R., Lorenz, A., and Kulzer, E. 1981b. Body temperature and metabolism in the red-backed mousebird (*Colius castanotus*) during fasting and torpor. *Comp. Biochem. Physiol.* 69A: 689 - 692.
- Prinzinger, R., Preßmar, A., and Schleucher, E. 1991. Body temperature in birds. *Comp. Biochem. Physiol.* 99A: 499 - 506.
- Reinertsen, R. E. 1983. Nocturnal hypothermia and its energetic significance for small birds living in the arctic and subarctic regions. A review. *Polar Res.* 1: 269 - 284.
- Reinertsen, R. E. 1996. Physiological and ecological aspects of hypothermia. In: Carey, C. (Eds.) *Avian energetics and nutritional ecology*. Chapman & Hall, New York.
- Reinertsen, R. E. and Haftorn, S. 1986. Different metabolic strategies of northern birds for nocturnal survival. *J. Comp. Physiol.* 156: 655 - 663.

- Reynolds, P. S. and Lee, R. M. 1996. Phylogenetic analysis of avian energetics: passerines and non-passerines do not differ. *Am. Nat.* 147: 735 - 759.
- Rich, P. V. and Haarhoff, P. J. 1985. Early Pliocene Coliidae (Aves, Coliiformes) from Langebaanweg, South Africa. *Ostrich* 56: 20 - 41.
- Schaub, R., Prinzinger, R., and Schleucher, E. 1999. Energy metabolism and body temperature in the Blue-naped mousebird (*Urocolius macrourus*) during torpor. *Ornis Fennica* 76: 211 - 219.
- Schmidt-Nielsen, K. 1990. Animal physiology: adaptation and environment. Cambridge University Press, Cambridge.
- Sibley, C. G. and Ahlquist, J. E. 1990. Phylogeny and classification of birds. Yale University Press, New Haven.
- Song, X., Körtner, G., and Geiser, F. 1997. Thermal relations of metabolic rate reduction in a hibernating marsupial. *Am. J. Physiol.* 273: R2097 - R2104 -
- Stephens, T. W. and Caro, J. F. 1998. To be lean or not to be lean: is leptin the answer? *Exp. Clin. Endocrinol. Diabetes* 106: 1 - 15.
- Waite, T. A. 1991. Nocturnal hypothermia in gray jays *Perisoreus canadensis* wintering in interior Alaska. *Ornis Scand.* 22: 107 - 110.
- Wang, L. C. H. and Wolowyk, M. W. 1987. Torpor in mammals and birds. *Can. J. Zool.* 66: 133 - 137.
- Withers, P. C. 1977. Measurement of VO_2 , VCO_2 , and evaporative water loss with a flow-

through mask. *J. Appl. Physiol.* 42: 120 - 123.

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

Zhang, Y. Y., Proenca, R., Maffei, M., Barone, M., Leopold, L., and Friedman, J. M. 1994.
Positional cloning of the mouse *obese* gene and its human homologue. *Nature* 372:
425 - 432.

Chapter 3. Thermoregulation in speckled mousebirds (*Colius striatus*) under semi-natural conditions: the role of clustering behaviour.

Introduction

Several behavioural and physiological avenues exist whereby birds can reduce their energy expenditure during the rest-phase of the circadian cycle, including microhabitat selection (Andreev 1999), communal roosting (Reinertsen 1983) and facultative increases in the amplitude of circadian rhythms of metabolism and body temperature (T_b) (Reinertsen 1983). Microhabitat selection, communal roosting and facultative hypothermia are important in the energy balance of birds inhabiting both temperate (e.g. Reinertsen 1983; Andreev 1999) and tropical environments (e.g. Carpenter 1974; Hiebert 1993).

Reductions in rest-phase energy expenditure associated with communal roosting have been observed in several social species, including red-billed woodhoopoes *Phoeniculus purpureus* (Boix-Hinzen and Lovegrove 1998), at least three mousebird species (Prinzinger et al. 1981; Brown and Foster 1992; McKechnie and Lovegrove 2001), grey partridges *Perdix perdix* (Putala et al. 1995), common bushtits *Psaltriparus minimus* (Chaplin 1982) and blacktailed gnatcatchers *Auriparus flaviceps* (Walsberg 1990). In some cases, rest-phase energy expenditure was reduced by > 40% (Prinzinger et al. 1981; Walsberg 1990; McKechnie and Lovegrove 2001).

Communal roosting is particularly important in temperate and sub-arctic areas subject to pronounced seasonal variation in food availability and quality (Reinertsen 1983; Du Plessis et al. 1994). However, it is well-developed in the Afrotropical endemic order Coliiformes, or mousebirds. The distinctive clustering behaviour shown by mousebirds results in energy savings of 40 - 50% (Prinzinger et al. 1981; Brown and Foster 1992; McKechnie and

Lovegrove 2001). Moreover, there is evidence that clustering behaviour may represent an important component of thermoregulation in mousebirds. Brown and Foster (1992) noted that rest-phase T_b (ρT_b) in single speckled mousebirds *Colius striatus* was more labile than in clustering birds. McKechnie and Lovegrove (2001) found that rest-phase thermoregulation in white-backed mousebirds (*Colius colius*) was characterized by patterns of ambient temperature (T_a)-dependent decreases in T_b . Clustering behaviour appeared to be vital in the reduction of these cooling rates and in the avoidance of pathological hypothermia at low T_a .

In addition to exhibiting well-developed communal roosting, mousebirds exhibit a pronounced capacity for heterothermy (Bartholomew and Trost 1970; Prinzinger et al. 1981; Hoffmann and Prinzinger 1984; Chapter 2). The fact that mousebirds exhibit clustering behaviour as well as the capacity for daily torpor is interesting, as these energy-saving mechanisms have generally been considered in isolation of each other. The mousebirds offer an opportunity to investigate the interaction between these pathways for reduction in energy expenditure. It may be significant that all records of torpor in mousebirds are from single birds under laboratory conditions. In at least one mousebird species (*C. colius*), patterns of thermoregulation under laboratory conditions differ significantly between single birds and clustering birds (McKechnie and Lovegrove 2001). The energy savings associated with clustering behaviour may obviate the need to utilise torpor under natural conditions (McKechnie and Lovegrove 2001; Chapter 2).

I tested the hypothesis that under natural conditions of T_a and photoperiod, thermoregulation in speckled mousebirds *C. striatus* differs significantly between single birds and clustering birds. Specifically, I tested the predictions that a) in contrast to the rest-phase cooling exhibited by single *C. striatus* under laboratory conditions (Chapter 2), clustering birds under semi-natural conditions defend an approximately constant ρT_b , and b) clustering

behaviour moderates the use of hypothermic responses. In addition, I was interested in whether the patterns of T_a -dependent cooling shown by single *C. striatus* under laboratory conditions (Chapter 2) were representative of thermoregulation in this species under semi-natural conditions. I also investigated the extent to which previous laboratory studies of thermoregulation in this species (Bartholomew and Trost 1970; Hoffmann and Prinzinger 1984; Brown and Foster 1992; Chapter 2) reflected patterns exhibited under natural cycles of T_a and photoperiod.

Materials and Methods

Ten speckled mousebirds were trapped in Pietermaritzburg, South Africa, during June 1999, using a walk-in trap baited with fruit. They were housed in an outdoor aviary (3m long, 2m high, 1m wide) in the School of Botany and Zoology at the University of Natal. They were fed ad libitum on a variety of fruit, including pawpaws, bananas, grapes, apples and tomatoes. Each bird was marked with coloured celluloid rings for identification. The birds were exposed to natural conditions of T_a , air movement and photoperiod, but artificial feeding conditions. They were weighed every second day during the ad libitum feeding treatments, and daily during the restricted feeding treatments. All experiments were carried out during August 1999.

Body temperature measurement

Temperature-sensitive FM transmitters (Sirtrack, New Zealand) with an average mass of 1.6g and frequencies between 146.0 and 146.5 MHz were used to measure T_b in the mousebirds. The transmitters were calibrated in a water bath at temperatures between 10° and 45°C, using a standard mercury thermometer (0.05°C), with an accuracy traceable to the US National Bureau of Standards. They were implanted into the peritoneal cavities of the mousebirds

under inhalation anaesthesia (Isoflurane in oxygen; induction and maintenance, 2.5%; flow rate, ca. $0.5\ell.\text{min}^{-1}$).

Signals from the transmitters were recorded using a custom-built multi-channel data logger. This data logger controlled a single side-band mode communications receiver (Model IC-R10, ICOM) and recorded pulse intervals of all ten transmitters in 10-minute intervals. Ambient temperature in the aviary was measured by the data logger using a monolytic temperature transducer (LM335). Data were stored on an EPROM and downloaded daily. Electronics and software were developed by Gerhard Körtner.

Experimental protocol

Data collection commenced immediately after implantation on the 3rd of August 1999 but data recorded within 48 hours of surgery were excluded from the analyses. All ten birds were kept in a single aviary for seven days after implantation. Thereafter, during a five day period, each bird in the group was removed from the group aviary and placed in a separate aviary overnight, before being returned to the group aviary the following day. Two birds were placed in separate aviaries each night, and group size in the main aviary was maintained at eight birds. Each bird spent 24 hours (12h00 - 12h00) away from the group, which facilitated measurement over an entire circadian T_b cycle without the influence of clustering behaviour.

To investigate the effects of restricted food on rest-phase thermoregulation, I deprived the birds of food for one day. This was repeated three times while all the birds were in a single aviary. Finally, I placed each bird in a single aviary (as described above) and deprived it of food for 24 hours. During this final period, some of the transmitter batteries ran flat and I was able to obtain reliable traces of T_b for only five individuals.

Data analysis

The rest-phase was subjectively judged to commence following the rapid reduction in T_b which typically occurred immediately following sunset. Single birds generally did not exhibit well-defined T_b downregulation at the onset of the rest-phase. Hence, I assumed that the rest-phase in single birds commenced at the same time as that of clustering birds on the same evening. The rest-phase was subjectively judged to end immediately preceding the rapid reheating which typically occurred at around sunrise. I calculated the maximum circadian amplitude of T_b cycles (R_T) as the difference between minimum rest-phase T_b ($\rho T_{b,\min}$) and the maximum active-phase T_b ($\alpha T_{b,\max}$), following Aschoff (1982).

I calculated cooling rates by fitting least-square linear regressions (Zar 1999) to ρT_b as a function of time during the rest-phase. Rest-phase T_b patterns in both *C. colius* and *C. striatus* are best described by linear models (McKechnie and Lovegrove 2001; Chapter 2). The coefficients of these regressions were used as measures of cooling rate.

Values are presented as mean \pm S.E. To assess the specific effects of group size and food availability I used repeated-measures analysis of co-variance (RM-ANCOVA; Zar 1999). The minimum and average T_a s recorded between sunset and sunrise (site-specific times obtained from the Department of Agrometeorology, University of Natal) were used as co-variates. Assumptions concerning the homogeneity of variances / covariances were confirmed using Sen & Puri's nonparametric test.

Results

Random visits to the aviaries at night suggested that the birds clustered from shortly after sunset until immediately prior to sunrise the next morning. Some movement within the clusters was evident, and it appeared that an individual's position in the cluster varied during

the course of the night. The body mass (M_b) during ad libitum feeding was $52.4 \pm 1.4\text{g}$, and decreased to $46.3 \pm 1.0\text{g}$ during the restricted feeding treatment. The mean M_b loss during restricted feeding was $11.7 \pm 0.8\%$ of ad libitum M_b .

Ad libitum feeding

Birds which spent the night in clusters exhibited typical endothermic patterns of circadian T_b rhythms, namely a rapid reduction at the onset of the rest-phase followed by the defence of an approximately constant ρT_b (Figure 1a-d). Steady-state ρT_b was followed by rapid reheating to active phase T_b (αT_b) at sunrise the following morning. These patterns were reflected in the approximately normal frequency distribution of ρT_b observed in clustering birds, with range of ρT_b from ca. 32°C to 42°C (Figure 2a). In several cases, some thermolability was evident with rapid transient increases and decreases in ρT_b (e.g. Figure 1a). In general, the ρT_b s of individual birds in the cluster during the course of the rest-phase were highly synchronised during both ad libitum and restricted feeding (Figure 3).

Patterns of ρT_b in single birds differed from those exhibited by clustering birds. The initial down-regulation of T_b and the subsequent defence of a constant ρT_b was largely absent (Figure 1e-h). Instead, T_b gradually decreased from active-phase levels to the minimum ρT_b ($\rho T_{b\text{min}}$), which typically occurred immediately prior to the increase in endogenous heat production associated with sunrise. The $\rho T_{b\text{min}}$ values recorded in single birds were significantly lower than those observed in clustering birds (RM-ANCOVA, $F_{1,135} = 10.755$, $P < 0.05$). A greater degree of thermolability was evident in single birds, compared to clustering birds (Figure 2b). The range of ρT_b was slightly wider than that of clustering birds, from ca. 31°C to 43°C (Figure 2b). Furthermore, the coefficients of linear regressions fitted to ρT_b as a function of time (i.e. cooling rates) were significantly higher in single birds (RM-ANCOVA,

$F_{1,135} = 55.852, P < 0.05$). The cooling rates of single birds were approximately three times greater than those of birds in a cluster (Table 1). As mentioned in Chapter 2, these cooling rates should not be interpreted as accurate measurements of heat loss, but merely as approximations of deviation from typical endotherm T_b homeostasis. The R_T of single birds was significantly greater than that of clustering birds (RM-ANCOVA, $F_{1,135} = 16.143, P < 0.05$; Table 1).

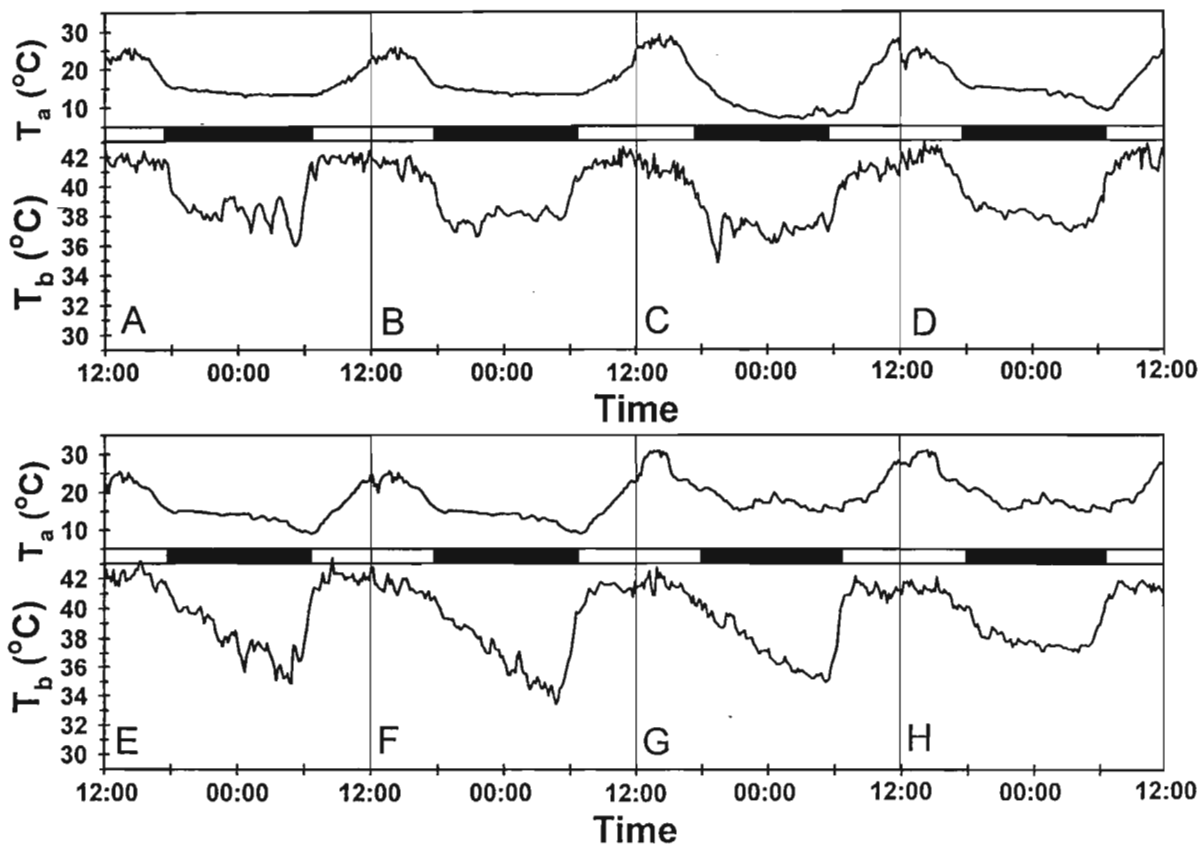


Figure 1. Traces of T_a and circadian T_b rhythms in speckled mousebirds (*Colius striatus*) held in outdoor aviaries and fed ad libitum. Traces A - D were recorded in birds in a group which clustered at night. Traces E - H were recorded in single birds placed in separate aviaries. The horizontal bars indicate the period between sunset and sunrise. Note that only in clustering birds were the initial reduction of T_b at the onset of the rest-phase, and subsequent defence of a constant T_b setpoint evident.

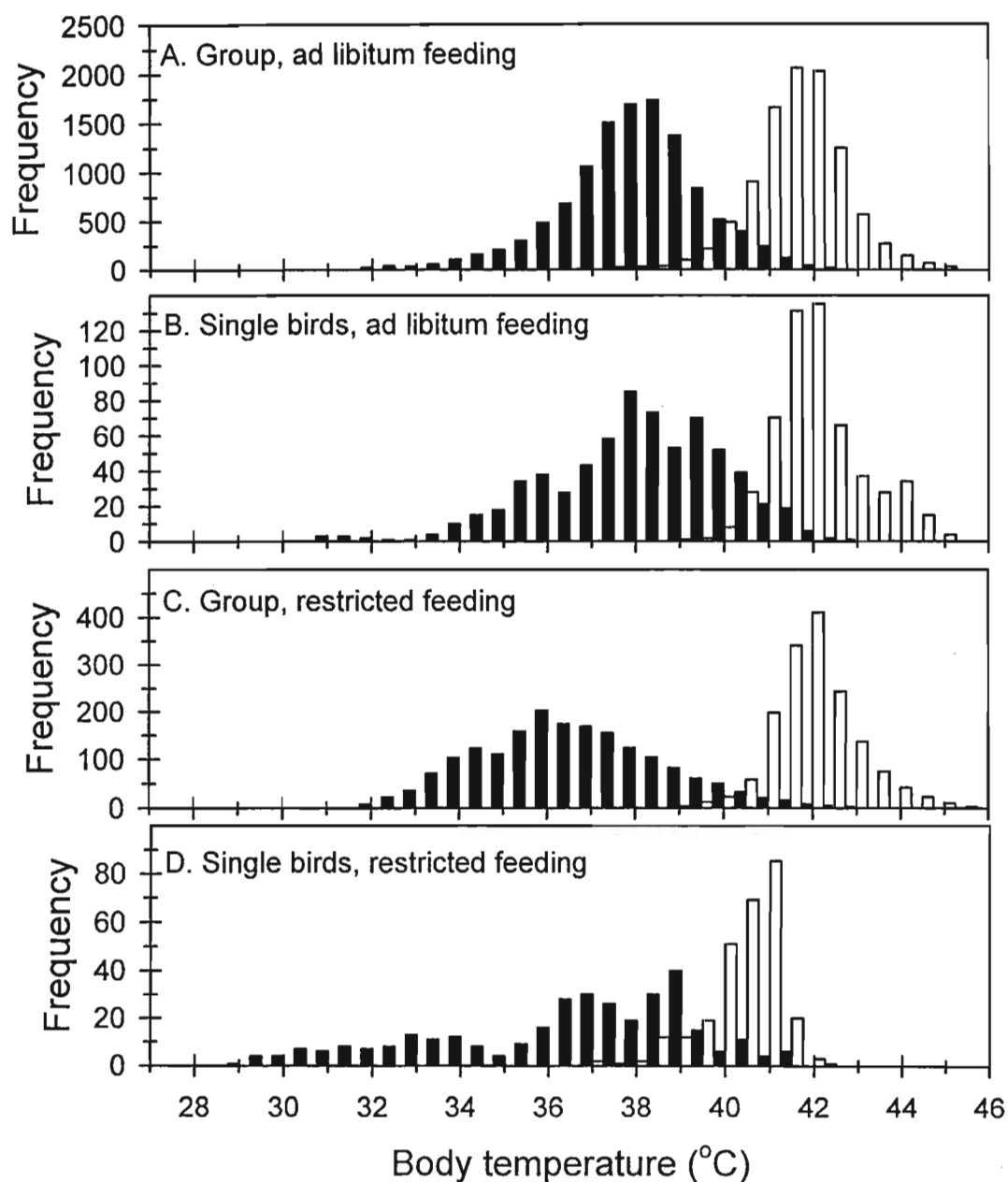


Figure 2. Frequency histograms of T_b recorded in speckled mousebirds (*Colius striatus*) held in outdoor aviaries. Light bars indicate active-phase T_b (recorded between sunrise and sunset) and dark bars indicate rest-phase T_b (recorded between sunset and sunrise). The data were recorded in groups of birds (A,C) and single birds (B,D) and during ad libitum (A,B) and restricted (C,D) feeding treatments.

Table 1. Minimum rest-phase body temperature (ρT_b min), rest-phase cooling rate, and the amplitude of circadian T_b rhythms (R_T) in speckled mousebirds *Colius striatus* under semi-natural conditions in outdoor aviaries.

	ρT_b min ($^{\circ}\text{C}$)		Cooling rate ^a ($^{\circ}\text{C}\cdot\text{h}^{-1}$)		R_T ($^{\circ}\text{C}$)	
	Ad lib	Restricted	Ad lib	Restricted	Ad lib	Restricted
Clustering	35.9±0.1 (145) ^b	33.3±0.2 (23)	0.14±0.01 (145)	0.42±0.03 (23)	6.9±0.1 (145)	9.5±0.2 (23)
Single	34.9±0.6 (9)	30.7±1.2 (5)	0.49±0.09 (9)	0.47±0.13 (5)	8.1±0.6 (9)	11.8±0.5 (5)

a. Calculated as coefficient of least-squares linear regression fitted to ρT_b as a function of time

b. Numbers in parentheses indicate number of measurements

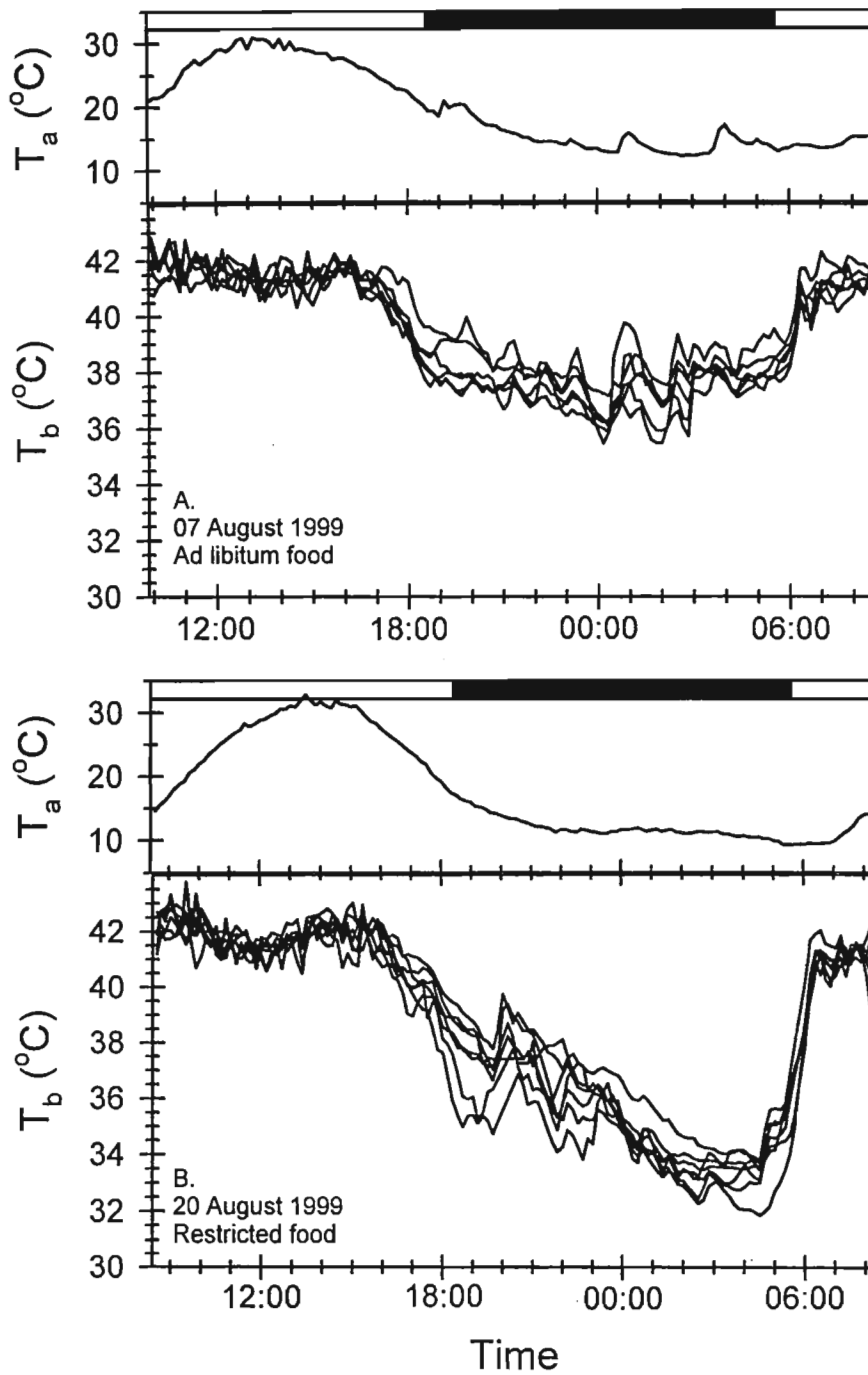


Figure 3. Traces of T_b recorded simultaneously in clustering speckled mousebirds (*Colius striatus*) held in outdoor aviaries. The dark bar indicates sunset - sunrise. Note the high degree of synchronicity between the ρT_b of different individuals. The traces shown in A were recorded during the ad libitum feeding treatment, and the traces in B during the restricted feeding treatment.

Restricted feeding

During the restricted food treatment (24 hours), during which the mousebirds lost $11.7 \pm 0.8\%$ of their M_b , R_T increased in both clusters (RM-ANCOVA, $F_{1,149} = 97.473$, $P \ll 0.05$) and single birds (RM-ANCOVA, $F_{1,2} = 96.856$, $P < 0.05$). Clustering birds did not maintain a constant ρT_b following the initial T_b down-regulation at the onset of the rest-phase (Figure 4a-d). Rather, the responses of clustering birds involved increased cooling rates, similar to those observed in single birds during the ad libitum food treatment (Table 1). During the restricted feeding treatment, both clustering and single birds showed a wider range of ρT_b than during the ad libitum feeding treatment (Figure 2c,d). Moreover, decreases in the modal ρT_b values were evident (Figure 2c,d). Similarly, the $\rho T_{b,min}$ of both clustering birds (RM-ANCOVA, $F_{1,149} = 82.339$, $p \ll 0.05$) and single birds (RM-ANCOVA, $F_{1,2} = 203.931$, $P < 0.05$) was significantly lower than during the ad libitum feeding treatment (Table 1). The cooling rates of birds in clusters were significantly higher than during the ad libitum treatment (RM-ANCOVA, $F_{1,149} = 82.454$, $p \ll 0.05$; Table 1). However, the cooling rates exhibited by single birds did not change during restricted feeding (RM-ANCOVA, $F_{1,2} = 1.623$, $P > 0.05$; Table 1). Single birds during the restricted food treatment exhibited the widest ρT_b range from ca. 29°C to 43°C (Figure 2d). The lowest observed T_b was 29.1°C , recorded in a single bird during the restricted food treatment (Figure 4e). During the restricted feeding treatment, the $\rho T_{b,min}$ was significantly lower in single birds than in clustering birds (RM-ANCOVA, $F_{1,14} = 10.312$, $P < 0.05$) and the R_T was significantly greater (RM-ANCOVA, $F_{1,14} = 4.854$, $P < 0.05$).

Active-phase T_b

The birds maintained approximately constant T_b s during the active-phase, with a mean αT_b of $41.5 \pm 0.06^\circ\text{C}$ during the ad libitum food treatment ($n = 155$ bird-days). The mean maximum

αT_b ($\alpha T_{b,max}$) observed in each bird during the study was 43.7°C ($n = 10$). These high T_b s were typically recorded between 09h00 and 11h00 on sunny days, and appeared to coincide with bouts of sunning behaviour. During sunning behaviour, the mousebirds would cling to the sides of the aviaries with their underparts orientated towards incident solar radiation, and would pilo-erect their feathers to expose their skin.

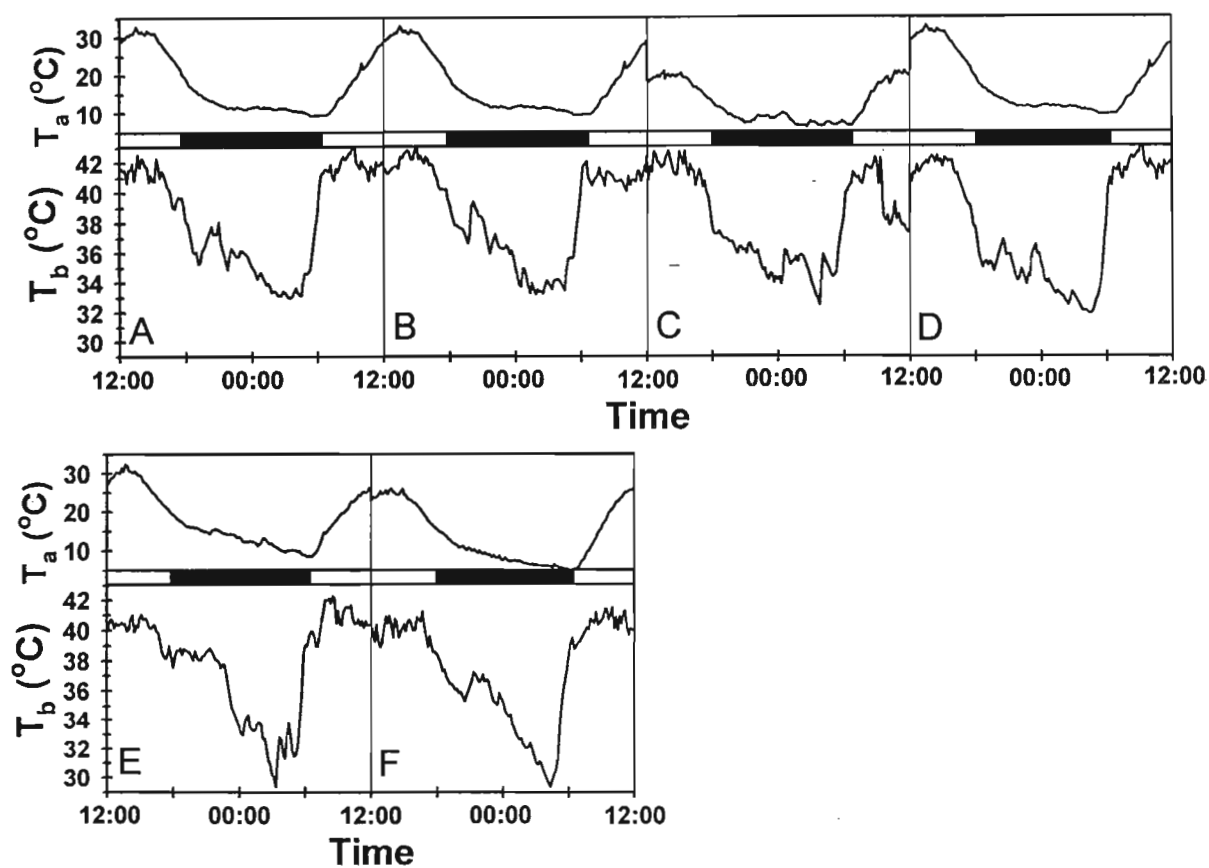


Figure 4. Traces of T_a and circadian T_b rhythms in speckled mousebirds (*Colius striatus*) held in outdoor aviaries and derived of food for 24 hours. Traces A - D were recorded in birds which clustered at night, and traces E - F were recorded in single birds placed in separate aviaries. The horizontal bars indicate the period between sunset and sunrise.

Discussion

The differences between thermoregulation in single and clustering birds supported my initial predictions, and illustrate the thermoregulatory role of clustering behaviour in *C. striatus*. In contrast to clustering birds, which defended approximately constant ρT_b setpoints, single birds exhibited patterns of rest-phase cooling consistent with previous laboratory observations (Chapter 2).

Clustering birds exhibited hypothermic responses to restricted feeding that were reduced in comparison to those of single birds. This observation supported my prediction that behavioural thermoregulation, namely clustering behaviour, moderates hypothermic responses to energetic stress in *C. striatus*.

Thermoregulation in single birds under laboratory and semi-natural conditions

The majority of data on avian thermoregulation originate from laboratory studies, and these data are frequently assumed to be representative of thermoregulation under natural conditions. However, there are several potential pathways whereby the thermal environment of a bird within a confined space, such as a respirometer, may be inadvertently altered. In particular, low rates of air flow may lead to a gradual increase in relative humidity within a respirometer, which in turn influences heat flux between a bird and its environment.

Comparisons of data collected under laboratory conditions with those collected under semi-natural or natural conditions are necessary to assess the degree to which laboratory measurements are representative of patterns shown by animals in their natural environments. For instance, Geiser et al. (2000) compared patterns of heterothermy in free-ranging and captive endotherms. Almost without exception, laboratory studies tended to underestimate the frequency, duration and depth of heterothermic responses (Geiser et al. 2000). Recent efforts

have been made to investigate thermoregulation in complex thermal environments, similar to those experienced by free-ranging endotherms (Wolf and Walsberg 1996; Wolf et al. 1996).

The patterns of linear rest-phase cooling I observed in single *C. striatus* during the ad libitum feeding treatment were consistent with previous laboratory observations (Chapter 2). In addition, the range of ρT_b in single birds during the ad libitum feeding treatment (ca. 31 °C to 43 °C) was similar to that observed under laboratory conditions (ca. 30 °C to 40 °C; Chapter 2). I used the average T_a between sunset and sunrise to calculate predicted cooling rates using the equation for cooling rate and T_a in Chapter 2. The observed cooling rates of single birds during the ad libitum feeding treatment were equivalent to $133 \pm 25\%$ of these predicted values. In Chapter 2, I found that a rapid decrease in T_a during the rest-phase caused a significant increase in cooling rate. I suspect that *C. striatus* showed slightly higher cooling rates under semi-natural conditions because T_a typically decreased during the course of the rest-phase, rather than remaining constant as was the case during most of the laboratory measurements (Chapter 2).

Role of clustering behaviour in normothermic thermoregulation

Mousebirds are highly social and rarely spend a night without clustering (Fry et al. 1988).

Hence, patterns of normothermic thermoregulation in free-ranging *C. striatus* are likely to be similar to the patterns shown by clustering individuals under semi-natural conditions.

Nocturnal thermoregulation in clustering *C. striatus* comprised three distinct phases: a decrease in T_b at the onset of the rest-phase, followed by the defence of an approximately constant ρT_b setpoint, and an increase in T_b to active-phase levels at sunrise. These patterns are consistent with typical avian circadian T_b patterns (e.g. Maddocks and Geiser 1997; Boix-Hinzen and Lovegrove 1998; McKechnie and Lovegrove 1999).

A comparison of the patterns of thermoregulation in single and clustering birds during the ad libitum feeding treatment suggests that clustering behaviour may be obligatory for the maintenance of typical endothermic circadian T_b cycles in *C. striatus*. However, the reason for the apparent absence of metabolic down-regulation in single birds at the onset of the rest-phase is unclear. Cooling rate and hence the ρT_b min attained prior to rewarming in single *C. striatus* was dependent on T_a , although the underlying physiological mechanism for these patterns of cooling is unclear (McKechnie and Lovegrove 2001; Chapter 2). It is possible that a facultative inhibition of metabolic suppression at the onset of the rest-phase served to minimise the reduction in ρT_b resulting from T_a -dependent cooling.

The traces of T_b in clustering *C. striatus* (Figure 1a-d), as well as the frequency distribution of ρT_b (Figure 2a) suggest that even when in a cluster, the ρT_b of this species is unusually labile. The normothermic ρT_b range of this species includes T_b s usually associated with avian hypothermic responses (Prinzinger et al. 1991). Several authors have noted that ρT_b in mousebirds is relatively variable (Bartholomew and Trost 1970; Prinzinger et al 1981; Brown and Foster 1992), and my results are consistent with these observations. The related observation that the ρT_b of individual mousebirds within a cluster was highly synchronized reflects the close contact that occurs between mousebirds while clustering. Contact between individuals presumably facilitates heat flow and reduces T_b gradients between individuals, resulting in temporal synchronicity of heat flux within the cluster.

Clustering behaviour and facultative hypothermic responses

Although clustering behaviour led to a reduction in the extent of hypothermic responses in *C. striatus*, clustering birds exhibited clear facultative hypothermic responses to energy shortages under semi-natural conditions. Hypothermic responses in clustering *C. striatus* were generally

characterized by increased cooling rates following the initial T_b down-regulation, rather than by more pronounced T_b reduction at the onset of the rest-phase and the subsequent defence of a reduced ρT_b setpoint. On the basis of a similar lack of metabolic suppression in mousebirds exposed to food deprivation (*C. striatus*) and low T_a (*C. colius*) under laboratory conditions, McKechnie and Lovegrove (2000) argued that patterns of thermoregulation in these two species do not accord with typical endothermic torpor patterns. Instead, these patterns may represent “proto-torpor”, an intermediate stage between Malan’s (1996) hypothesised ancestral patterns of thermoregulation, and typical avian heterothermic responses (McKechnie and Lovegrove 2000).

The most important proximate determinants of avian facultative hypothermic responses are food availability and T_a (Reinertsen 1996). However, my data show that in at least one mousebird species a further factor, namely group size, is critical in determining the extent of hypothermic responses. Hence, it is unlikely that clustering mousebirds under natural conditions routinely exhibit torpor comparable to that shown by single birds under laboratory conditions (Bartholomew and Trost 1970; Hoffmann and Prinzinger 1984; Chapter 2). Mousebirds are one of the best-known groups of avian heterotherms (Prinzinger et al. 1991; Reinertsen 1996), but this may be the result of their thermoregulation being investigated under artificial (laboratory) conditions. Moreover, the mousebirds seem to represent an exception to the observations of Geiser et al. (2000), who noted that heterothermy in free-ranging animals was generally more frequent and more pronounced than under laboratory conditions.

Coevolution of mousebird sociality and thermoregulation?

The primary benefits of avian sociality are generally assumed to be related to territory defence and predator avoidance (Wrangham and Rubenstein 1986). Nevertheless, the importance of

physiological constraints in the evolution of avian sociality has come under close scrutiny, and these studies form a conceptual framework in which to examine the relationship between thermoregulation and sociality in mousebirds.

Ligon et al. (1988) proposed that green (red-billed) woodhoopoes (*Phoeniculus purpureus*) are constrained to roost communally in cavities, despite associated high predation rates, because of a thermogenic inability to tolerate low nocturnal T_a . This “Thermoregulatory Insufficiency Hypothesis” was criticized (Ward et al. 1989), defended (Ligon et al. 1989) and subsequently refuted by Williams et al. (1991), whose measurements of oxygen consumption and T_b demonstrated that woodhoopoes in good body condition were able to defend a pT_b setpoint even at $T_a = -10^\circ\text{C}$. Nevertheless, Boix-Hinzen and Lovegrove (1998) showed that *P. purpureus* do significantly reduce their rest-phase energy expenditure by roosting communally.

The potential importance of energetic constraints on selection for philopatry has also been investigated in the acorn woodpecker (*Melanerpes formicivorus*) by Weathers et al. (1990). These authors observed several unusual physiological characteristics, such as the lack of a clearly-defined thermoneutral zone, and an inability to tolerate even moderate T_a . Whereas these characteristics may to an extent be due to phylogeny, the unusual patterns of thermoregulation in *M. formicivorus* may well be related to their communal roosting behaviour (Weathers et al. 1990).

The importance of clustering behaviour in the thermoregulation of at least two mousebird species (McKechnie and Lovegrove 2001; present study) suggests that the primary benefits of sociality in these species are thermoregulatory, since clustering behaviour appears to be obligatory for the maintenance of typical endotherm circadian T_b cycles. The thermoregulatory importance of clustering behaviour suggests that in the Coliiformes,

sociality is a plesiomorphic trait. This argument is supported by the fact that clustering behaviour is ubiquitous in extant mousebirds (Fry et al. 1988). Hence, it would appear that social behaviour in the Coliiformes has evolved in tandem with thermoregulation. McKechnie and Lovegrove (2000) have argued that the characteristics of heterothermic responses in these two species suggest that sociality developed early in the mousebird lineage, and arrested the development of typical avian heterothermy. The patterns of thermoregulation shown by *C. striatus* under semi-natural conditions suggest that the evolution of normothermic thermoregulation in the Coliiformes was similarly influenced by sociality. The relative lability of ρT_b in single mousebirds may reflect the fact that the development of rest-phase thermoregulation in mousebirds has been influenced by their distinctive social behaviour.

However, there appears to be interspecific variation in the extent to which clustering behaviour is necessary for survival at low T_a . Whereas single *C. striatus* in good condition were able to thermoregulate at $T_a < 10^\circ\text{C}$ under laboratory conditions (Chapter 2), four out of nine single *C. colius* suffered pathological hypothermia at $T_a = 5^\circ\text{C}$ (McKechnie and Lovegrove 2001). The arid-zone *C. colius* is apparently more reliant on clustering behaviour than the mesic *C. striatus*, suggesting that reliance on behavioural thermoregulation may be correlated with habitat characteristics. It would appear that social thermoregulation has been more strongly selected for in *C. colius* than in *C. striatus*, possibly because of the greater selective pressures acting on the ability to reduce energy requirements in arid, unpredictable habitats (Lovegrove 2000). However, it is not possible to adequately infer adaptations from comparisons of two species (Garland and Adolph 1994), and this hypothesis requires further testing in other mousebird species, such as the white-headed mousebird *C. leucocephalus*, endemic to the east African arid zone (Fry et al. 1988).

Literature cited

- Andreev, A. V. 1999. Energetics and survival of birds in extreme environments. In: Adams, N. J. and Slotow, R. H. (Eds.) Proc. 22 Int. Ornithol. Congr., Durban. Ostrich 70(1).
- Aschoff, J. 1982. The circadian rhythm of body temperature as a function of body size. In: Taylor, C. R., Johansen, R., and Bolis, L. (Eds.) A companion to animal physiology. Cambridge University Press, Cambridge.
- Bartholomew, G. A. and Trost, C. H. 1970. Temperature regulation in the speckled mousebird, *Colius striatus*. *Condor* 72: 141 - 146.
- Boix-Hinzen, C. and Lovegrove, B. G. 1998. Circadian metabolic and thermoregulatory patterns of red-billed woodhoopoes (*Phoeniculus purpureus*): the influence of huddling. *J. Zool., Lond.* 244: 33 - 41.
- Brown, C. R. and Foster, G. G. 1992. The thermal and energetic significance of clustering on the speckled mousebird, *Colius striatus*. *J. Comp. Physiol.* B162: 664 - 685.
- Carpenter, F. L. 1974. Torpor in an Andean hummingbird: its ecological significance. *Science* 183: 545 - 547.
- Chaplin, S. A. 1982. The energetic significance of huddling in common bushtits (*Psaltriparus minimus*). *Condor* 99: 424 - 430.
- Du Plessis, M. A., Weathers, W. W., and Koenig, W. D. 1994. Energetic benefits of communal roosting by acorn woodpeckers during the non-breeding season. *Condor* 96: 631 - 637.

- Fry, C. H., Keith, S., and Urban, E. K. 1988. *The Birds of Africa Vol. 3*. Academic Press, London.
- Garland, T. and Adolph, S. C. 1994. Why not to do two-species comparative studies: limitations on inferring adaptation. *Physiol. Zool.* 67: 797 - 828.
- Geiser, F., Holloway, J. C., Körtner, G., Maddocks, T. A., Turbill, C., and Brigham, R. M. 2000. Do patterns of torpor differ between free-ranging and captive mammals and birds? In: Heldmaier, G. and Klingenspor, M. (Eds.) *Life in the cold: 11th International Hibernation Symposium*. Springer, Berlin.
- Hiebert, S. M. 1993. Seasonal changes in body mass and use of torpor in a migratory hummingbird. *Auk* 110: 787 - 797.
- Hoffmann, R. and Prinzinger, R. 1984. Torpor und Nahrungsausnutzung bei 4 Mausvogelarten (Coliiformes). *J. Ornithol.* 125: 225 - 237.
- Ligon, J. D., Carey, C., and Ligon, S. H. 1988. Cavity roosting, philopatry, and co-operative breeding in the green woodhoopoe may reflect a physiological trait. *Auk* 105: 123 - 127.
- Ligon, J. D., Carey, C., Ligon, S. H., and Farley, G. H. 1989. Response to Ward et al. *Auk* 106: 343 - 344.
- Lovegrove, B. G. 2000. The zoogeography of mammalian basal metabolic rate. *Am. Nat.* 156: 201 - 219.
- Maddocks, T. A. and Geiser, F. 1997. Energetics, thermoregulation and nocturnal

hypothermia in Australian silvereyes. *Condor* 99: 104 - 112.

Malan, A. 1996. The origins of hibernation: a reappraisal. In: Geiser, F., Hulbert, A. J., and Nicol, S. C. (Eds.) *Adaptations to the cold: Tenth International Hibernation Symposium*. University of New England Press, Armidale.

McKechnie, A. E. and Lovegrove, B. G. 1999. Circadian metabolic responses to food deprivation in black-shouldered kites. *Condor* 101: 426 - 432.

McKechnie, A. E. and Lovegrove, B. G. 2000. Heterothermy in mousebirds: evidence of avian proto-torpor? In: Heldmaier, G. and Klingenspor, M. (Eds.) *Life in the cold: 11th International Hibernation Symposium*. Springer, Berlin.

McKechnie, A. E. and Lovegrove, B. G. 2001. Thermoregulation and the energetic significance of clustering behavior in the white-backed mousebird (*Colius colius*). *Physiol. Biochem. Zool.* 74: 238 - 249.

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

Prinzinger, R., Preßmar, A., and Schleucher, E. 1991. Body temperature in birds. *Comp. Biochem. Physiol.* 99A: 499 - 506.

Putala, A., Hohtola, E., and Hissa, R. 1995. The effect of group size on metabolism in huddling grey partridge (*Perdix perdix*). *Comp. Biochem. Physiol.* 111B: 243 - 247.

Reinertsen, R. E. 1983. Nocturnal hypothermia and its energetic significance for small birds

- living in the arctic and subarctic regions. A review. *Polar Res.* 1: 269 - 284.
- Reinertsen, R. E. 1996. Physiological and ecological aspects of hypothermia. In: Carey, C. (Ed.) *Avian energetics and nutritional ecology*. Chapman & Hall, New York.
- Walsberg, G. E. 1990. Communal roosting in a very small bird: consequences for the thermal and respiratory environments. *Condor* 92: 795 - 798.
- Ward, D., Pinshow, B., Afik, D., Linder, Y., and Winkler, N. 1989. Cavity roosting, philopatry, and cooperative breeding in the green woodhoopoe may not reflect a physiological trait. *Auk* 106: 342 -
- Weathers, W. W., Koenig, W. D., and Stanback, M. T. 1990. Breeding energetics and thermal ecology of the acorn woodpecker in central coastal California. *Condor* 92: 341 - 359.
- Williams, J. B., Du Plessis, M. A., and Siegfried, W. R. 1991. Green woodhoopoes (*Phoeniculus purpureus*) and obligate cavity roosting provide a test of the thermoregulatory insufficiency hypothesis. *Auk* 108: 285 - 293.
- Wolf, B. O. and Walsberg, G. E. 1996. Thermal effects of radiation and wind on a small bird and implications for microsite selection. *Ecology* 77: 2228 - 2236.
- Wolf, B. O., Wooden, K. M., and Walsberg, G. E. 1996. Effects of complex radiative and convective environments on the thermal biology of the white-crowned sparrow (*Zonotrichia leucophrys gambelii*). *J. Exp. Biol.* 203: 803 - 811.
- Wrangham, R. W. and Rubenstein, D. I. 1986. Social evolution in mammals and birds. In: Rubenstein, D. I. and Wrangham, R. W. (Eds.) *Ecological aspects of social evolution: birds and mammals*. Princeton University Press, New Jersey.
- Zar, J. H. 1999. *Biostatistical analysis*. Prentice Hall, New Jersey.

Chapter 4. Rest-phase thermoregulation in free-ranging white-backed mousebirds (*Colius colius*).

Introduction

The mousebirds (Coliiformes) are a phylogenetically ancient order endemic to the Afrotropics (Sibley and Ahlquist 1990). In terms of avian energetics, mousebirds are of interest because they exhibit well-developed communal roosting (clustering behaviour) as well as a pronounced capacity for heterothermy (Bartholomew and Trost 1970; Hoffmann and Prinzinger 1984; McKechnie and Lovegrove 2000;2001; Chapter 2). As mechanisms of energy conservation, communal roosting and heterothermy are important in the energy budgets of a number of avian species (Dawson and Whittow 2000), but have generally been investigated in isolation of each other. In this respect, the mousebirds offer a useful model group to investigate the interaction between these two energy-saving mechanisms.

Substantial reductions in nocturnal energy expenditure associated with clustering behaviour have been observed in several mousebird species. Brown and Foster (1992) reported that clustering speckled mousebirds *C. striatus* reduced their energy expenditure by ca. 30%, whereas Prinzinger et al. (1981) observed energy savings of 25 - 45% in red-backed mousebirds (*C. castanotus*). Each white-backed mousebird (*C. colius*) in a group of six individuals reduced energy expenditure by an average of 50% during clustering (McKechnie and Lovegrove 2001). The energy savings associated with communal roosting in mousebirds are similar to those reported for a variety of other avian species (e.g. Chaplin 1982; Walsberg 1990; Putaala et al. 1995).

In addition to reducing energy requirements, clustering behaviour in mousebirds appears to play an important thermoregulatory role. McKechnie and Lovegrove (2001) found

that under laboratory conditions single *C. colius* exhibited linear decreases in rest-phase body temperature (ρT_b), during which the rate of cooling was determined by ambient temperature (T_a). At $T_a = 5^\circ\text{C}$, four out of nine birds became pathologically hypothermic. Clustering behaviour, in addition to reducing rest-phase energy requirements, resulted in significant reductions in these cooling rates (McKechnie and Lovegrove 2001).

In *C. colius*, clustering behaviour was necessary for the defence of a constant ρT_b and for the avoidance of pathological hypothermia at low T_a (McKechnie and Lovegrove 2001). These authors argued that clustering represents an obligatory component of thermoregulation in this species, and hypothesized that under natural conditions, the defence of approximately constant ρT_b in free-ranging white-backed mousebirds is facilitated by clustering behaviour. I found similar patterns of non-steady state rest-phase thermoregulation in *C. striatus*, although cooling rates were less dependent on T_a than in *C. colius* (Chapter 2). Under semi-natural conditions (outdoor aviaries), thermoregulation in clustering *C. striatus* differed significantly from that observed in single birds (Chapter 3). In particular, clustering behaviour appeared to facilitate the defence of typical endothermic circadian cycles of body temperature (T_b) and moderated the extent of hypothermic responses to food deprivation.

In this study, I examine the hypothesis that social thermoregulation, namely clustering behaviour, is important in free-ranging *C. colius*. I predicted that even at low T_a , clustering *C. colius* should defend relatively high ρT_b s, and should not exhibit the pronounced linear decreases in T_b previously observed in single birds under laboratory conditions (McKechnie and Lovegrove 2001). I also predicted that clustering behaviour should moderate the use of facultative hypothermic responses, and that free-ranging *C. colius* rarely use torpor.

Materials and methods

Study site

I conducted the study on the farm Tierberg (33°07'S, 22°16'E; 750m a.s.l.) near Prince Albert, South Africa, during June 2000. This area is characterized by sparse, dwarf shrubland, with a high proportion of succulent plants (Dean et al. 1993). I conducted the study during June, which is one of the two coldest months at Tierberg, since at this time of year the mousebirds are likely to experience the highest thermoregulatory costs (Dean et al. 1993). The following climatological data for Tierberg were obtained from the Computing Centre for Water Research, University of Natal: mean annual precipitation: 245mm; coefficient of variation of mean annual precipitation: 37%; mean daily maximum and minimum temperatures (June): 14.0°C and 1.1°C respectively. At Tierberg, white-backed mousebirds occur along drainage lines in vegetation consisting predominantly of *Acacia karoo*, *Diospyros* spp., *Euclea undulata*, *Rhus undulata* and *Rhizogum obovatum* (Dean et al. 1993). Rainfall at Tierberg occurs year-round, and the availability of fruit does not appear to show distinct seasonal cycles (Dean et al. 1993).

Body temperature measurement

Temperature-sensitive FM transmitters (Sirtrack, New Zealand) with an average mass of 1.6g and frequencies between 146.0 and 146.5 MHz were used to measure T_b in the mousebirds. The transmitters were calibrated in a water bath at temperatures between 10° and 45°C, using a standard mercury thermometer (0.05°C), with an accuracy traceable to the US National Bureau of Standards. They were implanted into the peritoneal cavities of the mousebirds under inhalation anaesthesia (Isoflurane in oxygen; induction and maintenance, 2.5%; flow rate, ca. 0.5l.min⁻¹).

Signals from the transmitters were recorded using a custom-built multi-channel data logger. The data logger controlled a single side-band mode communications receiver (Model IC-R10, ICOM) and recorded pulse intervals of all ten transmitters in 10-minute intervals, using a 6-element Yagi antenna. Ambient temperature was measured by the data logger using a monolithic temperature transducer (LM335). Data were stored on an EPROM and downloaded daily. Electronics and software were developed by Gerhard Körtner.

Data analysis

Data collection commenced immediately following implantation, but data recorded within 48 hours of surgery were excluded from the analyses. I obtained a total of 54 T_b traces from between 2 and 8 birds on the nights of the 12th to 28th June. For analyses of ρT_b , I considered the rest-phase to commence immediately following the rapid decreases in T_b that occurred shortly after sunset and to end immediately preceding the rapid increases in T_b shortly before departure from the roost site the following morning. Body temperatures were compared using repeated-measures analysis of co-variance (RM-ANCOVA; Zar 1999), using mean night-time T_a and minimum night-time T_a as co-variates. The birds appeared to exhibit a hypothermic response on only the night of the 21st June (see below), and I excluded these data from my analyses of normothermic thermoregulation. Results are presented as mean \pm S.E.

Results

General behaviour

The mousebirds spent the daylight hours foraging and sunbathing in the vegetation along the drainage line. Late each afternoon, they would move to a specific area along the drainage line, and spend the last half-hour before sunset sunning themselves. While sunning, the mousebirds

would cling to a suitable perch with their underparts orientated towards incident radiation, with the belly feathers raised to expose the skin. Immediately following sunset, they would cluster in a dense tree in the drainage line. The narrow reception angle of the Yagi antenna meant that the time of arrival at the roost site could be determined to within 10 minutes by the time of the first T_b measurements. The average time between sunset and the commencement of clustering was < 10 minutes. The group of mousebirds that clustered at this site appeared to consist of 12 individuals. The tree in which the birds clustered was exposed to solar radiation until sunset, but was shaded by a hill until ca. 45 minutes after sunrise. In the mornings, the birds left the roost while it was still shaded, on average < 10 minutes before sunrise. The same site was used every night, with the exception of the night of the 21st June. On this night, the birds clustered in a low bush on the surrounding open plain. This site was 0.95km from the usual roost site. I suspect that the birds used a different roost site on this night because of the presence of a pale chanting goshawk (*Melierax canorus*), which I observed flying and perching within ca. 50m of the regular roost site shortly prior to sunset.

Ambient temperature

During the study period, the mean night-time temperature (sunset - sunrise) was $3.4 \pm 0.5^\circ\text{C}$ (range -0.7 to 12.9°C). The mean minimum night-time temperature was $0.0 \pm 0.5^\circ\text{C}$ (range -3.4 to 9.2°C). Typically, the temperature reached a minimum shortly before sunrise (Figure 1-3). On most nights there was no wind.

Normothermic ρT_b

Several observations can be made from the traces of ρT_b (representative traces shown in Figures 1-3). Firstly, the ρT_b of clustering *C. colius* was unusually labile. The frequency

distribution of ρT_b (Figure 4) shows that ρT_b varied between 33°C and 40°C, with a median of ca. 37°C. The $\rho T_{b,\min}$ showed a significant positive relationship ($F_{1,48} = 8.216$; $P < 0.05$) with mean T_a between sunset and sunrise, and was best described by a linear model (Figure 5a).

Secondly, the ρT_b s of the mousebirds appeared to decrease gradually during the night (Figure 1,2). This observation is confirmed by the fact that in all traces, minimum ρT_b ($\rho T_{b,\min}$) during the final hour of the rest-phase ($34.8 \pm 0.2^\circ\text{C}$) was significantly lower (RM-ANCOVA, $F_{1,90} = 75.108$, $P < 0.05$) than $\rho T_{b,\min}$ during the first hour ($37.4 \pm 0.2^\circ\text{C}$). Hence, ρT_b decreased on average by approximately 3°C during the course of the rest-phase. The mean cooling rate, calculated by fitting linear regressions to ρT_b as a function of time, was $0.22 \pm 0.01^\circ\text{C}\cdot\text{h}^{-1}$. This cooling rate is equivalent to ca. 25% of the mean cooling rate exhibited by single birds at $T_a = 5^\circ\text{C}$ under laboratory conditions (McKechnie and Lovegrove 2001). Cooling rate was negatively correlated with mean T_a between sunset and sunrise ($F_{1,47} = 12.121$; $P < 0.05$; Figure 5b) as well as with minimum T_a ($F_{1,47} = 4.327$; $P < 0.05$). The relationship between cooling rate and mean T_a was best described by a linear model (Figure 5b).

Thirdly, the ρT_b s of individual mousebirds within the cluster were highly synchronised (Figure 1-3), although on some occasions a ρT_b gradient of up to 3°C existed between individuals. I was unable to explain the fact that on the night of the 17th June (Figure 1), one of the birds (transmitter frequency = 146.220 MHz) maintained ρT_b several degrees higher than the remainder of the flock. The elevated T_b of this individual may have reflected some post-surgery stress, but the fact that the transmitter had been implanted 4 days earlier makes this unlikely.

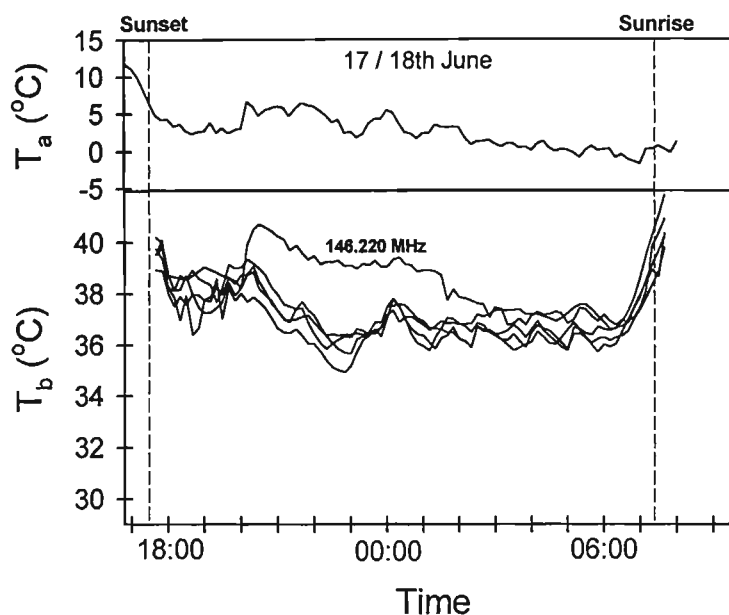


Figure 1. Body temperature (T_b) of five free-ranging white-backed mousebirds *Colius colius* (lower graph) and ambient temperature (T_a) (upper graph) on the night of the 17th/18th June 2000 at Tierberg. The times that the birds arrived and departed from the roost site coincide with the commencement and termination of T_b measurements. One of the birds (transmitter frequency = 146.220 MHz) maintained T_b higher than other members of the group.

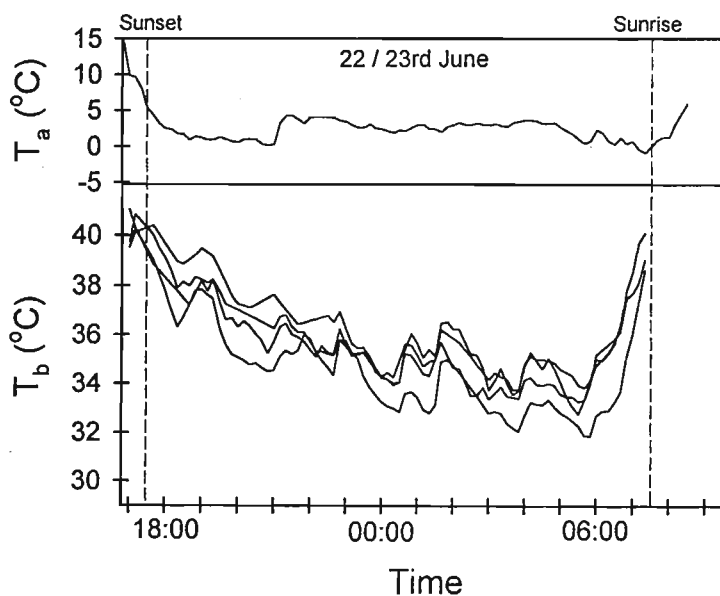


Figure 2. Body temperature (T_b) of four free-ranging white-backed mousebirds *Colius colius* (lower graph) and ambient temperature (T_a) (upper graph) on the night of the 22nd/23rd June 2000 at Tierberg. The times that the birds arrived and departed from the roost site coincide with the commencement and termination of T_b measurements.

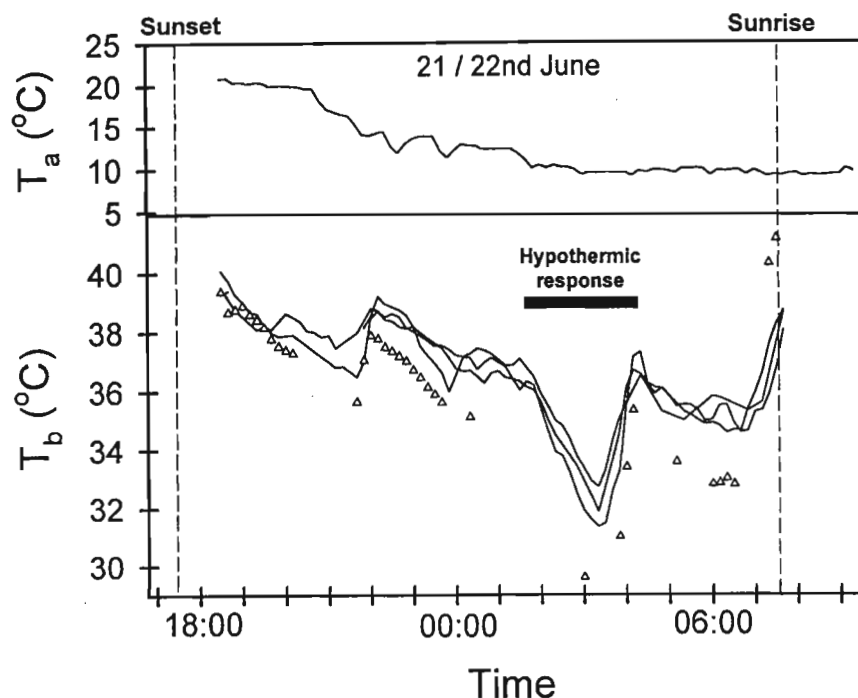


Figure 3. Body temperature (T_b) of four free-ranging white-backed mousebirds *Colius colius* (lower graph) and ambient temperature (T_a) (upper graph) on the night of the 21st/22nd June 2000 at Tierberg. The times that the birds arrived and departed from the roost site coincide with the commencement and termination of T_b measurements. The triangles represent intermittent data, but have been included as this bird exhibited the lowest T_b recorded during the study.

Hypothermic response - 21st June

With the exception of the night of the 21st June, the birds did not show any clear hypothermic responses to the low T_a . On the night of the 21st however, the birds rapidly decreased ρT_b to between 29 and 33°C at ca. 03h00 (Figure 3). Thereafter, ρT_b returned to normal levels. This clearly represented a facultative hypothermic response. Even though the night was relatively warm, the birds clustered in a more exposed site than usual, and experienced strong wind and rain. The fact that the birds exhibited a hypothermic response on this particular night probably reflects increased thermoregulatory demands. I suspect that the decrease in ρT_b coincided with a bout of heavy rain.

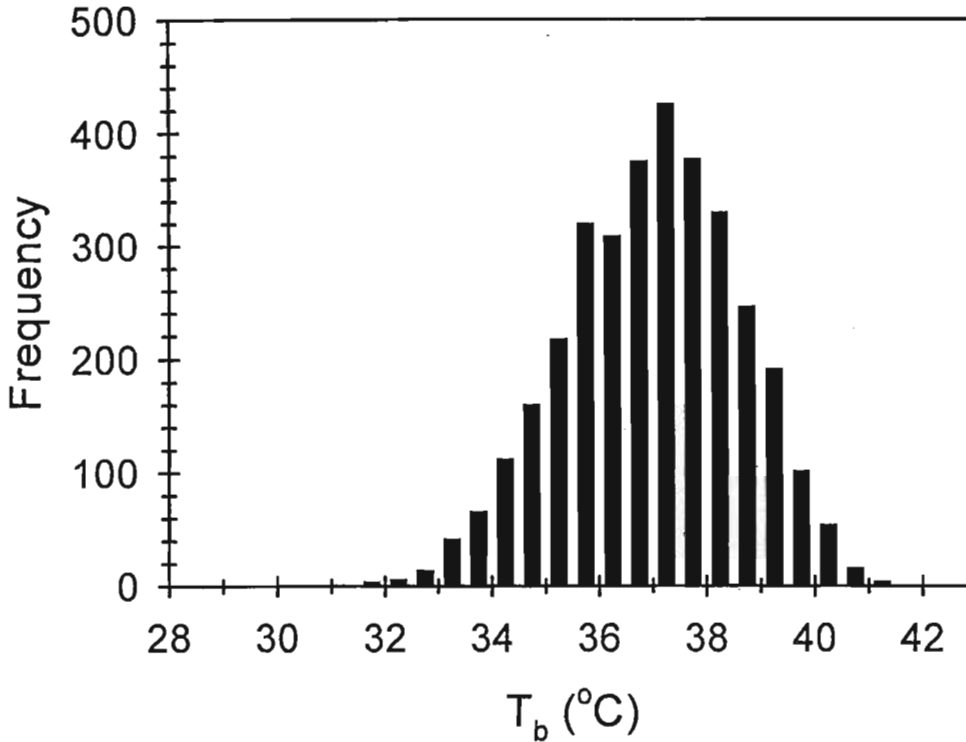


Figure 4. Frequency histogram of normothermic rest-phase body temperature (ρT_b) recorded in eight free-ranging white-backed mousebirds *Colius colius* between the 12th and 28th June 2000 at Tierberg. Data from the night of the 21st/22nd June have not been included, since the birds exhibited a hypothermic response.

Other observations

The T_b s of the mousebirds immediately prior to departure from the roost in the morning ranged from 36.6°C to 42.5°C, with a mean of $39.0 \pm 0.2^\circ\text{C}$. Typically, the birds left the roost before sunrise, at which time T_a was still close to the overnight minimum. These observations suggest that the birds increased their T_b by means of endogenous heat production, and that solar radiation did not play any role in raising T_b to active-phase (diurnal) levels.

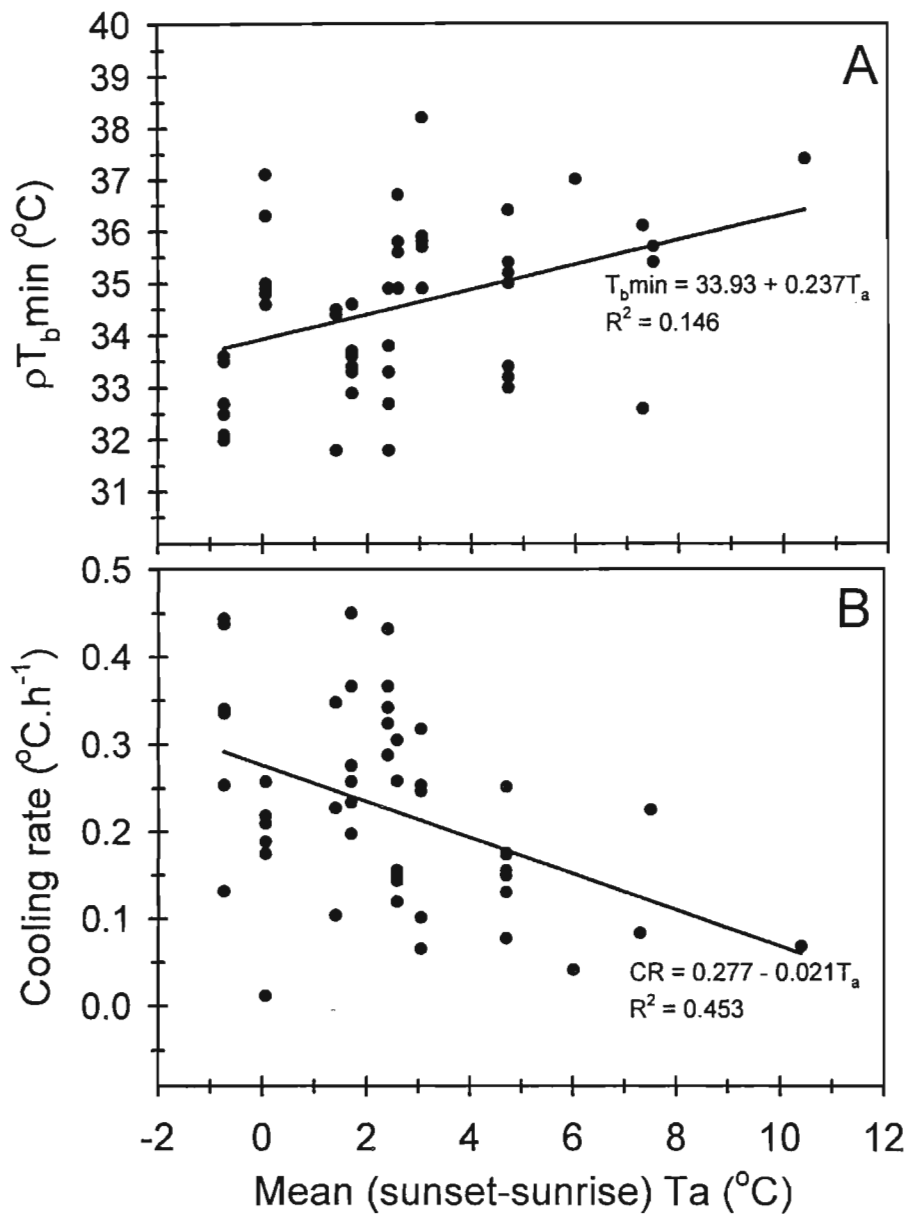


Figure 5. Minimum rest-phase body temperature ($\rho T_{b\text{min}}$) (A) and rest-phase cooling rate (B) in eight free-ranging white-backed mousebirds *Colius colius*, plotted against mean ambient temperature (T_a) between sunset and sunrise.

Discussion

Thermoregulatory role of clustering behaviour

Thermoregulation in clustering *C. colius* under natural conditions was markedly different to that previously observed in single birds under laboratory conditions (McKechnie and Lovegrove 2001). In the latter study, single birds at $T_a = 5^\circ\text{C}$ exhibited rest-phase cooling rates of $0.8^\circ\text{C}\cdot\text{h}^{-1}$ and a minimum ρT_b of ca. 26°C , and in some cases, pathological hypothermia. In contrast, free-ranging birds maintained $\rho T_b > \text{ca. } 33^\circ\text{C}$ and displayed relatively low cooling rates, even at $T_a < 0^\circ\text{C}$.

Despite the apparent thermoregulatory importance of clustering behaviour, the ρT_b of the mousebirds was nevertheless more labile than that of most birds. Whereas avian ρT_b is typically defended within a narrow range with respect to a set-point T_b (Dawson and Whittow 2000; for examples see Maddocks and Geiser 1997; Boix-Hinzen and Lovegrove 1998; McKechnie and Lovegrove 1999), ρT_b in free-ranging *C. colius* was relatively labile (Figure 4) and was partially dependent on T_a (Figure 5). Several authors have noted that normothermic ρT_b in mousebirds is atypically labile (Bartholomew and Trost 1970; Brown and Foster 1992; McKechnie and Lovegrove 2001; Chapter 2), and my results confirm that similar thermolability is evident in clustering *C. colius* under natural conditions. Although avian ρT_b during hypothermic responses is frequently correlated with T_a (Reinertsen 1996), a correlation of normothermic ρT_b with T_a is more unusual.

Although some rest-phase cooling was evident, the mousebirds maintained substantially higher ρT_b s than were observed in single *C. colius* under laboratory conditions (McKechnie and Lovegrove 2001). My observations illustrate the importance of clustering behaviour in reducing rest-phase cooling rates and the avoidance of pathological hypothermia, and support my predictions concerning the thermoregulatory role of clustering behaviour.

All mousebird species investigated so far show ρT_b that is highly labile compared to typical patterns of avian thermoregulation (Prinzinger et al. 1981; Hoffmann and Prinzinger 1984; McKechnie and Lovegrove 2001; Chapter 2). The labile patterns of thermoregulation shown by clustering *C. colius* in the wild presumably reflect this phylogenetic effect. Nevertheless, these labile ρT_b patterns are likely to have adaptive value in the arid habitats this species occupies. The pattern of gradual rest-phase cooling exhibited by *C. colius* under laboratory conditions (McKechnie and Lovegrove 2001) and to some extent under natural conditions (present study), requires lower energy expenditure than typical avian homeothermy which is characterized by the defence of a constant ρT_b of ca. 38 - 39°C (Prinzinger et al. 1991). Any avenue whereby rest-phase energy expenditure is reduced is likely to be adaptive in arid areas characterized by unpredictable food supplies (Lovegrove 2000). Tieleman and Williams (2000) have shown that both basal metabolic rate (BMR) and field metabolic rate (FMR) are reduced in birds inhabiting arid habitats. I would argue that the labile ρT_b of free-ranging *C. colius* probably contribute to this species' ability to survive even in the most arid southern African habitats (Harrison et al. 1997).

Facultative hypothermic responses

It is noteworthy that the pronounced capacity for heterothermy usually associated with the Coliiformes was not evident in the thermoregulation of free-ranging white-backed mousebirds. Despite June being one of the coldest months at Tierberg, with the amount of time available for foraging reduced due to shorter daylength, I did not observe torpor during two and a half weeks of observations. With the exception of the night of the 21st June, during which the mousebirds exhibited a decrease in ρT_b to between 29 and 33°C (Figure 3), there was no evidence of heterothermy. My data hence support the argument that the energy savings

mousebirds make by means of social thermoregulation i.e. clustering behaviour, probably obviate the need to employ hypothermia as an energy saving response.

Recently, Geiser et al. (2000) compared thermoregulation in captive and free-ranging mammals and birds, and concluded that almost without exception, laboratory studies have underestimated the frequency, duration and depth of torpor and hibernation under natural conditions. The mousebirds appear to represent an exception to this general pattern. Whereas torpor has been well-described in captive birds (Bartholomew and Trost 1970; Prinzinger et al. 1981; Hoffmann and Prinzinger 1984; Chapter 2), the use of hypothermia appears to be limited under semi-natural (Chapter 3) and natural conditions (present study). It would appear that the pronounced capacity for heterothermy usually associated with the Coliiformes is not representative of their thermoregulation under natural conditions. I would argue that the fact that the mousebirds are one of the best-known groups of avian heterotherms is due to the fact that thermoregulation has predominantly been examined in captive single birds under laboratory conditions. Nevertheless, the T_b traces recorded on the night of the 21st June (Figure 3) show that under some circumstances, clustering mousebirds may exhibit facultative hypothermic responses. I believe that the most interesting observation arising from Figure 3 concerns the fact that the hypothermic response was synchronised between different individuals (discussed below).

Synchronised patterns of ρT_b

The synchronized hypothermic response shown by the birds on the night of the 21st June is particularly noteworthy. I envisage two possible explanations for this pattern of a rapid reduction in ρT_b followed immediately by re-warming to normothermic levels. Firstly, the increase in cooling rate at ca. 02h00 may reflect a rapid increase in the rate of heat loss from

the cluster (e.g. onset of rain). According to this explanation, the ρT_b of the clustering birds decreased until some threshold T_b was reached. Once this threshold was reached, the birds increased their metabolic heat production. This increase in heat production returned ρT_b to normothermic levels at ca. 04h30. This explanation is consistent with the observation that ρT_b in *C. colius* is dependent on T_a under laboratory conditions (McKechnie and Lovegrove 2001) and in free-ranging birds. Moreover, single speckled mousebirds (*C. striatus*) increased cooling rates following a rapid 10°C decrease in T_a (Chapter 2). However, I was unable to confirm that the decrease in ρT_b shown by the clustering *C. colius* did indeed coincide with the onset of rain.

The second possible explanation for the synchronised hypothermic response is that it represented a facultative decrease in metabolic heat production, and hence ρT_b . According to this explanation, the mousebirds responded to energetic stress by means of a facultative decrease in metabolic rate, resulting in a drop in ρT_b . However, evaluating this possibility would require traces of metabolic rate as well as ρT_b .

If the latter explanation is correct, and the decrease in ρT_b shown by the mousebirds on the night of the 21st June did indeed represent a synchronised facultative hypothermic response, how was the extent of this response determined? The extent of the hypothermic response may have been determined by a) the average energy status of the individuals within the cluster, or b) the energy status of the most energetically stressed individual in the cluster. However, the relative position of an individual within the roughly spherical cluster may also be important. For instance, a mousebird near the centre of the cluster probably experiences minimal contact with the surrounding air, and presumably lower rates of heat loss than an individual on the periphery of the cluster. If the extent of a hypothermic response is determined by the average energy status of the birds in the cluster, it

is possible that the most energetically-stressed birds may remain near the centre of the cluster, whereas less stressed birds remain near the periphery. An investigation of cluster dynamics would require a rigorous laboratory study in which the energy intake of individual mousebirds is manipulated and an individual's relative position within a cluster closely monitored.

Ruf and Arnold (2000) observed similar patterns of synchronized heterothermic T_b s in hibernating alpine marmots (*Marmota marmota*). The degree of group synchrony was the most important determinant of M_b loss in individual marmots (Ruf and Arnold 2000). Juvenile marmots frequently displayed delayed arousal relative to adults, and derived energetic benefits by means of passive heat gains (Ruf and Arnold 2000). It is possible that a similar mechanism operates in clustering mousebirds. Individuals with the greatest degree of energetic stress may balance their energy budget by means of passive heat gain from other birds in the cluster.

Literature cited

- Bartholomew, G. A. and Trost, C. H. 1970. Temperature regulation in the speckled mousebird, *Colius striatus*. *Condor* 72: 141 - 146.
- Boix-Hinzen, C. and Lovegrove, B. G. 1998. Circadian metabolic and thermoregulatory patterns of red-billed woodhoopoes (*Phoeniculus purpureus*): the influence of huddling. *J. Zool., Lond.* 244: 33 - 41.
- Brown, C. R. and Foster, G. G. 1992. The thermal and energetic significance of clustering on the speckled mousebird, *Colius striatus*. *J. Comp. Physiol. B* 162: 664 - 685.
- Chaplin, S. A. 1982. The energetic significance of huddling in common bushtits (*Psaltriparus minimus*). *Condor* 99: 424 - 430.
- Dawson, W. R. and Whittow, G. C. 2000. Regulation of body temperature. In: Sturkie, P. D. (Ed.) *Avian Physiology*. Academic Press, New York.
- Dean, W. R. J., Williams, J. B., and Milton, S. J. 1993. Breeding of the white-backed mousebird *Colius colius* in relation to rainfall and the phenology of fruiting plants in the southern Karoo, South Africa. *J. Afr. Zool.* 107: 105 - 111.
- Geiser, F., Holloway, J. C., Körtner, G., Maddocks, T. A., Turbill, C., and Brigham, R. M. 2000. Do patterns of torpor differ between free-ranging and captive mammals and birds? In: Heldmaier, G. and Klingenspor, M. (Eds.) *Life in the cold: 11th International Hibernation Symposium*. Springer, Berlin.
- Harrison, J. A., Allan, D. G., Underhill, L. G., Herremans, M., Tree, A. J., Parker, V., and

- Brown, C. J. 1997. The atlas of southern African birds. Volume 1: Non-passerines. Birdlife South Africa, Johannesburg.
- Hoffmann, R. and Prinzinger, R. 1984. Torpor und Nahrungsausnutzung bei 4 Mausvogelarten (Coliiformes). *J. Ornithol.* 125: 225 - 237.
- Lovegrove, B. G. 2000. The zoogeography of mammalian basal metabolic rate. *Am. Nat.* 156: 201 - 219.
- Maddocks, T. A. and Geiser, F. 1997. Energetics, thermoregulation and nocturnal hypothermia in Australian silvereyes. *Condor* 99: 104 - 112.
- McKechnie, A. E. and Lovegrove, B. G. 1999. Circadian metabolic responses to food deprivation in black-shouldered kites. *Condor* 101: 426 - 432.
- McKechnie, A. E. and Lovegrove, B. G. 2000. Heterothermy in mousebirds: evidence of avian proto-torpor? In: Heldmaier, G. and Klingenspor, M. (Eds.) Life in the cold: 11th International Hibernation Symposium. Springer, Berlin.
- McKechnie, A. E. and Lovegrove, B. G. 2001. Thermoregulation and the energetic significance of clustering behavior in the white-backed mousebird (*Colius colius*). *Physiol. Biochem. Zool.* 74: 238 - 249.
- Prinzinger, R., Göppel, R., Lorenz, A., and Kulzer, E. 1981. Body temperature and metabolism in the red-backed mousebird (*Colius castanotus*) during fasting and torpor. *Comp. Biochem. Physiol.* 69A: 689 - 692.
- Prinzinger, R., Preßmar, A., and Schleucher, E. 1991. Body temperature in birds. *Comp.*

Biochem. Physiol. 99A: 499 - 506.

Putala, A., Hohtola, E., and Hissa, R. 1995. The effect of group size on metabolism in huddling grey partridge (*Perdix perdix*). *Comp. Biochem. Physiol.* 111B: 243 - 247.

Reinertsen, R. E. 1996. Physiological and ecological aspects of hypothermia. In: Carey, C. (Ed.) Avian energetics and nutritional ecology. Chapman & Hall, New York.

Ruf, T. and Arnold, W. 2000. Mechanisms of social thermoregulation in hibernating alpine marmots (*Marmota marmota*). In: Heldmaier, G. and Klingenspor, M. (Eds.) Life in the cold: 11th International Hibernation Symposium. Springer, Berlin.

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

Tieleman, B. I. and Williams, J. B. 2000. The adjustment of avian metabolic rates and water fluxes to desert environments. *Physiol. Biochem. Zool.* 73: 461 - 479.

Walsberg, G. E. 1990. Communal roosting in a very small bird: consequences for the thermal and respiratory environments. *Condor* 92: 795 - 798.

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

Chapter 5. Thermoregulation and metabolic responses to food deprivation in an Afrotropical arid-zone passerine, the red-headed finch (*Amadina erythrocephala*).

Introduction

Avian facultative hypothermic responses are typically divided into hibernation, torpor and (controlled) rest-phase hypothermia (Prinzinger et al. 1991, Reinertsen 1996). The distinction between the latter two responses is unclear. Prinzinger et al. (1991) suggested that body temperature (T_b) $< 25^\circ\text{C}$ indicates torpor, whereas Reinertsen (1996) argued that $T_b < 30^\circ\text{C}$ represents torpor. However, the use of discrete T_b ranges to distinguish between avian physiological states is questionable (Chapter 1), and responsiveness to environmental stimuli is a more meaningful criterion for distinguishing between categories of avian hypothermic responses (Merola-Zwartjes and Ligon 2000). Unfortunately, few data are available on the relationship between relative responsiveness and T_b , and for the purposes of this study I follow Reinertsen (1996) and assume that $T_b < 30^\circ\text{C}$ is indicative of torpor.

The capacity for heterothermy appears to depend on phylogeny. Torpor is wide-spread in the nightjars and relatives (Dawson and Fisher 1969; Brigham and Firman 1990; Brigham 1992; Körtner et al. 2000), the hummingbirds (Carpenter 1974, Hiebert 1990, Bech et al. 1997) and the mousebirds (Prinzinger et al. 1981; Hoffmann and Prinzinger 1984; McKechnie and Lovegrove 2000). In contrast, it is relatively rare in passerines. Torpor has been observed in the house martin *Delichon urbica* (Prinzinger and Siedle 1988), and anecdotal reports of torpor exist for several other members of the Hirundinidae (Lasiewski and Thompson 1966, Serventy 1970). A reduction in metabolic rate to 44% of resting metabolism and a minimum T_b of 26.8°C was observed in the golden-collared manakin *Manacus vitellinus* (Tyrannidae) (Bartholomew et al. 1983). Furthermore, unpublished descriptions of torpor exist for several

sunbirds (Nectariniidae) (S. W. Nicolson pers. comm.; C. T. Downs pers. comm.).

The majority of passerines, however, do not appear to use torpor. Members of the Paridae which overwinter in Arctic and subarctic regions depress their T_b s to between 30 - 35°C, but apparently do not enter torpor (Haftorn 1972, Grossman and West 1977, Mayer et al. 1982, Reinertsen and Haftorn 1983). Similarly, members of the Passeridae (Steen 1958), Fringillidae (Steen 1958), Muscicapidae (Biebach 1977) and Corvidae (Waite 1991) have been observed to reduce T_b by less than 10°C below normothermic levels. Collectively, these data suggest that passerines generally do not use torpor when faced with low ambient temperature (T_a) or food shortages.

There is a strong link between the metabolic traits of endotherms and environmental predictability. In general, the basal metabolic rate (BMR) of desert mammals (Shkolnik and Schmidt-Nielsen 1976, Armitage et al. 1990, Lovegrove 2000a) and birds (Dawson and Bennett 1973, Frumkin et al. 1986, Hinsley et al. 1993) are lower than those of their mesic counterparts. Recently, Tieleman and Williams (2000) have shown that both the BMR and field metabolic rate (FMR) of desert birds are lower than those of mesic species, although BMR divergence appears to only occur in certain zoogeographical zones (Chapter 6).

Habitat-specific variance in BMR is thought to reflect an underlying slow-fast metabolic continuum correlated with broad-scale patterns of climatic predictability (Lovegrove 2000a). In addition to the well-documented differences between desert and mesic species, the BMR of mammals and birds is higher in the more predictable Palearctic and Nearctic environments relative to the climatically variable Australasian, Afrotropical and Indomalayan zones (Lovegrove 2000a; Chapter 6).

Endotherms inhabiting relatively unpredictable habitats appear to experience selection for reduced energy expenditure. The adaptive value of the ability to reduce energy expenditure

by means of facultative hypothermia is hence likely to be high in areas subject to unpredictable fluctuations in resource availability in time and space (Lovegrove 2000b). I would argue that species inhabiting the most unpredictable environments are likely to provide the best indication of a taxon's phylogenetic capacity for heterothermy, since these species experience the strongest selection for energy conservation.

In this study I investigated thermoregulation in a small, Afrotropical arid-zone Estrilidid, the red-headed finch *Amadina erythrocephala*. This species occurs in the arid and semi-arid western parts of southern Africa (Harrison et al. 1997). I predicted that *A. erythrocephala* responds to restricted feeding by a reduction in rest-phase metabolism and T_b , but does not reduce T_b by more than 10°C . I also predicted that the BMR of *A. erythrocephala* should be significantly lower than predicted by published allometric equations for avian BMR, but should be similar to the value predicted for Afrotropical species.

Materials and methods

I trapped nine *A. erythrocephala* (5 males and 4 females) with a body mass (M_b) of 21.5 ± 0.2 g (mean \pm SE) on the farm Benfontein ($28^{\circ}51'$ S; $24^{\circ}47'$ E) near Kimberley, South Africa during October 1999. The birds were trapped using mist-nets, and were subsequently transported by road to School of Botany and Zoology, University of Natal in Pietermaritzburg. The birds were housed in an outdoor aviary 3m long, 1m wide and 2m high. They were provided with woven cane nests, and were provided with water and wild bird seed ad libitum. All experiments were carried out between March and May 2000.

Body temperature measurements

I obtained continuous scotophase measurements of cloacal T_b using copper-constantan thermocouple wire (type 0.005, California Fine Wire Company). The thermocouples were inserted to a depth of approximately 1.5cm. At this depth, a slight withdrawal of the thermocouple wire did not result in a decrease in the T_b reading. The wire was secured to the feathers by means of a small piece of adhesive tape. Each thermocouple wire was connected to a digital thermometer and the output was recorded on Windows-based recording software written by Barry Lovegrove. Each thermocouple was calibrated to 0.1°C using a water bath and a mercury thermometer (accuracy traceable to the U.S. Bureau of Standards) before measurements commenced, and was re-calibrated every few days during the experimental period. The sampling interval for T_b measurements was 3 - 5 minutes, depending on the number of birds used. On occasions when the thermocouple wire was dislodged during the night, the data were discarded and the measurements repeated a few days later.

Metabolic measurements

Oxygen consumption (VO_2) was measured as an indirect measure of metabolic rate. All metabolic measurements were made in 3.96 l respirometers (22cm high, 12cm wide, 15cm long) constructed from clear Perspex®. The respirometers were placed in a 1 m³ sound-proof temperature cabinet. Measurements of VO_2 and carbon dioxide production (VCO_2) were made using an open flow-through system, as described in Chapter 2. Air was drawn through the respirometers at flow rates of ca. 0.8 l.min⁻¹, chosen to maintain less than one percent oxygen depletion between the incurrent and excurrent air. Metabolic rates were calculated using Equation 3a in Withers (1977). The birds were weighed before and after each experiment. Mass-specific VO_2 was calculated assuming a linear decrease in M_b during the measurements.

Experimental protocol

The experimental photoperiod was matched to the prevailing photoperiod at the time i.e. that experienced by the birds in the outdoor aviary. Because the birds tended to move around and dislodge the thermocouple when the cabinet lights were on, I placed the birds in the respirometers immediately before commencement of the experimental scotophase. This meant that the birds were not necessarily post-absorptive at the commencement of measurements. With the exception of measurements of total rest-phase energy expenditure, I restricted my data analysis to the second half of the rest-phase, and assumed that metabolic measurements during this period were representative of post-absorptive metabolism.

Measurements of T_b , VO_2 and VCO_2 were made in 8 - 10 birds at $T_a = 0, 5, 10, 15, 20, 25, 30, 35$ and 40°C in a randomly chosen sequence. The birds were maintained in the respirometers for the entire rest phase at each T_a , and were removed at ca. 07h00 the following morning, ca. 1.5 hours after the commencement of the experimental photoperiod. During the measurements at $T_a = 40^\circ\text{C}$, I reduced T_a to 30°C near the end of the scotophase to reduce the likelihood of the birds becoming hyperthermic with the circadian increase in VO_2 with the onset of the photophase.

The influence of restricted feeding on thermoregulation was investigated by starving the birds from 09h00 i.e. approximately nine hours before the birds were placed in the respirometer. Measurements were made at $T_a = 0, 5, 10, 15$ and 20°C , in a random sequence.

Data analysis

Values are presented as mean \pm S.E. Results were compared using repeated-measures analysis of variance (R-M ANOVA), or covariance (R-M ANCOVA) following Zar (1999).

Assumptions concerning the homogeneity of variances / covariances were verified using

Cochran C, Hartley and Bartlett Tests for univariate data, and Sen & Puri's nonparametric test for multivariate data. I used the procedure of Yeager and Ultsch (1989) to objectively determine the deviations from steady-state thermoregulation indicating the commencement and end of the rest-phase for each set of measurements. Minimum VO_2 (VO_{2min}) was calculated as the mean of the three lowest consecutive values i.e. over a 18 min period. To calculate the lower critical limit of thermoneutrality (T_{lc}), I calculated a linear regression of VO_2 and T_a for $T_a \leq 30^\circ C$ for each bird. The T_{lc} of each bird was calculated as the T_a corresponding with the minimum VO_2 measurement for that bird. Minimum thermal conductance (C_{min}) was calculated at each experimental T_a using the simplified Newtonian equation $C = VO_2(T_b - T_a)$, where C is the thermal conductance in $ml\ O_2 \cdot g^{-1} \cdot (h \cdot ^\circ C)^{-1}$ (Schmidt-Nielsen 1990). To calculate rest-phase energy expenditure I multiplied the mean rest-phase VO_2 by a conversion factor calculated from a regression of respiratory quotient (RQ) and Joule equivalence, using the data in Table 4-2 in Withers (1992). To calculate M_b loss for each bird during the restricted feeding trial, I subtracted the M_b from the average M_b exhibited by the same individual during the ad libitum treatment.

I compared the BMR of *A. erythrocephala* to allometrically predicted values by calculating phylogenetically-corrected 95% prediction intervals (Garland and Ives 2000). These authors have shown that prediction intervals which account for a particular species' position in a phylogeny can be calculated and used to test hypotheses concerning deviations from allometrically predicted values. In Chapter 6, I found that non-migratory avian BMR shows significant zoogeographical variation, and that in the Afrotropics and Australasia, the BMR of mesic and arid species are convergent. This zoogeographic variation implies that hypotheses concerning BMR deviation from predicted values should be tested using zone-specific data sets. I hence calculated 95% prediction intervals using BMR and phylogenetic

data for 27 Afrotropical species (same data as used in Chapter 6, but excluding the datum for *A. erythrocephala*). Because the BMR of Afrotropical species does not differ between arid and mesic habitats (Chapter 6), I included data for both mesic and arid species in the analysis.

Results

Body mass and metabolic substrate

The mean M_b of the birds during the ad libitum feeding treatment was 22.9 ± 0.1 g prior to being placed in the respirometers, and 20.4 ± 0.1 g after removal from the respirometers the following morning. On average, the birds lost 2.5 ± 0.1 g (approximately 11% of their initial M_b) during each night, and this did not vary significantly with T_a (R-M ANOVA, $F_{7,58} = 1.212$, $P > 0.05$).

When starved, the birds lost $9.6 \pm 0.7\%$ of their M_b (range: 3.1% - 17.6%), and their M_b was significantly lower than during the ad libitum treatment (R-M ANOVA $F_{1,84} = 71.575$, $P \ll 0.05$; Table 1). The mean overnight mass loss during the restricted feeding treatment was significantly lower than during the ad libitum treatment (RM-ANCOVA, $F_{1,50} = 41.166$, $P < 0.05$), with a mean of 1.5 ± 0.1 g. Three birds died during the restricted feeding trials, after losing 13.6%, 15.5% and 17.4% of their M_b respectively, suggesting a tolerance threshold for food deprivation of approximately 14% M_b loss.

During the ad libitum treatment, the mean rest-phase respiratory quotient (RQ) decreased significantly with decreasing T_a (R-M ANOVA, $F_{7,47} = 7.999$, $P < 0.05$). At $T_a = 35^\circ\text{C}$, the mean RQ was 0.981, whereas at $T_a = 0^\circ\text{C}$, the mean RQ was 0.859. During restricted feeding, the mean RQ was significantly lower than during the ad libitum treatment (R-M ANCOVA, $F_{1,50} = 93.071$, $P \ll 0.05$), confirming a shift towards fat metabolism.

Body temperature

The minimum rest-phase T_b (ρT_b min) of the birds at thermoneutrality ($T_a = 30.8 \pm 1.4^\circ\text{C}$) was $39.6 \pm 0.2^\circ\text{C}$. Below the T_{lc} the ρT_b min did not vary significantly between the experimental $T_{a,s}$ (R-M ANOVA $F_{6,44} = 1.148$, $P > 0.05$; Figure 1a). During the restricted feeding treatment, the ρT_b min was significantly lower than during the ad libitum treatment (R-M ANOVA, $F_{1,44} = 23.541$, $P < 0.05$). The reduction in ρT_b min appeared to result from the defence of lower T_b setpoints than during the ad libitum treatment (Figures 1a, 2). The lowest T_b recorded during the restricted feeding treatment in a bird that suffered no obvious adverse effects was 34.8°C . One of the birds which died attempted to defend a set-point T_b of approximately 34.0°C and appeared to become pathologically hypothermic at approximately $T_b = 31^\circ\text{C}$. During the restricted feeding treatment, the ρT_b min was independent of body mass, as I could not detect any correlation between M_b loss and ρT_b min ($F = 0.007$; $P > 0.05$).

Oxygen consumption and energy expenditure

The mean minimum VO_2 at thermoneutrality was $1.75 \pm 0.06 \text{ ml O}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1}$ ($n = 9$) and the BMR was hence estimated as $35.07 \pm 1.23 \text{ J} \cdot \text{g}^{-1} \cdot \text{h}^{-1}$. This BMR falls within the 95% prediction intervals calculated for *A. erythrocephala* (Figure 3) and hence does not deviate significantly from the expected value for a 22g Afrotropical species.

Below the T_{lc} , the mean minimum rest-phase VO_2 (ρVO_2 min) increased with decreasing T_a (Figure 1b). During the restricted feeding treatment, ρVO_2 min was significantly lower than during ad libitum feeding (R-M ANCOVA, $F_{1,50} = 8.331$, $P < 0.05$). The mean rest-phase energy expenditure was significantly reduced during the restricted feeding treatment (R-M ANCOVA, $F_{1,50} = 15.413$, $P < 0.05$; Table 1; Figure 4b). The reduction in energy

Table 1. Changes in body mass, minimum rest-phase body temperature ($\rho T_{b\min}$), minimum rest-phase oxygen consumption $\rho VO_{2\min}$ and rest-phase energy expenditure associated with food deprivation in red-headed finches (*Amadina erythrocephala*).

Treatment	T_a	Body mass (g)	$\rho T_{b\min}$ (°C)	$\rho VO_{2\min}$ (ml O ₂ .g ⁻¹ .h ⁻¹)	Energy expenditure (J.g ⁻¹ .h ⁻¹)
Ad libitum	0	22.9 ± 0.3 (8) ^a	39.3 ± 0.3 (8)	6.02 ± 0.19 (8)	135.9 ± 4.6 (8)
	5	23.6 ± 0.4 (7)	39.0 ± 0.3 (7)	5.27 ± 0.31 (7)	120.0 ± 6.7 (7)
	10	22.7 ± 0.3 (8)	39.5 ± 0.3 (8)	4.50 ± 0.16 (8)	102.8 ± 3.2 (8)
	15	24.2 ± 0.2 (7)	39.4 ± 0.2 (7)	3.78 ± 0.14 (7)	87.4 ± 3.3 (7)
	20	22.9 ± 0.3 (8)	38.7 ± 0.5 (8)	3.33 ± 0.12 (8)	78.1 ± 2.6 (8)
Restricted	0	21.4 ± 0.4 (5)	37.6 ± 1.0 (3)	5.36 ± 0.34 (5)	119.3 ± 6.9 (5)
	5	20.8 ± 0.2 (6)	38.1 ± 0.2 (6)	4.71 ± 0.19 (6)	105.3 ± 4.2 (6)
	10	21.3 ± 0.3 (7)	37.9 ± 0.5 (5)	4.26 ± 0.11 (7)	93.5 ± 2.4 (7)
	15	21.7 ± 0.3 (6)	38.3 ± 0.4 (6)	3.67 ± 0.08 (6)	83.2 ± 1.7 (6)
	20	21.0 ± 0.4 (7)	37.9 ± 0.3 (5)	3.11 ± 0.14 (7)	68.9 ± 1.9 (7)

a. Sample sizes in parentheses

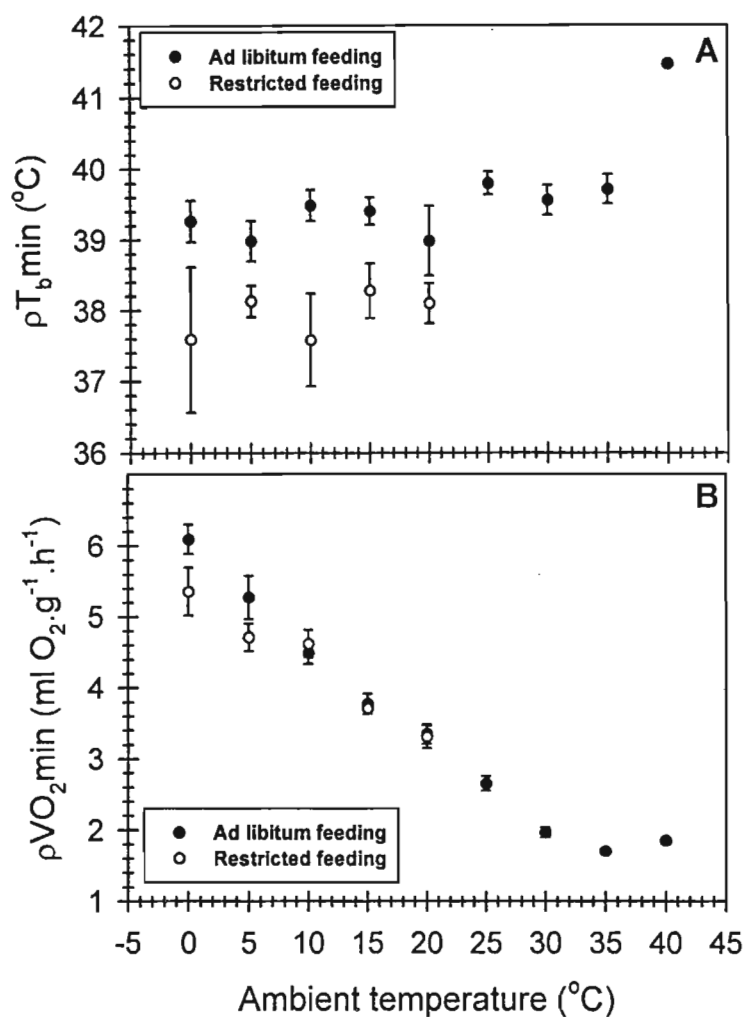


Figure 1. Mean \pm SE minimum rest-phase body temperature ($\rho T_{b,\min}$) (A) and minimum rest-phase oxygen consumption ($\rho VO_2,\min$) (B) at a range of ambient temperatures in red-headed finches *Amadina erythrocephala*.

expenditure did not vary between the five experimental T_a s, and averaged $10.8 \pm 1.8\%$ (Table 1). Furthermore, I found no significant correlation between energy expenditure reduction and M_b loss ($F = 2.993$; $P > 0.05$) or $\rho T_{b,\min}$ ($F = 4.137$, $P > 0.05$).

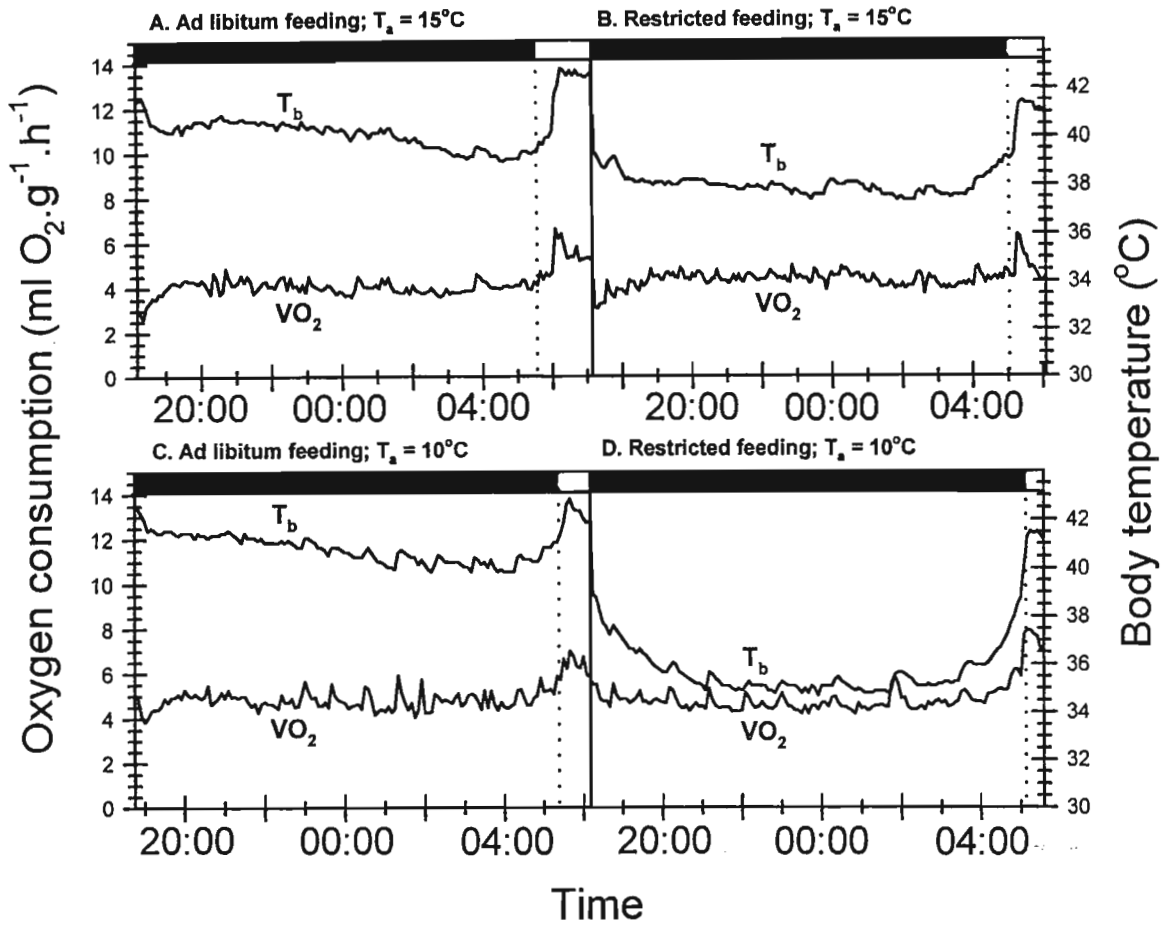


Figure 2. Representative traces of body temperature and oxygen consumption in red-headed finches *Amadina erythrocephala* at $T_a = 15^{\circ}\text{C}$ (top graphs) and 10°C (bottom graphs) during the ad libitum (left graphs) and restricted (right graphs) feeding treatments.

Thermal conductance

The mean C_{\min} at $T_a = 30^{\circ}\text{C}$ ($T_{lc} = 30.8^{\circ}\text{C}$) was $0.20 \pm 0.01 \text{ ml O}_2 \cdot \text{g}^{-1} \cdot (\text{h} \cdot ^{\circ}\text{C})^{-1}$. Below the T_{lc} this decreased to $0.15 \pm 0.01 \text{ ml O}_2 \cdot \text{g}^{-1} \cdot (\text{h} \cdot ^{\circ}\text{C})^{-1}$ at $T_a = 0^{\circ}\text{C}$ (Figure 4a). At $T_a = 40^{\circ}\text{C}$, C_{\min} increased approximately four-fold to $0.82 \pm 0.07 \text{ ml O}_2 \cdot \text{g}^{-1} \cdot (\text{h} \cdot ^{\circ}\text{C})^{-1}$.

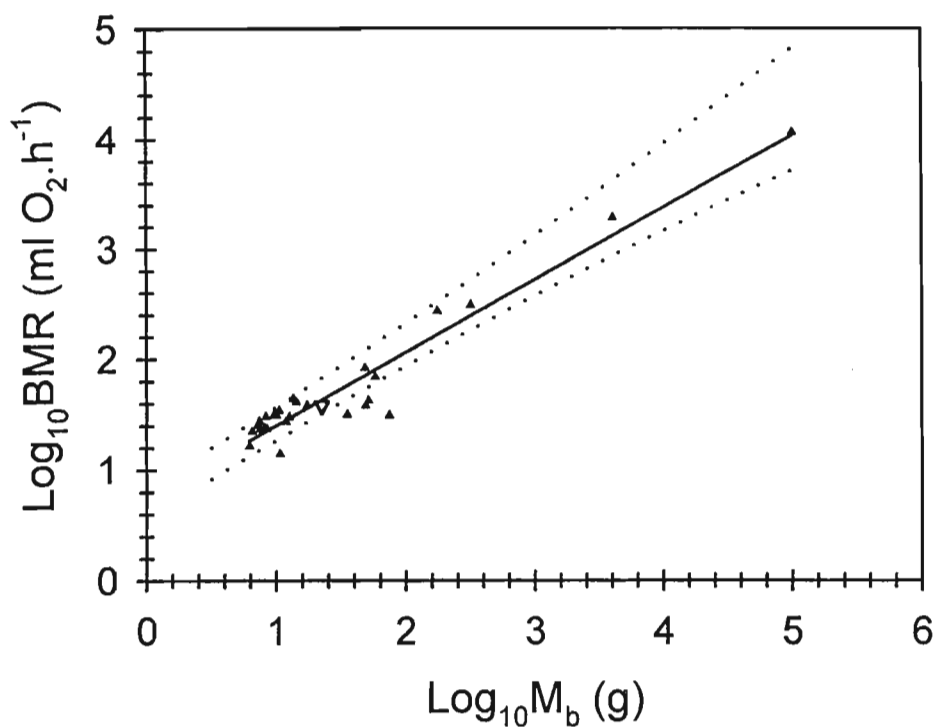


Figure 3. $\text{Log}_{10}\text{BMR}$ and $\text{log}_{10}\text{Mb}_b$ of 27 species of Afrotropical birds (for sources see Chapter 6). The datum for the red-headed finch (*Amadina erythrocephala*) is shown as an inverted, clear triangle. The solid line represents a conventional least-squares regression for the data, and the dotted lines show the phylogenetically-corrected 95% prediction intervals for the BMR of *A. erythrocephala*, calculated following Garland and Ives (2000).

Discussion

My data suggest that *A. erythrocephala* does not possess the capacity for torpor, and provide further support for the notion that passerines generally do not possess the capacity to employ torpor in response to energetic stress. Even above the tolerance limit for M_b loss, which appeared to be around 14%, *A. erythrocephala* showed no evidence of the ability to reduce T_b to below ca. 34°C.

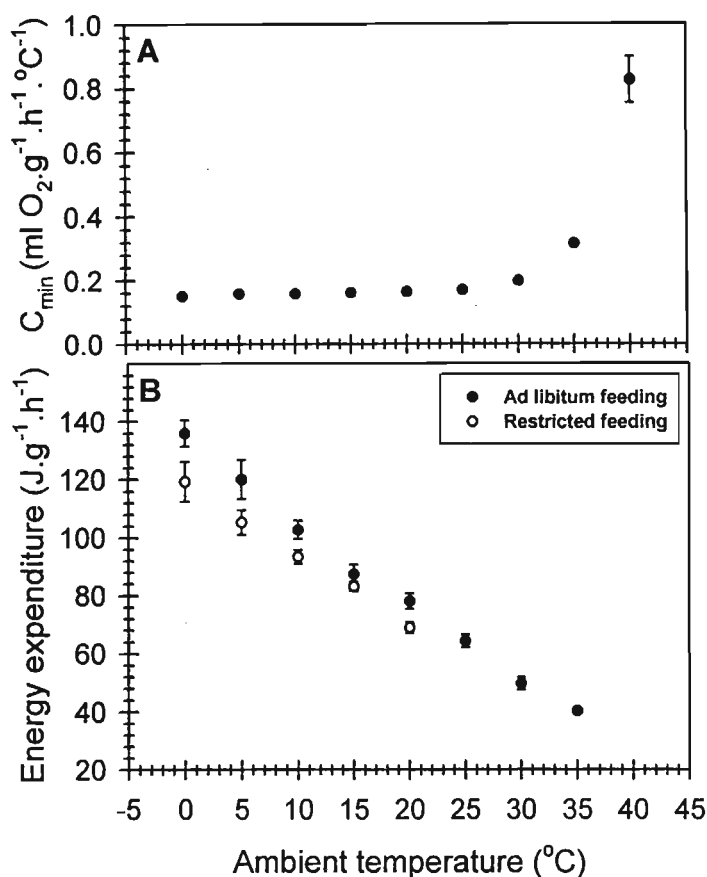


Figure 4. Mean \pm SE minimum rest-phase thermal conductance (C_{\min}) (A) during ad libitum feeding and rest-phase energy expenditure (B) at a range of ambient temperatures in red-headed finches *Amadina erythrocephala*.

Basal metabolic rate

The BMR of *A. erythrocephala* was 38 - 46% lower than predicted by three published allometric equations for avian BMR (Lasiewski and Dawson 1967; Aschoff and Pohl 1970; Reynolds and Lee 1996), but was virtually identical to the value predicted by the equation of Bennett and Harvey (1987), who analysed avian BMR among families, rather than species (Table 2). Moreover, the observed BMR was 10.6% greater than the value predicted by a phylogenetically-corrected regression calculated from data for 27 species of Afrotropical non-migrants (Chapter 6). The phylogenetically-corrected 95% prediction intervals for *A. erythrocephala* (Figure 3) confirm that the measured BMR does not deviate significantly from

the predicted value for a 22g Afrotropical non-migratory bird.

Table 2. Comparison of the observed BMR ($35 \text{ J.g}^{-1}.\text{h}^{-1}$) of the red-headed finch (*Amadina erythrocephala*) with predicted values calculated from various published allometric equations.

Equation	Predicted ($\text{J.g}^{-1}.\text{h}^{-1}$)	Difference (%)
Lasiewski and Dawson (1967) ¹	64.9	- 45.6
Aschoff and Pohl (1970) ¹	57.0	- 38.5
Bennett and Harvey (1987) ^{2,3}	35.3	- 0.79
Reynolds and Lee (1996) ^{2,4}	56.9	- 38.4
Chapter 6 ^{2,4,5}	31.7	+ 10.6

1. Equation for passerines
2. Passerines and non-passerines combined
3. Calculated using mean value for each of 78 families
4. Phylogenetically-corrected regression
5. Calculated for Afrotropical species only

The above comparisons are consistent with the patterns of avian BMR variance described in Chapter 6. Firstly, the BMR of Afrotropical species is lower than Holarctic species. The large differences between my observed BMR for *A. erythrocephala* and the values predicted by published allometric equations which were calculated for species (Lasiewski and Dawson 1967; Aschoff and Pohl 1970; Reynolds and Lee 1996), probably reflects a strong Holarctic bias in these allometries. Secondly, the fact that the observed BMR for *A. erythrocephala* did not differ significantly from the value predicted by an equation based on both mesic and arid Afrotropical species, further illustrates the convergence between the BMR of arid and mesic species in the Afrotropics. This aridity-mimic effect, which is evident in Afrotropical and

Australasian birds (Chapter 6) is thought to be associated with unpredictable rainfall patterns in the mesic areas of the latter zones, largely due to El Niño Southern Oscillation (ENSO) events (Lovegrove 2000a).

Normothermic thermoregulation

The pattern of steady-state rest-phase thermoregulation and the defence of a constant setpoint ρT_b shown by *A. erythrocephala* is consistent with the patterns shown by most endotherms. The mean $\rho T_{b,min}$ observed at thermoneutrality during the ad libitum feeding treatment ($39.6 \pm 0.2^\circ\text{C}$) was 0.7°C higher than Prinzinger et al.'s (1991) mean rest-phase T_b for passerines ($38.9 \pm 0.9^\circ\text{C}$), and was 1.0°C higher than their mean value for all birds ($38.6 \pm 1.0^\circ\text{C}$). The birds appeared to be capable of effective thermoregulation at all experimental T_a s, and there was no evidence for rest-phase hypothermia in response to cold. However, the possibility that *A. erythrocephala* may utilise rest-phase hypothermia at $T_a < 0^\circ\text{C}$ cannot be excluded.

Several passerines which overwinter in the Arctic appear to employ rest-phase hypothermia in response to low T_a (Haftorn 1972, Reinertsen and Haftorn 1983, 1986, Reinertsen 1983, 1985, Waite 1991). For instance, willow tits (*Parus montanus*) fed ad libitum reduced their T_b by up to ca. 6°C (Reinertsen and Haftorn 1983). The extent of T_b depression appeared to depend on T_a , as well as the state of acclimatization (Reinertsen and Haftorn 1983).

However, it is unlikely that roosting *A. erythrocephala* ever experience $T_a < 0^\circ\text{C}$. Red-headed finches typically roost and breed in nests built by red-billed buffalo weavers (*Bubalornis niger*), white-browed sparrow weavers (*Plocepasser mahali*) or sociable weavers (*Philetairus socius*) (Maclean 1993). The insulating effects of these nests are likely to result in chamber temperatures significantly higher than external air temperatures, particularly in the

huge communal nests of the latter species. White et al. (1975) found that the nocturnal temperatures within occupied chambers in sociable weaver nests may be 18°C higher than external T_a . Hence, by utilising such roost sites, *A. erythrocephala* probably avoid exposure to very low T_a .

Responses to food deprivation

The shallow hypothermic responses exhibited by *A. erythrocephala* are consistent with the responses described for a number of passerines. In temperate regions, members of the Corvidae (Waite 1991), Muscicapidae (Biebach 1977), Paridae (Grossman and West 1977, Mayer et al. 1982, Reinertsen and Haftorn 1983, 1986, Reinertsen 1983, 1985), Passeridae (Steen 1958) and Fringillidae (Steen 1958, Ketterson and King 1977) have been reported to reduce T_b by less than 10°C below normothermic levels. In tropical regions, similar shallow hypothermia has been reported in the Tyrannidae (Bucher and Worthington 1982, Bartholomew et al. 1983), Meliphagidae (Collins and Briffa 1984) Passeridae (present study), Fringillidae (Merola-Zwartjes 1998) and Zosteropidae (Maddocks and Geiser 1997).

A reduction in rest-phase energy expenditure of approximately 10% is consistent with the energy savings associated with rest-phase hypothermia in *P. montanus* (Reinertsen and Haftorn 1983) and with the patterns exhibited by black-capped chickadees (*P. atricapillus*) and willow tits (*P. montanus*) (Chaplin 1976, Reinertsen and Haftorn 1983). However, the lack of a correlation between minimum rest-phase T_b during hypothermic responses and M_b was unexpected, since such a correlation appears to be usual in small passerines (Reinertsen 1996). My results are more consistent with those of Paladino (1986), who recorded hypothermic responses in white-crowned sparrows (*Zonotrichia leucophrys*) which were apparently independent of M_b . However, the possibility that hypothermic responses in *A.*

erythrocephala may be correlated with fat reserves cannot be ruled out. There is experimental evidence that the protein leptin may be a peripheral signalling component of a mechanism whereby body fat reserves are determined (Zhang et al. 1994, Stephens and Caro 1998). The possibility exists that in *A. erythrocephala* the depth of hypothermic responses may be determined by such a “lipostat”, although assessing this possibility is beyond the scope of this study.

Rest-phase hypothermia in *A. erythrocephala* appears to occur in response to restricted food supply, rather than in response to cold. This supports Reinertsen’s (1983) suggestion that hypothermia in species inhabiting tropical and semi-tropical areas is predominantly associated with restricted food supplies, whereas hypothermia in arctic and sub-arctic species is typically a response to cold.

General

Like most passerines investigated so far, *A. erythrocephala* appears to be able to utilise shallow rest-phase hypothermia, but not torpor. It has been suggested that the capacity for such shallow hypothermia may be universal in birds (Prinzinger et al. 1991). The majority of species investigated do indeed appear to be able to utilise rest-phase hypothermia in response to energetic stress (Reinertsen 1996), although the apparent absence of hypothermic responses in Tengmalm’s owls *Aegolius funereus* (Hohtola et al. 1994) and black-shouldered kites *Elanus caeruleus* (McKechnie and Lovegrove 1999) suggests that this capacity may not necessarily be ubiquitous.

Dawson and Whittow (2000) have suggested that the that the lack of torpor in passerines may reflect a phylogenetic constraint on cooling tolerance. Notwithstanding a few families which appear to have overcome this phylogenetic constraint (most notably the

Hirundiniidae and Nectariniidae), there are numerous passerines in which, a priori, torpor might be expected to occur. For instance, the prevalence of deep torpor and hibernation in many small Arctic and sub-Arctic mammals is in contrast to the apparent absence of heterothermy in passerine inhabitants of these regions (Reinertsen and Haftorn 1983,1986 Reinertsen 1983,1985). Similarly, there are numerous small nectarivorous and insectivorous passerines in which the capacity for torpor could conceivably confer selective advantages.

The origins of endothermic hibernation and torpor have recently come under close scrutiny. Malan (1996) and Grigg and Beard (2000) proposed that heterothermy represents a plesiomorphic trait with a monophyletic origin. These authors argued that endotherm heterothermic responses represent a release of the inhibition of a primitive reptilian tendency towards wide-amplitude circadian T_b cycling. However, Geiser (1998) pointed out that the phylogenetic distribution of endotherm heterothermic responses suggests that heterothermy evolved independently in several taxa, and urged caution in accepting Malan's (1996) monophyletic hypothesis. Although there are presently insufficient data to evaluate these alternative hypotheses in birds, the relative rarity of torpor in the passerines is consistent with the predictions of Malan's (1996) model, which predicts that heterothermy should be more widespread in phylogenetically older avian groups.

In conclusion, I note that all data on hypothermic responses of passerines have been measured under laboratory conditions. These proximate responses to artificial conditions do not necessarily reflect patterns of thermoregulation in the field. Geiser et al. (2000) compared laboratory and field patterns of heterothermy and showed that, almost without exception, laboratory studies underestimate the depth, frequency and duration of torpor exhibited by both mammals and birds under natural conditions. Although the available evidence strongly suggests that the majority of passerines are not capable of torpor, this possibility should not be

ruled out until it is confirmed in free-ranging birds under natural conditions.

Literature cited

- Armitage, K. B., Melcher, J. C., and Ward, J. M. 1990. Oxygen consumption and body temperature in yellow-bellied marmot populations from montane-mesic and lowland-xeric environments. *J. Comp. Physiol.* 160: 491 - 502.
- Aschoff, J. and Pohl, H. 1970. Der Ruheumsatz von Vögeln als Funktion der Tageszeit und der Körpergröße. *J. Ornithol.* 111: 38 - 47.
- Bartholomew, G. A., Vleck, C. M., and Bucher, T. L. 1983. Energy metabolism and nocturnal hypothermia in two tropical passerine frugivores, *Manacus vitellinus* and *Pipra mentalis*. *Physiol. Zool.* 56: 370 - 379.
- Bech, C., Abe, A. S., Steffensen, J. F., Berger, M., and Bicudo, J. E. P. W. 1997. Torpor in three species of Brazilian hummingbirds under semi-natural conditions. *Condor* 99: 780 - 788.
- Bennett, P. M. and Harvey, P. H. 1987. Active and resting metabolism in birds: allometry, phylogeny and ecology. *J. Zool., Lond.* 213: 327 - 363.
- Biebach, H. 1977. Reduktion des Energiestoffwechsels und der Körpertemperatur hungernder Amseln (*Turdus merula*). *J. Ornithol.* 118: 294 - 300.
- Brigham, R. M. 1992. Daily torpor in a free-ranging goatsucker, the common poorwill (*Phalaenoptilus nuttallii*). *Physiol. Zool.* 65: 457 - 472.
- Brigham, R. M. and Firman, M. C. 1990. Activity periods and use of torpor by two goatsuckers, the poorwill, *Phalaenoptilus nuttallii*, and the common nighthawk,

Chordeiles minor. *Bat Research News* Winter 1990: 72 - 73.

Bucher, T. L. and Worthington, A. 1982. Nocturnal hypothermia and oxygen consumption in manakins. *Condor* 84: 327 - 331.

Carpenter, F. L. 1974. Torpor in an Andean hummingbird: its ecological significance. *Science* 183: 545 - 547.

Chaplin, S. A. 1976. The physiology of hypothermia in the black-capped chickadee (*Parus atricapillus*). *J. Comp. Physiol. B* 112: 335 - 344.

Collins, B. G. and Briffa, P. 1984. Nocturnal energy expenditure by honeyeaters experiencing food shortage and low environmental temperatures. *Comp. Biochem. Physiol.* 78A: 77 - 81.

Dawson, W. R. and Bennett, A. F. 1973. Roles of metabolic level and temperature regulation in the adjustment of western plumed pigeons (*Lophophaps ferruginea*) to desert conditions. *Comp. Biochem. Physiol.* 44A: 249 - 266.

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

Dawson, W. R. and Whittow, G. C. 2000. Regulation of body temperature. In: Sturkie, P. D. (Ed.) *Avian Physiology*. Academic Press, New York.

Frumkin, R., Pinshow, B., and Weinstein, Y. 1986. Metabolic heat production and evaporative heat loss in desert phasianids: chukar and sand partridge. *Physiol. Zool.* 59: 592 - 605.

- Garland, T. and Ives, A. R. 2000. Using the past to predict the present: confidence intervals for regression equations in phylogenetic comparative methods. *Am. Nat.* 155: 346 - 364.
- Geiser, F. 1998. Evolution of daily torpor and hibernation in birds and mammals: importance of body size. *Clin. Exp. Pharmacol. Physiol.* 25: 736 - 740.
- Geiser, F., Holloway, J. C., Körtner, G., Maddocks, T. A., Turbill, C., and Brigham, R. M. 2000. Do patterns of torpor differ between free-ranging and captive mammals and birds? In: Heldmaier, G. and Klingenspor, M. (Eds.) *Life in the cold: 11th International Hibernation Symposium*. Springer, Berlin.
- Grigg, G. and Beard, L. 2000. Hibernation by echidnas in mild climates: hints about the evolution of endothermy. In: Heldmaier, G. and Klingenspor, M. (Eds.) *Life in the cold: 11th International Hibernation Symposium*. Springer, Berlin.
- Grossman, A. F. and West, G. C. 1977. Metabolic rate and temperature regulation in winter-acclimatized black-capped chickadees, *Parus atricapillus*, in interior Alaska. *Ornis Scand.* 8: 127 - 138.
- Haftorn, S. 1972. Hypothermia of tits in the Arctic winter. *Ornis Scand.* 3: 153 - 166.
- Harrison, J. A., Allan, D. G., Underhill, L. G., Herremans, M., Tree, A. J., Parker, V., and Brown, C. J. 1997. *The atlas of southern African birds. Volume 2: Passerines*. Birdlife South Africa, Johannesburg.
- Hiebert, S. M. 1990. Energy costs and temporal organization of torpor in the rufous hummingbird (*Selasphorus rufus*). *Physiol. Zool.* 63: 1082 - 1097.

- Hinsley, S. A., Ferns, P. N., Thomas, D. H., and Pinshow, B. 1993. Black-bellied sandgrouse (*Pterocles orientalis*) and pin-tailed sandgrouse (*Pterocles alchata*): closely related species with differing bioenergetic adaptations to arid zones. *Physiol. Zool.* 66: 20 - 42.
- Hoffmann, R. and Prinzinger, R. 1984. Torpor und Nahrungsausnutzung bei 4 Mausvogelarten (Coliiformes). *J. Ornithol.* 125: 225 - 237.
- Hohtola, E., Pyörnilä, A., and Rintamäki, H. 1994. Fasting endurance and cold resistance without hypothermia in a small predatory bird: the metabolic strategy of Tengmalm's owl, *Aegolius funereus*. *J. Comp. Physiol.* 164: 130 - 437.
- Ketterson, E. D. and King, J. R. 1977. Metabolic rate and behavioral responses to fasting in the white-crowned sparrow (*Zonotrichia leucophrys gambelli*). *Physiol. Zool.* 50: 115 - 129.
- Körtner, G., Brigham, R. M., and Geiser, F. 2000. Winter torpor in a large bird. *Nature* 407: 318.
- Lasiewski, R. C. and Dawson, W. R. 1967. A re-examination of the relation between standard metabolic rate and body weight in birds. *Condor* 69: 13 - 23.
- Lasiewski, R. C. and Thompson, H. J. 1966. Field observations of torpidity in the violet-green swallow. *Condor* 68: 102 - 103.
- Lovegrove, B. G. 2000a. The zoogeography of mammalian basal metabolic rate. *Am. Nat.* 156: 201 - 219.

- Lovegrove, B. G. 2000b. Daily heterothermy in mammals: coping with unpredictable environments. In: Heldmaier, G. and Klingenspor, M. (Eds.) *Life in the cold: 11th International Hibernation Symposium*. Springer, Berlin.
- Maclean, G. L. 1993. *Roberts' birds of southern Africa*. John Voelcker Bird Book Fund, Cape Town.
- Maddocks, T. A. and Geiser, F. 1997. Energetics, thermoregulation and nocturnal hypothermia in Australian silvereyes. *Condor* 99: 104 - 112.
- Malan, A. 1996. The origins of hibernation: a reappraisal. In: Geiser, F., Hulbert, A. J., and Nicol, S. C. (Eds.) *Adaptations to the cold: Tenth International Hibernation Symposium*. University of New England Press, Armidale.
- Mayer, L., Lustick, C., and Battersby, B. 1982. The importance of cavity roosting and hypothermia in the energy balance of the winter acclimatized Carolina chickadee. *Int. Biometeor.* 26: 231 - 238.
- McKechnie, A. E. and Lovegrove, B. G. 1999. Circadian metabolic responses to food deprivation in black-shouldered kites. *Condor* 101: 426 - 432.
- McKechnie, A. E. and Lovegrove, B. G. 2000. Heterothermy in mousebirds: evidence of avian proto-torpor? In: Heldmaier, G. and Klingenspor, M. (Eds.) *Life in the cold: 11th International Hibernation Symposium*. Springer, Berlin.
- Merola-Zwartjes, M. 1998. Metabolic rate, temperature regulation, and the energetic implications of roost nests in the bananaquit (*Coereba flaveola*). *Auk* 115: 780 - 786.

- Merola-Zwartjes, M. and Ligon, J. D. 2000. Ecological energetics of the Puerto Rican tody: heterothermy, torpor and intra-island variation. *Ecology* 81: 990 - 1002.
- Paladino, F. V. 1986. Transient nocturnal hypothermia in white-crowned sparrows. *Ornis Scand.* 17: 78 - 80.
- Prinzinger, R., Göppel, R., Lorenz, A., and Kulzer, E. 1981. Body temperature and metabolism in the red-backed mousebird (*Colius castanotus*) during fasting and torpor. *Comp. Biochem. Physiol.* 69A: 689 - 692.
- Prinzinger, R., Preßmar, A., and Schleucher, E. 1991. Body temperature in birds. *Comp. Biochem. Physiol.* 99A: 499 - 506.
- Prinzinger, R. and Siedle, K. 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. 1983. Nocturnal hypothermia and its energetic significance for small birds living in the arctic and subarctic regions. A review. *Polar Res.* 1: 269 - 284.
- Reinertsen, R. E. 1985. Hypothermia in northern passerine birds. In: Heller, H. C., Musacchia, X. J., and Wang, L. C. H. (Eds.) *Living in the cold: physiological and biochemical adaptations*. Elsevier, New York.
- Reinertsen, R. E. 1996. Physiological and ecological aspects of hypothermia. In: Carey, C. (Ed.) *Avian energetics and nutritional ecology*. Chapman & Hall, New York.
- Reinertsen, R. E. and Haftorn, S. 1983. Nocturnal hypothermia and metabolism in the Willow

- Tit *Parus montanus* at 63°N. *J. Comp. Physiol.* 151: 109 - 118.
- Reinertsen, R. E. and Haftorn, S. 1986. Different metabolic strategies of northern birds for nocturnal survival. *J. Comp. Physiol.* 156: 655 - 663.
- Reynolds, P. S. and Lee, R. M. 1996. Phylogenetic analysis of avian energetics: passerines and non-passerines do not differ. *Am. Nat.* 147: 735 - 759.
- Schmidt-Nielsen, K. 1990. *Animal physiology: adaptation and environment.* Cambridge University Press, Cambridge.
- Serventy, D. L. 1970. Torpidity in the white-backed swallow. *Emu* 70: 27 - 28.
- Shkolnik, A. and Schmidt-Nielsen, K. 1976. Temperature regulation in hedgehogs from temperate and desert environments. *Physiol. Zool.* 49: 56 - 64.
- Steen, J. 1958. Climatic adaptation in small northern birds. *Ecology* 39: 625 - 629.
- Stephens, T. W. and Caro, J. F. 1998. To be lean or not to be lean: is leptin the answer? *Exp. Clin. Endocrinol. Diabetes* 106: 1 - 15.
- Tieleman, B. I. and Williams, J. B. 2000. The adjustment of avian metabolic rates and water fluxes to desert environments. *Physiol. Biochem. Zool.* 73: 461 - 479.
- Waite, T. A. 1991. Nocturnal hypothermia in gray jays *Perisoreus canadensis* wintering in interior Alaska. *Ornis Scand.* 22: 107 - 110.
- White, F. N., Bartholomew, G. A., and Howell, T. R. 1975. The thermal significance of the nest of the Sociable Weaver *Philetairus socius*: winter observations. *Ibis* 117: 171 - 179.

Withers, P. C. 1977. Measurement of VO_2 , VCO_2 , and evaporative water loss with a flow-through mask. *J. Appl. Physiol.* 42: 120 - 123.

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

Yeager, D. P. and Ultsch, G. R. 1989. Physiological regulation and conformation: a BASIC program for the determination of critical points. *Physiol. Zool.* 62: 888 - 907.

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

Zhang, Y. Y., Proenca, R., Maffei, M., Barone, M., Leopold, L., and Friedman, J. M. 1994. Positional cloning of the mouse *obese* gene and its human homologue. *Nature* 372: 425 - 432.

Chapter 6. Avian basal metabolic rate: a zoogeographical perspective.

Introduction

The focus of analyses of avian basal metabolic rate (BMR) during the 1960s, 70s, and early 80s was the calculation of generalised allometric equations describing the relationship between BMR and body mass (M_b) (Lasiewski and Dawson 1967; Zar 1968; Prinzinger and Hänssler 1980). The last two decades have seen a shift towards studies which attempt to explain the variance surrounding the relationship between BMR and M_b (e.g. Weathers 1979; Bennett and Harvey 1987; McNab 1988) in the hope of elucidating adaptive associations between BMR and various ecological and life history traits.

These recent approaches reflect the contemporary convergence between physiology and evolutionary biology and the emerging field of evolutionary physiology (Garland and Carter 1994), as well as the search for mechanisms and processes underlying an energetic basis of fitness (Brown et al. 1993; Kozłowski 1996; Kozłowski and Weiner 1997; Chown and Gaston 1997). Quantifying resource acquisition in excess of maintenance requirements is implicit in several energetic definitions of fitness (Brown et al. 1993; Chown and Gaston 1997). For instance, Brown et al. (1993) assumed that the rate at which energy intake is converted into production scales to the same exponent (0.75) as metabolic rate and M_b . However, the validity of a single scaling exponent for mammals is questionable, because the exponent can vary from 0.42 - 1.03 between and within zoogeographical zones, depending on habitat effects and relative body size (small vs. large) (Lovegrove 2000). A more realistic approach, which moves away from the assumption of a functional dependence of energetic traits on body size, has been proposed by Kozłowski and Weiner (1997). These authors incorporated intra- and inter-specific variance in energetic traits into a model based on the

assumption that body size optimization occurs through optimal resource allocation. In this model, interspecific allometries resulted from body size optimization and intraspecific production and mortality parameters (Kozłowski and Weiner 1997).

The importance of understanding BMR variance for defining fitness in energetic terms was the stimulus for a recent analysis which examined the correlation between broad-scale patterns of climatic predictability and mammalian BMR variance (Lovegrove 2000). This study showed that mammalian BMR varies significantly between zoogeographical zones. Moreover, scaling exponents for large (>500g) and small (<500g) mammals were markedly different. For small mammals, the BMR of Afrotropical, Australasian and Indomalayan species was significantly lower than that of Holarctic species (Lovegrove 2000). On the other hand, BMR variance in large mammals was dependent on relative mobility, which is largely determined by locomotory mode (Lovegrove 2000).

A slow-fast metabolic continuum hence exists in mammals, for which gradients of resource predictability constitute the underlying selective mechanism (Lovegrove 2000). Because any mechanism which results in variance in energetic traits is likely to be important in defining fitness in energetic terms, I consider an examination of the link between resource predictability and avian BMR variance to be important. In addition, avian BMR provides a compelling test of Lovegrove's (2000) model, simply because birds are potentially much more mobile than mammals.

Within zoogeographical zones, gradients of resource predictability are partly determined by the relative influence of the El Niño Southern Oscillation (ENSO) phenomenon (Lovegrove 2000). Lovegrove (2000) showed that a large component of the variance in mammalian BMR can be explained by the influence of ENSO on zonal rainfall patterns. Small mammals inhabiting zones where ENSO causes periodic negative rainfall anomalies, namely

the Afrotropical, Australasian and Indomalayan zones, exhibited significantly lower BMRs than mammals inhabiting Holarctic zones largely unaffected by ENSO. The latter paper is one of several recent studies which illustrate the importance of selection pressures associated with ENSO. For instance, Grant and Grant (1993) provided the first observable evidence of evolution at work in their documented changes in bill dimensions in a Galapagos finch *Geospiza fortis*, arising directly from changes in the relative abundance of large and small seeds associated with the severe El Niño event of 1982 - 83. Based on seed size-ratio changes, Grant and Grant (1993) predicted, and subsequently observed, a significant decrease in bill width.

In this paper, I test the generality of Lovegrove's (2000) model linking resource predictability to BMR variance. In short, I test whether similar BMR patterns are evident in birds. Specifically, Lovegrove's (2000) model predicts that a) the BMR of Afrotropical, Indomalayan and Australasian birds should be lower than those of Holarctic and Neotropical species, and b) that birds inhabiting arid regions should exhibit lower BMR than mesic counterparts. Furthermore, the model predicts an aridity-mimic effect whereby selection for low BMR associated with unpredictable rainfall caused by ENSO in certain mesic zones should mimic that of counterpart desert species (Lovegrove 2000). A specific prediction of the aridity-mimic effect is marked divergence of the BMR of arid and mesic birds in the Palearctic and Nearctic, but convergence in Afrotropical and Australasian species (Lovegrove 2000).

However, Lovegrove (2000) emphasised the importance of relative mobility and body size in terms of BMR selection. This criterion requires careful consideration in avian analyses because of the relatively low costs and ease of long-distance bird movement by flight. Long-distance migrations between zones obviate zone-specific selection pressures in migratory

birds. Hence, I limited my data set to non-migratory species. Nevertheless, selection pressures on non-migratory avian BMR may well be moderated by the inherently greater mobility associated with flight, although this latter consideration is offset by the higher metabolic maintenance requirements of a bird compared to those of a similarly sized mammal (Daan et al. 1990).

Materials and Methods

I obtained measurements of BMR ($\text{ml O}_2 \cdot \text{h}^{-1}$) and M_b (g) for 219 species (Appendix 1) from Prinzing et al. (1981); Wasser (1986); Bennett and Harvey (1987); Prinzing et al. (1989); Weathers et al. (1990); Williams et al. (1991); Hinsley et al. (1993); McNab and Bonaccorso (1995); Liknes and Swanson (1996); Smith (1996); Maddocks and Geiser (1997); Weathers (1997); Merola-Zwartjes (1998); Boix-Hinzen and Lovegrove (1998); Bech and Nicol (1999); Vitali et al. (1999); Schleucher (1999a;b); McKechnie and Lovegrove (2001); Chapters 1,5. Where possible, I consulted the original references to confirm that measurements were representative of basal metabolism i.e. that measured in unstressed animals at thermoneutral ambient temperatures during the rest-phase. All BMR and M_b measurements were \log_{10} -transformed. I excluded pelagic and migratory species from the analysis. I included species which showed seasonal movements within a particular zone, but excluded those which seasonally migrate between zones. I also excluded species occurring in more than one zone, with the exception of a few species which marginally entered a second zone because of contiguous landmasses (e.g. Neotropical - Palearctic) or the proximity of islands (e.g. Australasian - Indomalayan).

Each species was classified as inhabiting a mesic or arid habitat (Appendix 1). I followed the arid/mesic classification of Williams (1996). For species which were not

included in Williams' (1996) data set, I subjectively based my classification on published habitat descriptions.

I constructed a phylogeny (Appendix 2), based primarily on Sibley and Ahlquist's (1990) average linkage (UPGMA) phylogeny using PDTREE (Garland et al. 1993). I consulted the following additional references to resolve relationships within specific taxa: Marten and Johnson (1986); Zink and Dittmann (1991); Zink et al. (1991); Randi et al. (1991); Christidis et al. (1991); Christidis and Schodde (1993); Raikow (1994); Bleiweiss et al. (1994); Ellsworth et al. (1995;1996); Livezey (1996); Zink and Blackwell (1996); Espinosa de los Monteros and Cracraft (1997); Zink and Blackwell (1998); Espinosa de los Monteros (1998); Eberhard (1998); Gerwin and Zink (1998); Patten and Fugate (1998); Lanyon and Omland (1999); Johnson and Sorenson (1999); Johnson and Lanyon (1999); Brown and Toft (1999). I excluded genera if no information on phylogenetic position was available. In cases where phylogenetic position, but no branch length, was available, I placed the daughter branch(es) at one half the length of the parent branch.

In a re-analysis of the data set used by Reynolds and Lee (1996), Garland and Ives (2000) showed that passerines exhibit a relatively low rate of phenotypic evolution compared to non-passerines. These authors employed differential branch length transformations to adequately standardise independent contrasts and found that adequate standardisation was achieved by raising each segment of the phylogeny to the power of -0.2 and thereafter rescaling the passerine subclade to a total height of 4.0. I similarly found that the absolute values of passerine contrasts were significantly lower than within the non-passerines after raising each segment of my phylogeny to the power of -0.2 (Mann-Whitney $U = 3981$; $P = 0.00003$). I hence followed Garland and Ives' (2000) approach of differential transformation, but found that rescaling the passerine subclade to a height of 7.0, rather than 4.0, resulted in

adequate standardisation, with no significant differences in the magnitude of passerine and non-passerine contrasts (Mann-Whitney $U = 5877$; $P = 0.913$).

I tested for differences in BMR between zones using conventional and phylogenetically independent (PI) analysis of covariance (ANCOVA), after verifying homogeneous zone slopes of the BMR vs. M_b regressions (Zar 1999). PI ANCOVA were performed using the program PDANOVA on 1000 tip values simulated by PDSIMUL (Garland et al. 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 three evolutionary models: 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) speciation with bounds, correlation set to zero. For bounds, I used a minimum M_b of 1g [the M_b of the smallest extant bird species, *Calypte helenae*, is 1.6g, (Calder 1985)] and a maximum M_b of 450 000g [estimated M_b for the extinct *Aepyornis maximus*, (Calder 1985)]. To obtain BMR bounds, I calculated a phylogenetically corrected regression of BMR and M_b for the species in my data set using PDTREE (Garland et al. 1993; Garland and Ives 2000) and calculated predicted BMRs for *C. helenae* and *A. maximus* of 6.778 ml $O_2 \cdot h^{-1}$ and 36588.95 ml $O_2 \cdot h^{-1}$ respectively. The bounds algorithm was set to “replace”. No trends were set.

Results

The conventional linear regression for all species in the data set was $\log_{10} \text{BMR} = 0.660 \cdot \log_{10} M_b + 0.831$ ($r^2 = 0.953$). The phylogenetically independent (PI) regression, calculated using the methods described in Garland and Ives (2000), was $\log_{10} \text{BMR} = 0.690 \cdot \log_{10} M_b + 0.707$. For the purposes of future comparison, I have calculated PI regressions

for \log_{10} body mass and \log_{10} BMR, taking the zone and habitat variation described below into account, using the procedures described in Garland and Ives (2000) (Table 1).

Table 1. Phylogenetically corrected linear regressions ($\log_{10}\text{BMR} = a + b.\log_{10}M_b$) for non-migratory avian basal metabolic rate ($\text{ml O}_2.\text{h}^{-1}$) and body mass (g) for zoogeographical zones and habitat types. All regressions were calculated using the procedures of Garland and Ives (2000).

Zone	Habitat	b	a	N
Afrotropics	Arid	0.638	0.755	7
	Mesic	0.764	0.468	21
	Combined ^a	0.695	0.608	28
Australasia	Arid	0.615	0.886	13
	Mesic	0.722	0.617	20
	Combined ^a	0.703	0.660	33
Indomalaya ^b	Mesic	0.686	0.763	22
Nearctic	Arid	0.741	0.569	15
	Mesic	0.739	0.659	49
Neotropics ^b	Mesic	0.630	0.909	19
Palaearctic ^b	Mesic	0.704	0.740	47

a. No significant differences between BMR of arid and mesic species

b. Insufficient data to calculate regression for arid species

Aridity effects

The slopes of regressions for arid and mesic species were not significantly different (Table 2).

The BMR of arid-zone species was significantly lower than that of mesic species for two of the three evolutionary models used in the PI analysis, as well as for the conventional analysis (Table 2).

Zonal effects

Regression slopes for mesic species did not vary significantly between zones (Table 2), but all three models showed significant BMR differences between zones (Table 2). The magnitudes of these differences are illustrated with mean residuals calculated from a common regression (Figure 1). Note that the data in this plot are not independent of phylogeny, and hence variance estimates may be underestimated. Moreover, the relatively high mean residual for Neotropical mesic species is largely due to the large number of hummingbirds (8 of 21 species) in the Neotropical data set. Removal of the hummingbird data reduces the mean residual for the Neotropical mesic species from 0.051 ± 0.030 to 0.006 ± 0.025 (Figure 1). The mean BMR residuals of mesic Afrotropical, Indomalayan and Australasian species were lower than those of Palearctic, Nearctic and Neotropical species (Posterior Tukey Test). I also compared the BMR of arid species from the Afrotropical, Australasian and Nearctic zones, and found no significant variation (Table 1). Small sample sizes precluded analyses of arid species for the Neotropical ($n = 3$), Palearctic ($n = 3$) and Indomalayan ($n = 0$) zones.

Within-zone arid-mesic BMR convergence

I compared the BMR of arid and mesic species within the Afrotropical, Australasian and Nearctic zones, after verifying homogenous regression slopes (Table 3). I was unable to make similar comparisons for the Indomalayan, Neotropical and Palearctic zones due to small sample sizes for arid species. For the Nearctic, the BMR of arid species was significantly lower than that of mesic species (Table 3). However, for both the Afrotropical and Australasian zones, there was no significant difference in the BMR of mesic and desert arid birds (Table 2).

Table 2. ANCOVA of avian \log_{10} body mass (g) and \log_{10} BMR ($\text{ml O}_2\cdot\text{h}^{-1}$). The covariate was \log_{10} body mass (g). Critical values for F were calculated as the 95th percentiles of null distributions of F generated using the PDSIMUL module of PDAP (Garland et al. 1993). Branch lengths for passerines and non-passerines were differentially transformed following Garland and Ives (2000).

Source of variation	SS	df	MS	F	Brownian							
					Conventional		Gradual ^a		Speciational ^a		Gradual (corr.) ^b	
					Critical value	P	Critical value	P	Critical value	P	Critical value	P
<i>Habitat effects (Mesic / arid, n = 219)</i>												
Slopes	0.003	1	0.003	0.164	5.100	0.522	6.459	0.751	5.846	0.722	5.643	0.745
Habitats	0.174	1	0.174	9.121	5.100	0.002	8.888	0.045	7.902	0.028	9.201	0.052
<i>Zone effects - mesic species (n = 178)</i>												
Slopes	0.076	5	0.015	0.968	2.650	0.479	5.249	0.815	5.408	0.814	5.907	0.815
Zones	0.722	5	0.144	9.257	2.650	0.000	7.185	0.016	7.755	0.017	8.104	0.023
<i>Zone effects - arid species (excl. Palaearctic, Neotropics, Indomalaya) (n = 35)</i>												
Slopes	0.002	2	0.001	0.042	4.110	0.855	4.507	0.975	4.341	0.960	4.463	0.970
Zones	0.017	2	0.009	0.419	4.110	0.613	5.301	0.794	5.942	0.808	5.808	0.812

a. Correlation set to zero, bounds as defined in text.

b. Correlation = default value i.e that of input distributions, bounds as defined in text.

Significance ($\alpha = 0.5$) indicated by bold type.

Table 3. ANCOVA comparing the \log_{10} BMR ($\text{ml O}_2 \cdot \text{h}^{-1}$) of desert and mesic birds from the Nearctic, Afrotropical and Australasian zones. The covariate was \log_{10} body mass (g). Critical values for F were calculated as the 95th percentiles of null distributions of F generated using the PDSIMUL module of PDAP (Garland et al. 1993). Branch lengths for passerines and non-passerines were differentially transformed following Garland and Ives (2000).

Source of variation	SS	df	MS	F	Brownian							
					Conventional		Gradual ^a		Speciational ^a		Gradual (corr.) ^b	
					Critical value	P	Critical value	P	Critical value	P	Critical value	P
<i>Arid/Mesic (Nearctic) (n = 64)</i>												
Slopes	0.007	1	0.007	0.451	5.340	0.432	4.651 >	0.565	4.058	0.516	4.624	0.534
Among groups	0.100	1	0.100	6.666	5.340	0.010	4.398	0.015	3.164	0.008	4.438	0.020
<i>Arid/Mesic (Afrotropical) (n = 28)</i>												
Slopes	0.000	1	0.000	0.017	5.690	0.546	4.551	0.906	4.758	0.904	4.560	0.903
Among groups	0.003	1	0.003	0.102	5.690	0.520	5.358	0.782	4.728	0.785	4.695	0.792
<i>Arid/Mesic (Australasia) (n = 33)</i>												
Slopes	0.006	1	0.006	0.223	5.570	0.489	5.034	0.658	4.450	0.666	4.504	0.644
Among groups	0.001	1	0.001	0.020	5.570	0.551	5.937	0.923	5.541	0.9041	5.644	0.912

a. Correlation set to zero, bounds as defined in text.

b. Correlation = default value i.e that of input distributions, bounds as defined in text.

Significance ($\alpha = 0.5$) indicated by bold type.

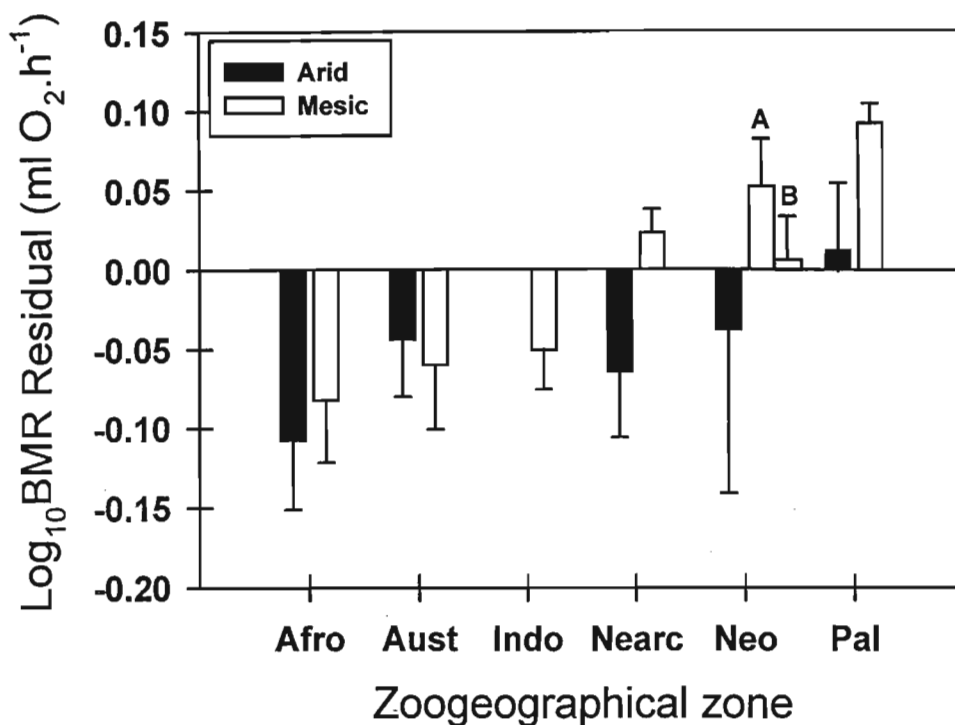


Figure 1. Mean \pm SE residual \log_{10} BMR ($\text{ml O}_2 \cdot \text{h}^{-1}$) calculated from the conventional linear regression of \log_{10} BMR and $\log_{10}M_b$ (g) for 219 avian species from six zoogeographical zones. Column A includes all Neotropical mesic species, whereas column B excludes the hummingbirds (Trochilidae).

Discussion

Lovegrove's (2000) model successfully predicted the observed variance in non-migratory avian BMR. Birds inhabiting the Afrotropics, Indomalaya and Australasia generally exhibit lower BMR than Palearctic, Nearctic or Neotropical species. The BMR of arid and mesic Afrotropical and Australasian species does not differ significantly. In contrast, the BMR of arid and mesic Nearctic species is significantly different. I suspect that the observation that PI ANCOVA of the entire data set yielded a significant difference between the BMR of arid species and mesic species for only two of three evolutionary models reflects this convergence.

A slow-fast metabolic continuum similar to that described by Lovegrove (2000) for mammals hence appears to exist for birds. The highest BMRs occur in species inhabiting

predictable, highly seasonal Holarctic habitats. Lovegrove (2000) suggested that in such predictable, seasonal environments, high BMR may be favoured if it optimises production and reproduction over longevity. In contrast, species inhabiting arid areas may experience selection for low BMR, if it optimises survival and longevity, which in turn optimizes long-term reproductive output (Lovegrove 2000). There also appears to be convergence between the BMR of arid and mesic species in regions where ENSO events cause periodic negative rainfall anomalies, suggesting that in these areas, mesic species experience selection pressures convergent with those experienced by arid species. Although the BMR of mesic Neotropical species initially appears to be higher than that of mesic Palearctic species, this is largely due to the over-representation of hummingbirds (Trochilidae) in the Neotropical data set (Figure 1). Moreover, ENSO events typically cause positive rainfall anomalies in the Neotropics (Stone et al. 1996). Hence, species in this region probably do not experience the same degree of selection for energy conservation as species inhabiting zones where ENSO events cause negative rainfall anomalies i.e. droughts.

A potential confounding effect in my analysis is the decrease in mean annual temperature with increasing latitude. Although Scholander et al. (1950) suggested that insulation rather than BMR is the major adaptation to temperature in mammals and birds, Weathers (1979) found that avian BMR showed broad correlations with ambient temperature, with species inhabiting cold climates at high latitudes exhibiting higher BMR than tropical species. Of course, this explanation for BMR variance in terms of ambient temperature is not mutually exclusive to my illustration of zoogeographical effects. However, several factors absent in previous analyses are essential in determining the role of ambient temperature on BMR variance. Firstly, the effects of inter-zonal variation need to be removed by restricting the analysis to one zone. The Nearctic or Palearctic zones are probably the only zones with a

sufficient range of ambient temperatures to investigate this correlation. Secondly, habitat (e.g. aridity) effects need to be removed, by restricting the analysis to mesic species. Thirdly, the effects of phylogeny need to be removed, using appropriate PI models.

Implicit in Lovegrove's (2000) model is the assumption that the global effect of aridity in selecting for low BMR is indicative of an underlying mechanism or selection process common in all habitats. Lovegrove (2000) argued that selection for BMR is primarily determined by the minimum temporal and spatial resource availability, and that the low BMR of desert mammals may provide evidence of ultimate evolutionary responses to resource unpredictability, determined primarily by rainfall variability. The low BMR of mesic mammals in ENSO-affected regions reflect similar selective pressures associated with resource unpredictability (Lovegrove 2000). My results suggest that observed variance in avian BMR may be explained by the same mechanism, i.e. in terms of resource predictability gradients.

Several authors have noted that birds inhabiting the tropics tend to exhibit lower BMRs than species from higher latitudes (Bennett and Harvey 1987; McNab 1988; Daan et al. 1990). For instance, Daan et al. (1990) argued that the smaller clutch and offspring sizes of endotherms inhabiting "stable, tropical" environments than similar sized species in arctic and temperate climates represent "an evolutionary adjustment to reduced nonreproductive adult mortality, which would shift the trade-off towards reduced investment in offspring, hence a smaller DEE_{par} [energy turnover during parental care], smaller metabolic machinery, and a lower BMR". However, I seriously question the notion of "stable, tropical" environments. ENSO events have been shown to influence fruiting events in both Malaysian (Van Schaik 1986; Ashton et al. 1988) and Panamanian (Wright et al. 1999) rain forests. Moreover, Wright et al. (1999) found that frugivorous and granivorous rain forest mammals on Barro Colorado

Island, Panama, were limited by unpredictable ENSO-associated variability in community-level fruit production. In terms of Lovegrove's (2000) model, the low BMR of endotherms inhabiting the tropics results from selection associated with unpredictable periods of low resource availability. Lovegrove's (2000) model effectively suggests that selection for lower BMR in tropical species arises from exactly the opposite mechanism to that proposed by Daan et al. (1990).

Implications for comparative studies

The broad-scale zoogeographical patterns of variation in non-migratory avian BMR described here provide a framework for investigating the relationships between BMR and various ecological and life-history traits. My results suggest that zoogeographical effects, as well as phylogeny, need to be considered when attempting to infer adaptive trends in non-migratory avian BMR. Hypotheses concerning the deviation of observed BMR from allometrically predicted values, for example, need to be tested using zone-specific data sets. Furthermore, hypotheses concerning habitat-related BMR variance need to be generated taking into account the arid-mesic convergence which appears to exist in certain zones.

One of the commonalities of models such as those proposed by Brown et al. (1993) and Kozłowski and Weiner (1997) is that resource allocation optimality is modelled in "saturated" or "aseasonal" environments. Lovegrove (2000) suggested that these assumptions of environmental non-stochasticity represent potentially serious shortcomings. The zoogeographical variance in mammalian BMR predicted by Lovegrove (2000), as well as my present results for birds, suggests that any model of energy allocation in endotherms needs to take into consideration zonal variation in maintenance metabolism associated with broad-scale climatic variability.

Although some aspects of Lovegrove's (2000) model apply exclusively to non-volant mammals, it does yield further testable predictions for non-migratory birds. Firstly, if life-history parameters such as age and size at maturity are correlated with physiological parameters, then the model should provide a basis for predicting life-history traits based on resource predictability criteria (Lovegrove 2000). Hence, it is possible that the slow-fast continuum in avian BMR is correlated with a slow-fast life history continuum. If the high BMR of endotherms inhabiting predictable, seasonal environments optimizes short-term reproduction, rather than longevity, then Holarctic species should be expected to reach maturity more quickly and exhibit higher breeding rates than species inhabiting more unpredictable Indomalayan, Afrotropical or Australasian environments (Lovegrove 2000).

Secondly, the model predicts that species inhabiting islands should exhibit lower BMRs than their mainland counterparts. This prediction arises from the reduced ability of island species to escape areas of localized reduced resource availability (Lovegrove 2000). If this prediction holds, it is possible that the low BMRs of Indomalayan species may be partly attributable to the large number of islands in this zone, in addition to the severe effects of ENSO in this region (Stone et al. 1996). This island effect should naturally be much less pronounced in birds than in mammals, but may well contribute to the BMR of birds inhabiting isolated islands, as well as species with insufficient mobility to move between islands.

The link between selective pressure for energy conservation and the evolution of flightlessness has received attention from several authors (Diamond 1991; McNab 1994). McNab (1994) concluded that flightlessness and reduced energy requirements through the reduction of pectoral muscle mass is most likely to occur on smaller islands where birds presumably face the most severe resource restrictions. This selection is likely to be particularly strong in species with the greatest resource requirements. The broad-scale patterns

of selection for energy conservation predicted by Lovegrove's model may represent an additional factor in the evolution of flightlessness. Although the large number of flightless species, both extant and recently extinct, in the western Pacific and the Indian oceans (Diamond 1991) may simply reflect the number of islands in these areas, the selection pressures for flightlessness in these areas may well be amplified by the effects of ENSO on the temporal and spatial variation of resource availability.

Finally, my data set highlights the paucity of avian BMR data for certain zones. At present, a major limiting factor in comparative studies is the low number of southern Hemisphere species for which BMR has been measured. Of the 219 species in my data set, 28 were Afrotropical, 32 were Australasian, 21 were Indomalayan and 21 were Neotropical. The remaining 117 species, or 53% of the data set, were Nearctic or Palearctic species. This represents a substantial imbalance when the relatively high numbers of species occurring in the Neotropics and Indomalaya are considered (Flegg 1985).

Literature cited

- Ashton, P. S., Givnish, T. J., and Appanah, S. 1988. Staggered flowering in the Dipterocarpaceae: new insights into floral induction and the evolution of mast fruiting in the aseasonal tropics. *Am. Nat.* 132: 44 - 66.
- Bech, C. and Nicol, S. C. 1999. Thermoregulation and ventilation in the tawny frogmouth, *Podargus strigoides*: a low-metabolic avian species. *Aust. J. Zool.* 47: 143 - 153.
- Bennett, P. M. and Harvey, P. H. 1987. Active and resting metabolism in birds: allometry, phylogeny and ecology. *J. Zool., Lond.* 213: 327 - 363.
- Bleiweiss, R., Kirsh, J. A. W., and Matheus, J. C. 1994. DNA-DNA hybridization evidence for subfamily structure among hummingbirds. *Auk* 111: 8 - 19.
- Boix-Hinzen, C. and Lovegrove, B. G. 1998. Circadian metabolic and thermoregulatory patterns of red-billed woodhoopoes (*Phoeniculus purpureus*): the influence of huddling. *J. Zool., Lond.* 244: 33 - 41.
- Brown, D. M. and Toft, C. A. 1999. Molecular systematics and biogeography of the cockatoos (Psittaciformes: Cacatuidae). *Auk* 116: 141 - 157.
- Brown, J. H., Marquet, P. A., and Taper, M. L. 1993. Evolution of body size: consequences of an energetic definition of fitness. *Am. Nat.* 142: 573 - 584.
- Calder, W. A. 1985. Article 'Size'. In: Campbell, B. and Lack, E. (Eds.) A dictionary of birds. Calton and Vermillion.
- Chown, S. L. and Gaston, K. J. 1997. The species-body size distribution: energy, fitness and optimality. *Funct. Ecol.* 11: 365 - 367.
- Christidis, L. and Schodde, R. 1993. Relationships and radiations in the Meliphagine honeyeaters, *Meliphaga*, *Lichenostomus* and *Xanthotis* (Aves: Meliphagidae): protein

evidence and its integration with morphology and ecogeography. *Aust. J. Zool.* 41: 293 - 316.

Christidis, L., Schodde, R., Shaw, D. D., and Maynes, S. F. 1991. Relationships among the Australo-Papuan parrots, lorikeets and cockatoos (Aves: Psittaciformes): protein evidence. *Condor* 93: 302 - 317.

Daan, S., Masman, D., and Groenewold, A. 1990. Avian basal metabolic rates: their association with body composition and energy expenditure in nature. *Am. J. Physiol.* 259: R333 - R340 -

Diamond, J. 1991. A new species of rail from the Solomon Islands and convergent evolution of insular flightlessness. *Auk* 108: 461 - 470.

Eberhard, J. R. 1998. Evolution of nest-building behaviour in *Agapornis* parrots. *Auk* 115: 455 - 464.

Ellsworth, D. L., Honeycutt, R. L., and Silvy, N. J. 1995. Phylogenetic relationships among north American grouse inferred from restriction endonuclease analysis of mitochondrial DNA. *Condor* 97: 492 - 502.

Ellsworth, D. L., Honeycutt, R. L., and Silvy, N. J. 1996. Systematics of grouse and ptarmigan determined by nucleotide sequences of the mitochondrial cytochrome-B gene. *Auk* 113: 811 - 822.

Espinosa de los Monteros, A. 1998. Phylogenetic relationships among the trogons. *Auk* 115: 937 - 954.

Espinosa de los Monteros, A. and Cracraft, J. 1997. Intergeneric relationships of the New World jays inferred from cytochrome b gene sequences. *Condor* 99: 490 - 502.

Flegg, J. J. M. 1985. Article 'Numbers'. In: Campbell, B. and Lack, E. (Eds.) A dictionary of birds. Calton and Vermillion.

- Garland, T. and Carter, P. A. 1994. Evolutionary physiology. *Ann. Rev. Physiol.* 56: 579 - 621.
- Garland, T., Dickerman, A. W., Janis, C. M., and Jones, J. A. 1993. Phylogenetic analysis of covariance by computer simulation. *Syst. Biol.* 42: 265 - 292.
- Garland, T. and Ives, A. R. 2000. Using the past to predict the present: confidence intervals for regression equations in phylogenetic comparative methods. *Am. Nat.* 155: 346 - 364.
- Gerwin, J. A. and Zink, R. M. 1998. Phylogenetic patterns in the Trochilidae. *Auk* 115: 105 - 118.
- Grant, B. R. and Grant, P. R. 1993. Evolution of Darwin's finches caused by a rare climatic event. *Proc. R. Soc. B251*: 111 - 117.
- Hinsley, S. A., Ferns, P. N., Thomas, D. H., and Pinshow, B. 1993. Black-bellied sandgrouse (*Pterocles orientalis*) and pin-tailed sandgrouse (*Pterocles alchata*): closely related species with differing bioenergetic adaptations to arid zones. *Physiol. Zool.* 66: 20 - 42.
- Johnson, K. P. and Lanyon, S. M. 1999. Molecular systematics of the grackles and allies, and the effect of additional sequence (CYT B and ND2). *Auk* 116: 759 - 768.
- Johnson, K. P. and Sorenson, M. D. 1999. Phylogeny and biogeography of dabbling ducks (genus: *Anas*): a comparison of molecular and morphological evidence. *Auk* 116: 792 - 805.
- Kozłowski, J. 1996. Energetic definition of fitness? Yes, but not that one. *Am. Nat.* 147: 1087 - 1091.
- Kozłowski, J. and Weiner, J. 1997. Interspecific allometries are by-products of body size optimization. *Am. Nat.* 149: 352 - 380.

- Lanyon, S. M. and Omland, K. E. 1999. A molecular phylogeny of the blackbirds (Icteridae): five lineages revealed by cytochrome-B sequence data. *Auk* 116: 629 - 639.
- Lasiewski, R. C. and Dawson, W. R. 1967. A re-examination of the relation between standard metabolic rate and body weight in birds. *Condor* 69: 13 - 23.
- Liknes, E. T. and Swanson, D. L. 1996. Seasonal variation in cold tolerance, basal metabolic rate, and maximal capacity for thermogenesis in white-breasted nuthatches *Sitta carolensis* and downy woodpeckers *Picoides pubescens*, two unrelated arboreal temperate residents. *J. Avian. Biol.* 27: 279 - 288.
- Livezey, B. C. 1996. A phylogenetic analysis of modern pochards (Anatidae: Aythyini). *Auk* 113: 74 - 93.
- Lovegrove, B. G. 2000. The zoogeography of mammalian basal metabolic rate. *Am. Nat.* 156: 201 - 219.
- Maddocks, T. A. and Geiser, F. 1997. Energetics, thermoregulation and nocturnal hypothermia in Australian silvereyes. *Condor* 99: 104 - 112.
- Marten, J. A. and Johnson, N. K. 1986. Genetic relationships of north American Cardueline finches. *Condor* 88: 409 - 420.
- McKechnie, A. E. and Lovegrove, B. G. 2001. Thermoregulation and the energetic significance of clustering behavior in the white-backed mousebird (*Colius colius*). *Physiol. Biochem. Zool.* 74: 238 - 249.
- McNab, B. K. 1988. Food habits and the basal rate of metabolism in birds. *Oecologia* 77: 343 - 349.
- McNab, B. K. 1994. Energy conservation and the evolution of flightlessness in birds. *Am. Nat.* 144: 628 - 642.
- McNab, B. K. and Bonaccorso, F. J. 1995. The energetics of Australasian swifts, frogmouths

and nightjars. *Physiol. Zool.* 68: 245 - 261.

Merola-Zwartjes, M. 1998. Metabolic rate, temperature regulation, and the energetic

implications of roost nests in the bananaquit (*Coereba flaveola*). *Auk* 115: 780 - 786.

Patten, M. A. and Fugate, M. 1998. Systematic relationships among the Emberizid sparrows.

Auk 115: 412 - 424.

Prinzinger, R., Göppel, R., Lorenz, A., and Kulzer, E. 1981. Body temperature and

metabolism in the red-backed mousebird (*Colius castanotus*) during fasting and torpor. *Comp. Biochem. Physiol.* 69A: 689 - 692.

Prinzinger, R. and Hänssler, I. 1980. Metabolism-weight relationship in small nonpasserine

birds. *Experimentia* 36: 1299 - 1300.

Prinzinger, R., Lübben, I., and Schuchmann, K. L. 1989. Energy metabolism and body

temperature in 13 sunbird species (Nectariniidae). *Comp. Biochem. Physiol.* 92A: 393 - 402.

Raikow, R. J. 1994. A phylogeny of the woodcreepers (Dendrocolaptinae). *Auk* 111: 104 -

114.

Randi, E., Fusco, G., Lorenzini, R., and Spina, F. 1991. Allozyme divergence and

phylogenetic relationships among the Strigiformes. *Condor* 93: 295 - 301.

Reynolds, P. S. and Lee, R. M. 1996. Phylogenetic analysis of avian energetics: passerines

and non-passerines do not differ. *Am. Nat.* 147: 735 - 759.

Schleucher, E. 1999a. Energy metabolism in an obligate frugivore, the superb fruit-dove

(*Ptilinopus superbus*). *Aust. J. Zool.* 47: 169 - 179.

Schleucher, E. 1999b. Energetics and body temperature in two convergent dove species from

extreme habitats. *Ornis Fennica* 76: 199 - 210.

Scholander, P. F., Hock, R., Walters, V., and Irving, L. 1950. Adaptation to cold in arctic and

tropical mammals and birds in relation to body temperature, insulation and basal metabolic rate. *Biol. Bull.* 99: 259 - 271.

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

Smith, G. A. 1996. Energy metabolism and amplitude of circadian metabolic cycles in bronze mannikins (*Spermestes cucullatus*). B.Sc (Hons) Project, University of Natal.

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

Van Schaik, C. P. 1986. Phenological changes in a Sumatran rain forest. *J. Trop. Ecol.* 2: 327 - 347.

Vitali, S. D., Withers, P. C., and Richardson, K. C. 1999. Standard metabolic rates of three nectarivorous meliphagid passerine birds. *Aust. J. Zool.* 47: 385 - 391.

Wasser, J. S. 1986. The relationship of energetics of falconiform birds to body mass and climate. *Condor* 88: 57 - 62.

Weathers, W. W. 1979. Climatic adaptation in avian standard metabolic rate. *Oecologia* 42: 81 - 89.

Weathers, W. W. 1997. Energetics and thermoregulation by small passerines of the humid, lowland tropics. *Auk* 114: 341 - 353.

Weathers, W. W., Koenig, W. D., and Stanback, M. T. 1990. Breeding energetics and thermal ecology of the acorn woodpecker in central coastal California. *Condor* 92: 341 - 359.

Williams, J. B. 1996. A phylogenetic perspective of evaporative water loss in birds. *Auk* 113: 457 - 472.

Williams, J. B., Withers, P. C., Bradshaw, S. D., and Nagy, K. A. 1991. Metabolism and water flux of captive and free-living Australian parrots. *Aust. J. Zool.* 39: 131 - 142.

- Wright, S. J., Carrasco, C., Calderón, O., and Paton, S. 1999. The El Niño Southern Oscillation, variable fruit production, and famine in a tropical forest. *Ecology* 80: 1632 - 1647.
- Zar, J. H. 1968. Standard metabolism comparisons between orders of birds. *Condor* 70: 278 -
- Zar, J. H. 1999. Biostatistical analysis. Prentice Hall, New Jersey.
- Zink, R. M. and Blackwell, R. C. 1998. Molecular systematics of the scaled quail complex (genus *Callipepla*). *Auk* 115: 394 - 403.
- Zink, R. M. and Blackwell, R. C. 1996. Patterns of allozyme, mitochondrial DNA, and morphometric variation in four sparrow genera. *Auk* 113: 59 - 67.
- Zink, R. M. and Dittmann, D. L. 1991. Evolution of brown towhees: mitochondrial DNA evidence. *Condor* 93: 98 - 105.
- Zink, R. M., Dittmann, D. L., and Rootes, W. L. 1991. Mitochondrial DNA variation and the phylogeny of *Zonotrichia*. *Auk* 108: 578 - 584.

Appendix 1. Basal metabolic rate (BMR), body mass (M_b), zoogeographical zone and habitat (arid/mesic) classification for all species used in analysis. The habitat classification follows Williams (1996) wherever possible. Habitat and zone codes, as well as sources of BMR and M_b data are listed below.

Species	Zone	Habitat	$\text{Log}_{10}M_b$ (g)	$\text{Log}_{10}\text{BMR}$ (ml $\text{O}_2\cdot\text{h}^{-1}$)	Source
<i>Struthio camelus</i>	Afro	A	5.000	4.053	1
<i>Dromaius novaehollandiae</i>	Aust	A	4.590	3.887	1
<i>Casurarius bennetti</i>	Aust	M	4.246	3.647	1
<i>Apteryx australis</i>	Aust	M	3.377	2.855	1
<i>Apteryx haasti</i>	Aust	M	3.405	2.871	1
<i>Apteryx owenii</i>	Aust	M	3.040	2.565	1
<i>Penelope purpurescens</i>	Neo	M	3.310	2.984	1
<i>Crax alberti</i>	Neo	M	3.447	3.068	1
<i>Crax daubentoni</i>	Neo	M	3.447	3.106	1
<i>Callipepla californica</i>	Nearc	A	2.140	2.131	1
<i>Callipepla gambelii</i>	Nearc	A	2.101	2.128	1
<i>Colinus virginianus</i>	Nearc	M	2.288	2.297	1
<i>Tetrao tetrix</i>	Pal	M	3.033	3.095	1
<i>Tetrao urogallus</i>	Pal	M	3.603	3.322	1
<i>Lagopus lagopus</i>	Pal	M	2.754	2.708	1
<i>Lagopus leucurus</i>	Nearc	M	2.513	2.623	1
<i>Bonasa umbellus</i>	Nearc	M	2.809	2.627	1
<i>Meleagris gallopavo</i>	Nearc	M	3.568	3.200	1
<i>Gallus gallus</i>	Indo	M	3.433	3.028	1
<i>Alectoris graeca</i>	Pal	M	2.801	2.653	1
<i>Alectoris chukar</i>	Pal	A	2.677	2.542	1
<i>Chauna chavaria</i>	Neo	M	3.418	3.087	1
<i>Aythya ferina</i>	Pal	M	2.912	3.014	1
<i>Aythya nyroca</i>	Pal	M	2.643	2.765	1
<i>Aythya fuligula</i>	Pal	M	2.759	2.681	1
<i>Netta rufina</i>	Pal	M	3.092	3.101	1
<i>Cygnus buccinator</i>	Nearc	M	3.948	3.556	1
<i>Anser anser</i>	Pal	M	3.512	3.285	1
<i>Aix sponsa</i>	Nearc	M	2.651	2.601	1
<i>Anas rubripes</i>	Nearc	M	2.956	2.802	1
<i>Melanerpes formicivorus</i>	Nearc	M	1.864	2.110	2

<i>Picoides pubescens</i>	Nearc	M	1.864	1.837	3
<i>Upupa epops</i>	Pal	M	1.826	1.992	1
<i>Phoeniculus purpureus</i>	Afro	M	1.870	1.493	4
<i>Trogon rufus</i>	Neo	M	1.724	1.884	1
<i>Colius striatus</i>	Afro	M	1.708	1.627	5
<i>Colius castonotus</i>	Afro	M	1.761	1.838	6
<i>Colius colius</i>	Afro	A	1.545	1.502	7
<i>Urocolius macrourus</i>	Afro	M	1.686	1.582	6
<i>Geococcyx californianus</i>	Nearc	A	2.454	2.415	1
<i>Centropus senegalensis</i>	Afro	M	2.243	2.428	1
<i>Cacatua galerita</i>	Aust	M	2.890	2.787	8
<i>Cacactua tenuirostris</i>	Aust	M	2.740	2.754	8
<i>Eolophus roseicapillus</i>	Aust	A	2.429	2.350	8
<i>Nymphicus hollandicus</i>	Aust	A	1.932	2.090	8
<i>Calyptorhynchus banksii</i>	Aust	A	2.729	2.726	8
<i>Agapornis roseicollis</i>	Afro	A	1.682	1.917	1
<i>Melopsittacus undulatus</i>	Aust	A	1.401	1.727	1
<i>Neopsephotus bourkii</i>	Aust	A	1.602	1.980	1
<i>Barnardius zonarius</i>	Aust	A	2.137	2.110	8
<i>Loriculus galgulus</i>	Indo	M	1.431	1.964	1
<i>Neophema elegans</i>	Aust	A	1.689	2.051	8
<i>Neophema pulchella</i>	Aust	M	1.602	2.014	1
<i>Neophema petrophila</i>	Aust	M	1.685	2.056	8
<i>Eulampis jugularis</i>	Neo	M	0.924	1.440	1
<i>Anthracothorax nigricollis</i>	Neo	M	0.886	1.734	1
<i>Oreotrochilus estella</i>	Neo	A	0.924	1.537	1
<i>Agleactis cupripennis</i>	Neo	M	0.857	1.651	1
<i>Patagona gigas</i>	Neo	A	1.281	1.706	1
<i>Orthorhynchus cristatus</i>	Neo	M	0.462	1.214	1
<i>Chlorostilbon mellisugus</i>	Neo	M	0.462	1.412	1
<i>Eugenes fulgens</i>	Nearc	M	0.820	1.257	1
<i>Lampornis clemenciae</i>	Nearc	A	0.898	1.257	1
<i>Acestrura mulsant</i>	Neo	M	0.519	1.139	1
<i>Strix aluco</i>	Pal	M	2.716	2.568	1
<i>Otus asio</i>	Nearc	A	2.220	2.018	1
<i>Otus trichopsis</i>	Nearc	M	2.079	1.899	1
<i>Aegolius acadicus</i>	Nearc	M	2.093	2.065	1
<i>Glaucidium gnoma</i>	Nearc	M	1.732	1.894	1
<i>Glaucidium cuculoides</i>	Indo	M	2.212	2.188	1

<i>Podargus strigoides</i>	Aust	M	2.580	2.268	9
<i>Podargus ocellatus</i>	Aust	M	2.161	2.003	1
<i>Podargus papuensis</i>	Aust	M	2.498	2.283	10
<i>Eurostopodus argus</i>	Aust	A	1.944	1.859	1
<i>Eurostopodus mysticalis</i>	Aust	M	2.210	1.935	10
<i>Phalaenoptilus nuttalli</i>	Nearc	A	1.544	1.440	1
<i>Caprimulgus macrurus</i>	Aust	M	1.836	1.745	10
<i>Zenaida macroura</i>	Nearc	A	1.961	2.062	1
<i>Columba palumbus</i>	Pal	M	2.176	2.165	1
<i>Columba uncinata</i>	Afro	M	2.502	2.484	1
<i>Streptopelia decaocto</i>	Pal	M	2.190	2.197	1
<i>Geophaps plumifera</i>	Aust	A	1.908	1.849	1
<i>Geopelia cuneata</i>	Aust	A	1.568	1.645	11
<i>Scardefella inca</i>	Nearc	A	1.607	1.651	1
<i>Ptilinopus superbus</i>	Aust	M	2.081	2.132	12
<i>Grus paradisea</i>	Afro	M	3.605	3.277	1
<i>Pterocles orientalis</i>	Pal	A	2.587	2.543	13
<i>Thinocorus rumicivorus</i>	Neo	A	1.744	1.741	1
<i>Scolopax rusticola</i>	Pal	M	2.633	2.584	1
<i>Larus atricilla</i>	Nearc	M	2.440	2.522	1
<i>Larus pacificus</i>	Aust	M	3.083	3.039	1
<i>Larus occidentalis</i>	Nearc	M	2.881	2.781	1
<i>Daptrius ater</i>	Neo	M	2.559	2.332	14
<i>Falco mexicanus</i>	Nearc	A	2.633	2.542	14
<i>Accipiter nisus</i>	Pal	M	2.130	2.227	1
<i>Accipiter striatus</i>	Nearc	A	1.919	2.098	14
<i>Accipiter cooperii</i>	Nearc	M	2.655	2.581	14
<i>Buteo buteo</i>	Pal	M	3.005	2.825	1
<i>Buteo lineatus</i>	Nearc	M	2.818	2.578	14
<i>Leptoptilos javanicus</i>	Indo	M	3.757	3.422	1
<i>Jabiru mycteria</i>	Neo	M	3.738	3.369	1
<i>Vultur gryphus</i>	Neo	M	4.014	3.480	1
<i>Pelecanus conspicillatus</i>	Aust	M	3.707	3.508	1
<i>Xiphorhynchus guttatus</i>	Neo	M	1.655	1.899	1
<i>Thamnophilus punctatus</i>	Neo	M	1.322	1.786	1
<i>Pipra mentalis</i>	Neo	M	1.090	1.754	1
<i>Manacus vitellinus</i>	Neo	M	1.190	1.616	1
<i>Sayornis phoebe</i>	Nearc	M	1.334	1.786	1
<i>Melithreptus lunatus</i>	Aust	M	1.155	1.649	15

<i>Lichenostomus virescens</i>	Aust	A	1.398	1.798	1
<i>Lichmera indistincta</i>	Aust	M	0.980	1.576	1
<i>Phylidonyris melanops</i>	Aust	M	1.274	1.720	15
<i>Chloropsis sonnerati</i>	Indo	M	1.599	1.827	1
<i>Hypothymis azurea</i>	Indo	M	1.033	1.397	1
<i>Corvus monedula</i>	Pal	M	2.286	2.473	1
<i>Corvus cryptoleucus</i>	Nearc	A	2.806	2.832	1
<i>Corvus ruficollis</i>	Pal	A	2.820	2.780	1
<i>Corvus frugilegus</i>	Pal	M	2.591	2.667	1
<i>Corvus brachyrhynchos</i>	Nearc	M	2.585	2.766	1
<i>Corvus corone</i>	Pal	M	2.714	2.770	1
<i>Corvus corax</i>	Pal	M	3.080	2.991	1
<i>Nucifraga caryocatactes</i>	Pal	M	2.167	2.379	1
<i>Perisoreus canadensis</i>	Nearc	M	1.852	2.081	1
<i>Pica nuttalli</i>	Nearc	M	2.182	2.416	1
<i>Cyanocitta cristata</i>	Nearc	M	1.907	2.170	1
<i>Cinclus mexicanus</i>	Nearc	M	1.701	1.913	1
<i>Tudus viscivorus</i>	Pal	M	2.034	2.293	1
<i>Turdus merula</i>	Pal	M	1.917	2.218	1
<i>Turdus philomelos</i>	Pal	M	1.798	2.111	1
<i>Copsychus saularis</i>	Indo	M	1.525	1.616	1
<i>Luscinia obscura</i>	Pal	M	1.127	1.491	1
<i>Phoenicurus ochrurus</i>	Pal	M	1.143	1.634	1
<i>Erithacus rubecula</i>	Pal	M	1.246	1.698	1
<i>Acridotheres cristatellus</i>	Indo	M	2.039	2.331	1
<i>Sturnus vulgaris</i>	Pal	M	1.875	2.202	1
<i>Sitta canadensis</i>	Nearc	M	1.049	1.616	1
<i>Auriparus flaviceps</i>	Nearc	A	0.833	1.466	1
<i>Parus ater</i>	Pal	M	1.033	1.625	1
<i>Parus major</i>	Pal	M	1.255	1.761	1
<i>Parus atricapillus</i>	Nearc	M	1.013	1.651	1
<i>Aegithalos caudatus</i>	Pal	M	0.949	1.548	1
<i>Psaltriparus minimus</i>	Nearc	M	0.740	1.333	1
<i>Hirundo tahitica</i>	Indo	M	1.149	1.503	1
<i>Regulus regulus</i>	Pal	M	0.740	1.515	1
<i>Alophoixus bres</i>	Indo	M	1.544	1.798	1
<i>Pycnonotus goiavier</i>	Indo	M	1.456	1.642	1
<i>Pycnonotus finlaysoni</i>	Indo	M	1.420	1.598	1
<i>Zosterops lateralis</i>	Aust	M	1.041	1.427	16

<i>Phylloscopus collybita</i>	Pal	M	0.914	1.466	1
<i>Malacopteron cinereum</i>	Indo	M	1.199	1.578	1
<i>Sylvia atricapilla</i>	Pal	M	1.340	1.869	1
<i>Lullula arborea</i>	Pal	M	1.521	1.939	1
<i>Alauda arvensis</i>	Pal	M	1.664	1.999	1
<i>Arachnothera longirostra</i>	Indo	M	1.114	1.526	1
<i>Arachnothera flavigaster</i>	Indo	M	1.560	1.727	1
<i>Aethopyga christinae</i>	Indo	M	0.716	1.376	17
<i>Aethopyga siparaja</i>	Indo	M	0.833	1.421	17
<i>Anthreptes collaris</i>	Afro	M	0.919	1.483	17
<i>Anthreptes orientalis</i>	Afro	A	1.072	1.438	17
<i>Nectarinia venusta</i>	Afro	M	0.851	1.400	17
<i>Nectarinia cuprea</i>	Afro	M	0.869	1.441	17
<i>Nectarinia veroxii</i>	Afro	M	0.924	1.377	17
<i>Nectarinia bifasciata</i>	Afro	M	0.792	1.218	17
<i>Nectarinia adelberti</i>	Afro	M	0.978	1.494	17
<i>Nectarinia amethystina</i>	Afro	M	1.000	1.494	17
<i>Nectarinia senegalensis</i>	Afro	M	1.100	1.479	17
<i>Nectarinia tacazze-</i>	Afro	M	1.130	1.643	17
<i>Nectarinia kilimensis</i>	Afro	M	1.152	1.614	17
<i>Passer domesticus</i>	Pal	M	1.407	1.774	1
<i>Prunella modularis</i>	Pal	M	1.225	1.761	1
<i>Vidua paradisaea</i>	Afro	M	1.021	1.537	1
<i>Spermestes cucullatus</i>	Afro	M	1.026	1.146	18
<i>Lonchura fuscans</i>	Indo	M	0.978	1.236	1
<i>Lonchura striata</i>	Indo	M	1.013	1.578	1
<i>Lonchura malacca</i>	Indo	M	1.072	1.397	1
<i>Lonchura maja</i>	Indo	M	1.107	1.426	1
<i>Padda oryzivora</i>	Indo	M	1.405	1.742	1
<i>Taeniopygia guttata</i>	Aust	A	1.068	1.578	1
<i>Amadina fasciata</i>	Afro	M	1.236	1.584	19
<i>Amadina erythrocephala</i>	Afro	A	1.350	1.581	20
<i>Uraeginthus bengalus</i>	Afro	A	0.908	1.382	1
<i>Estrilda troglodytes</i>	Afro	A	0.813	1.350	1
<i>Estrilda melpoda</i>	Afro	M	0.875	1.369	19
<i>Fringilla coelebs</i>	Pal	M	1.322	1.821	1
<i>Coccothraustes coccothraustes</i>	Pal	M	1.684	2.093	1
<i>Carduelis flammea</i>	Pal	M	1.146	1.706	1
<i>Carduelis spinus</i>	Pal	M	1.114	1.698	1

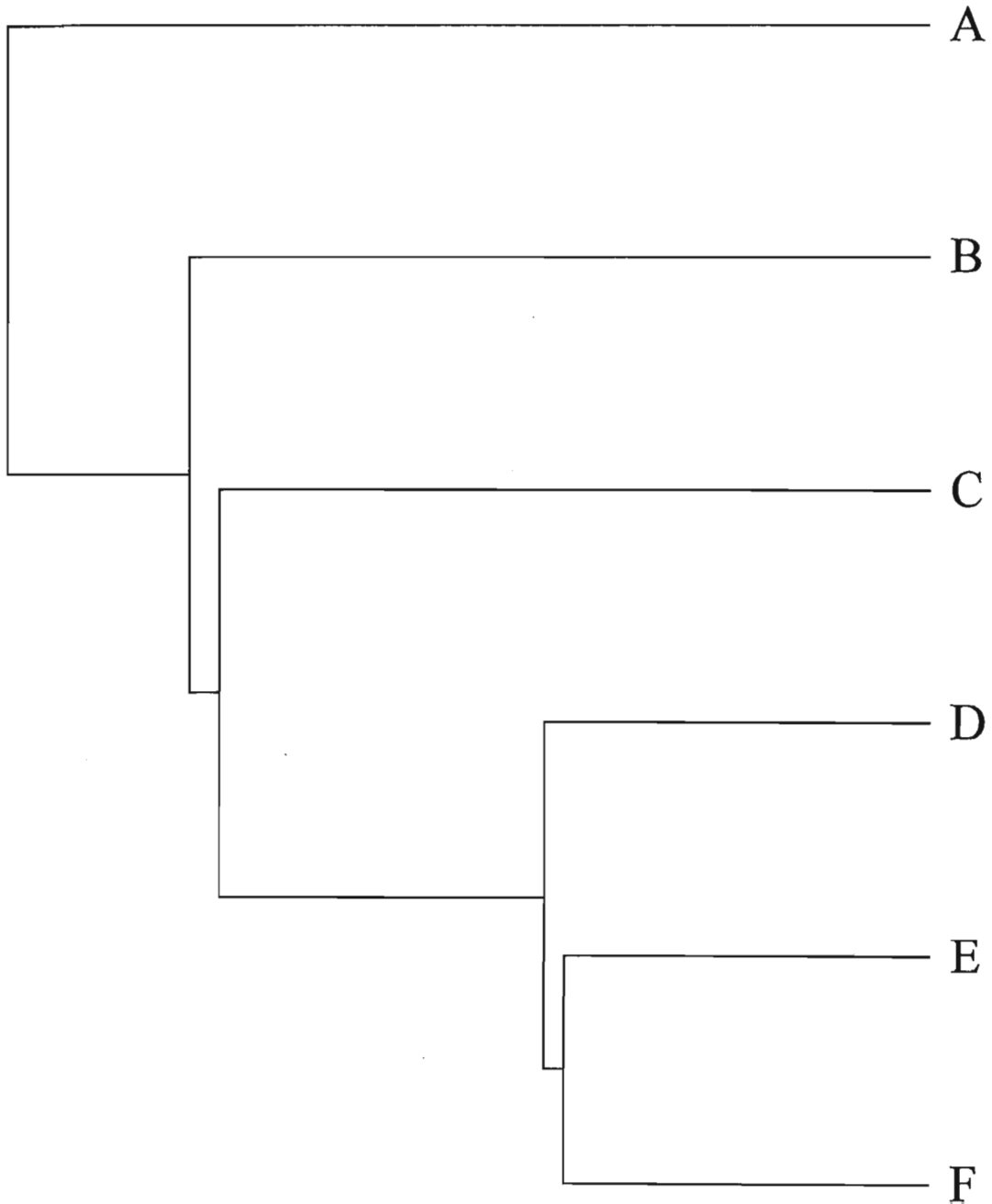
<i>Carduelis pinus</i>	Nearc	M	1.146	1.713	1
<i>Carduelis tristis</i>	Nearc	M	1.134	1.774	1
<i>Carduelis carduelis</i>	Pal	M	1.217	1.792	1
<i>Carduelis chloris</i>	Pal	M	1.450	1.926	1
<i>Loxia pytyopsittacus</i>	Pal	M	1.730	2.152	1
<i>Carpodacus mexicanus</i>	Nearc	M	1.310	1.741	1
<i>Carpodacus cassinii</i>	Nearc	M	1.438	1.780	1
<i>Passerella iliaca</i>	Nearc	M	1.487	1.821	1
<i>Melospiza melodia</i>	Nearc	M	1.281	1.651	1
<i>Melospiza georgiana</i>	Nearc	M	1.173	1.578	1
<i>Pipilo fuscus</i>	Nearc	M	1.640	2.071	1
<i>Pipilo aberti</i>	Nearc	A	1.668	2.111	1
<i>Junco hyemalis</i>	Nearc	M	1.255	1.720	1
<i>Zonotricha querula</i>	Nearc	M	1.522	1.903	1
<i>Zonotrichia leucophrys</i>	Nearc	M	1.417	1.780	1
<i>Zonotrichia albicollis</i>	Nearc	M	1.305	1.698	1
<i>Spizella passerina</i>	Nearc	M	1.076	1.537	1
<i>Spizella arborea</i>	Nearc	M	1.220	1.767	1
<i>Ammodramus savannarum</i>	Nearc	M	1.140	1.503	1
<i>Passerculus sandwichensis</i>	Nearc	M	1.201	1.598	1
<i>Pooecetes gramineus</i>	Nearc	M	1.332	1.683	1
<i>Amphispiza bilineata</i>	Nearc	A	1.064	1.548	1
<i>Emberiza schoeniclus</i>	Pal	M	1.246	1.727	1
<i>Emberiza citrinella</i>	Pal	M	1.428	1.889	1
<i>Dendroica coronata</i>	Nearc	M	1.061	1.526	1
<i>Dendroica dominica</i>	Nearc	M	0.991	1.453	1
<i>Dendroica pinus</i>	Nearc	M	1.079	1.503	1
<i>Agelaius phoeniceus</i>	Nearc	M	1.754	2.170	1
<i>Molothrus ater</i>	Nearc	M	1.628	2.045	1
<i>Cardinalis cardinalis</i>	Nearc	M	1.613	1.952	1
<i>Cardinalis sinuatus</i>	Nearc	A	1.505	1.843	1
<i>Coereba flaveola</i>	Neo	M	1.000	1.585	21

a. Sources: 1. Bennett and Harvey (1987); 2. Weathers et al. (1990); 3. Liknes and Swanson 1996; 4. Boix-Hinzen and Lovegrove (1998); 5. Chapter 2; 6. Prinzing et al. (1981); 7. McKechnie and Lovegrove (2001); 8. Williams et al. (1991); 9. Bech and Nicol (1999); 10. McNab and Bonaccorso (1995); 11. Schleucher (1999); 12. Schleucher (1999b); 13. Hinsley et al. (1993); 14. Wasser (1986); 15. Vitali et al. (1999); 16. Maddocks and Geiser (1997); 17. Prinzing et al. (1989); 18. Smith (1996); 19. Weathers (1997); 20. Chapter 5; 21. Merola-Zwartjies (1998)

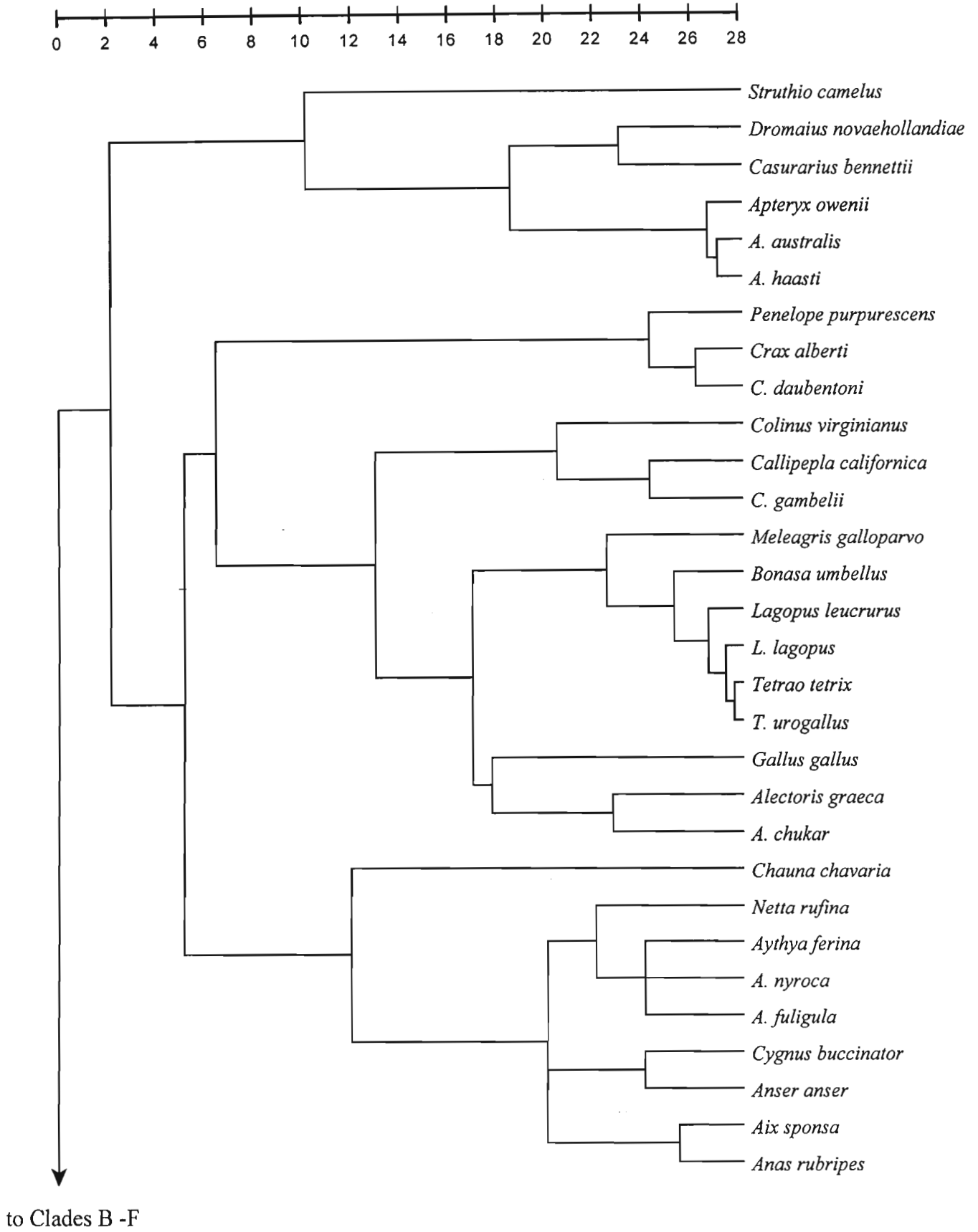
b. Habitat codes: A = arid; M = mesic

c. Zone codes: Afro = Afrotropics; Aust = Australasia; Indo = Indomalaya; Nearc = Nearctic; Neo = Neotropics; Pal = Palearctic

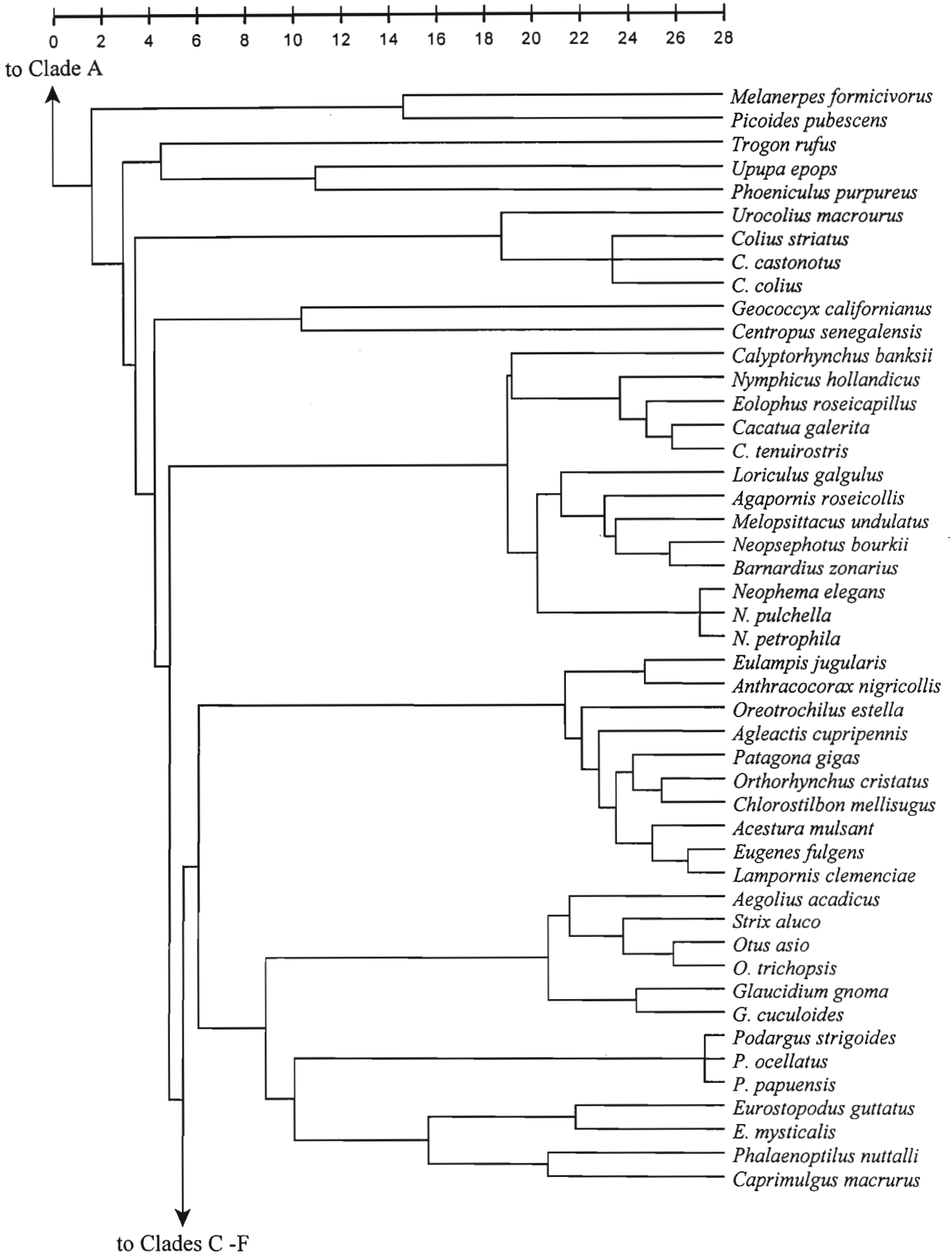
Appendix 2. Phylogeny for 219 non-migrant avian species used in analysis of basal metabolic rate, constructed using phylogenetic data from sources listed in text. Key to clade topology shown below, and detailed relationships for each clade shown in subsequent figures.



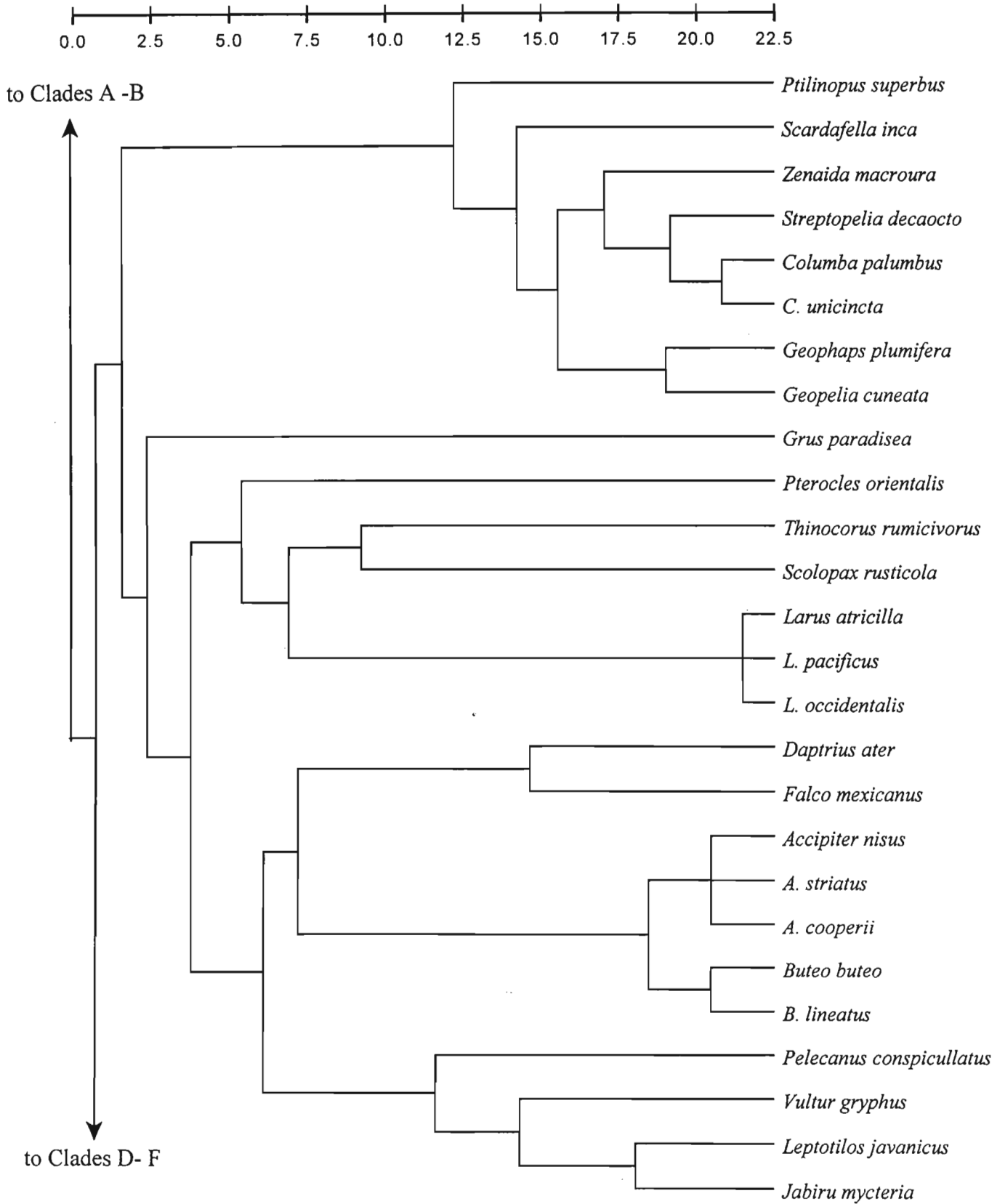
Clade A



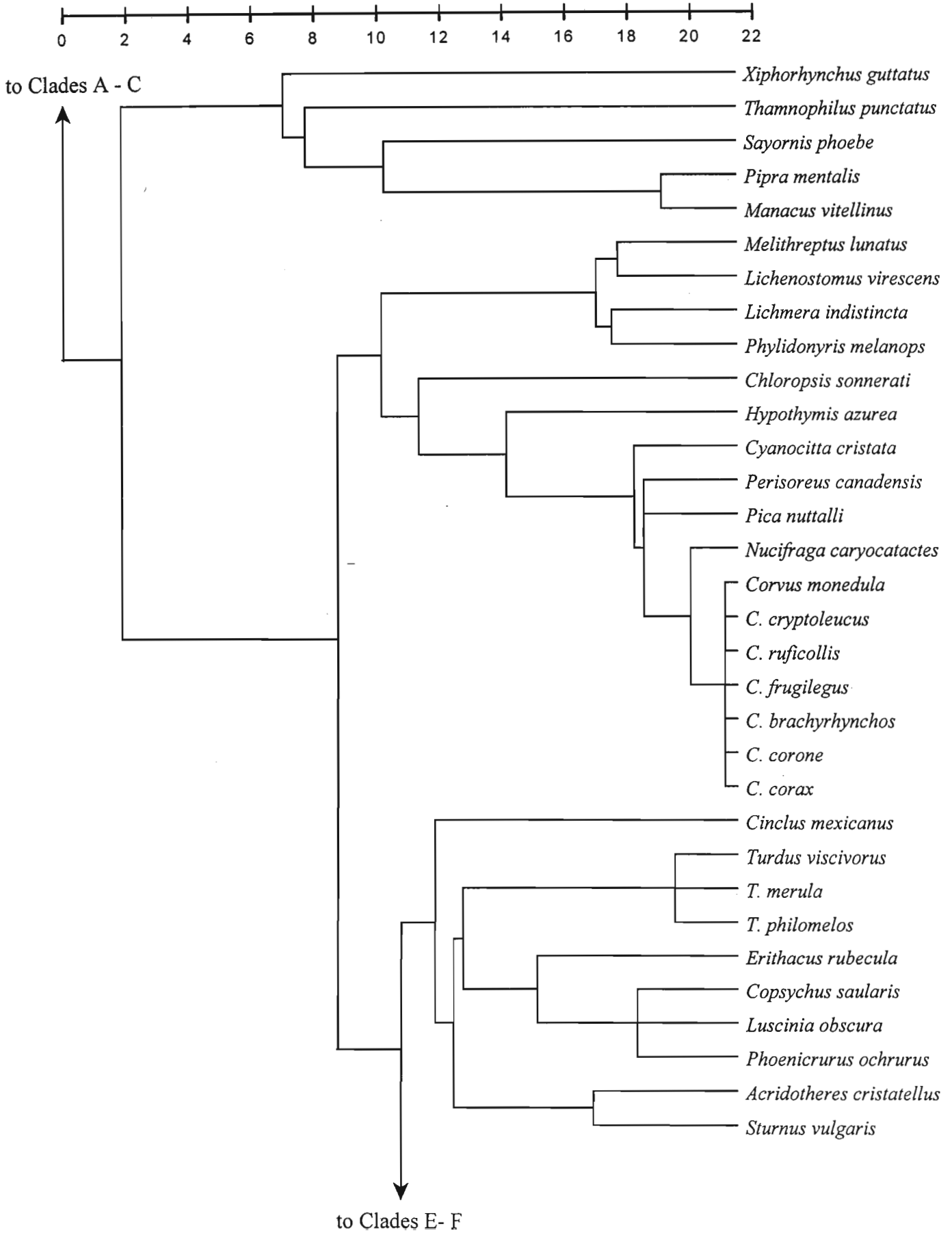
Clade B



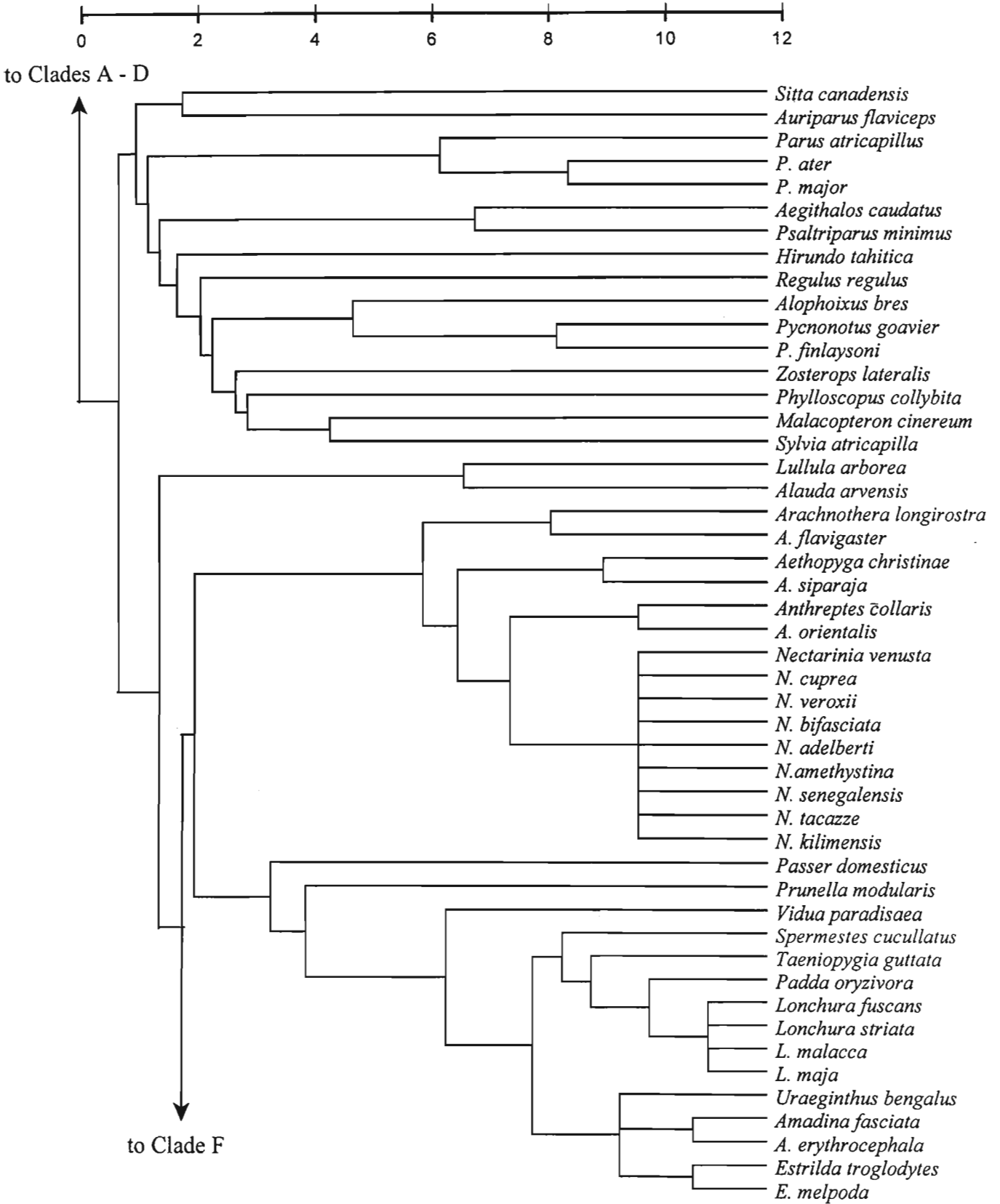
Clade C



Clade D



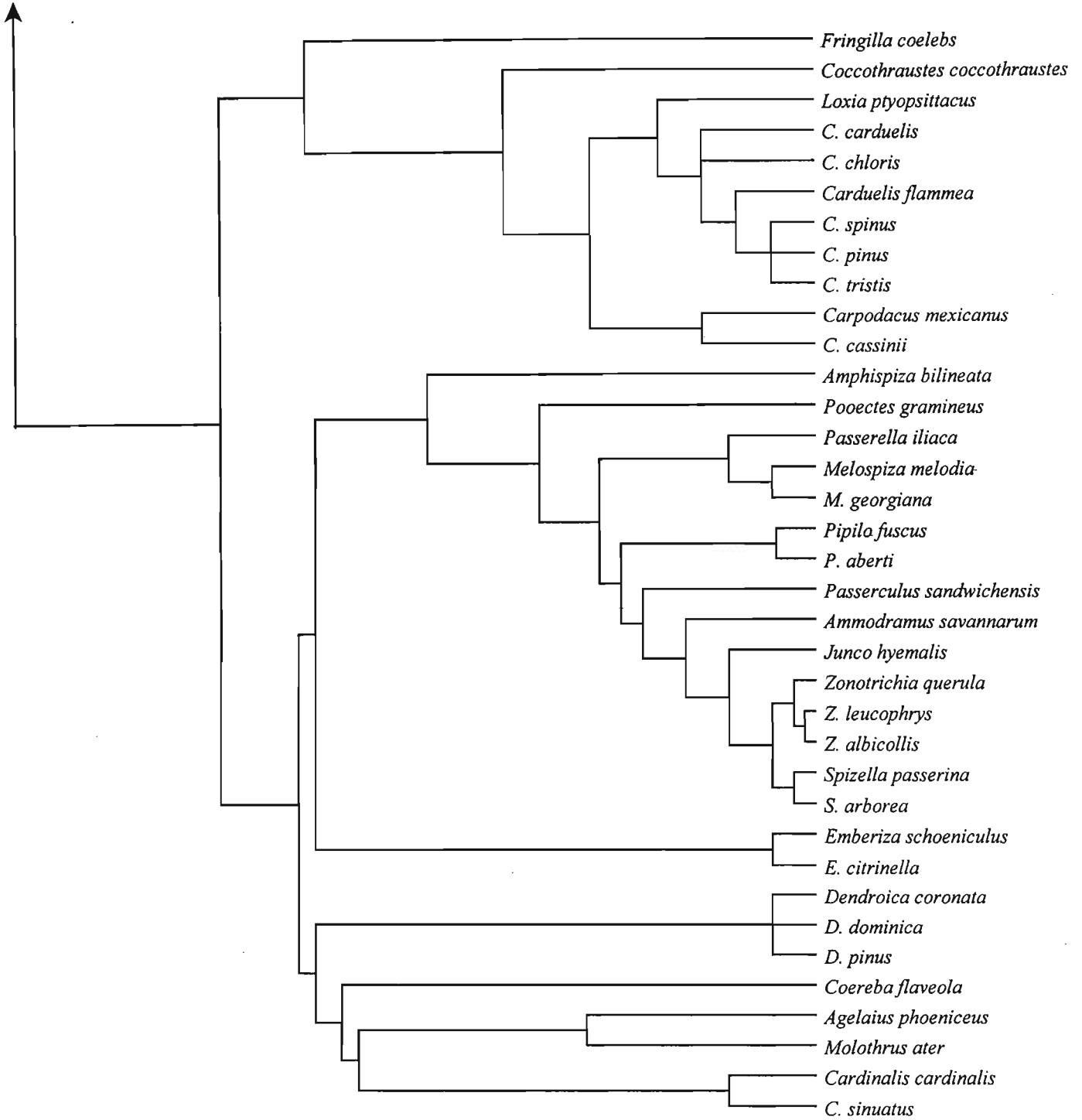
Clade E



Clade F



to Clades A - E



Chapter 7. Evolutionary and ecological determinants of avian torpor: a conceptual model.

Introduction

Avian thermoregulation is characterized by the metabolic defence of a relatively high body temperature (T_b) within a narrow circadian range (Schmidt-Nielsen 1990). However, facultative reductions in metabolic rate and T_b appear to be important in the energy balance of a number of species (Lyman et al. 1982; Reinertsen 1996). Three categories of avian facultative hypothermic responses are currently recognised. Rest-phase hypothermia (sensu Reinertsen 1996) refers to moderate reductions in metabolic rate and T_b (generally less than 10°C below normothermy) and appears to be widespread among birds. Torpor refers to a more substantial decrease in metabolic rate and T_b , characterised by a state of lethargy and reduced responsiveness to external stimuli (Bligh and Johnson 1973). Torpor is distinguished from the third category of avian hypothermia, hibernation, by being confined to a single circadian cycle (Geiser and Ruf 1995).

Whereas earlier authors considered torpor to represent a relatively rare, specialized adaptation to periods of energy stress (e.g. Bartholomew and Trost 1970; Wolf and Hainsworth 1972), recent evidence suggests it may be more common in birds than previously thought. For instance, torpor occurs routinely under natural conditions in several members of the Caprimulgidae and relatives (Brigham 1992; Brigham and Firman 1990; Körtner et al. 2000). Geiser et al. (2000) compared torpor in captive and free-ranging mammals and birds and concluded that laboratory studies underestimate the frequency, duration and depth of torpor. Moreover, torpor has recently been reported in two relatively large species. Körtner et al. (2000) observed torpor in the 500g tawny frogmouth (*Podargus strigoides*), and suggested

that avian torpor may be more wide-spread than previously suspected. In addition, Schleucher (in press) observed torpor in the 200g fruit-dove *Drepanotila holosericea* from New Caledonia. There is also evidence that torpor is not necessarily employed only during periods of energy shortage. In hummingbirds, the use of torpor is determined by a suite of proximate factors, including seasonal variation in the propensity for torpor (Carpenter 1974; Hiebert 1991), the perceived availability of food (Hiebert 1991) and temporal variation in assimilation efficiency (Hiebert 1991; McWhorter and Martinez del Rio 2000). Collectively, these observations suggest that the contribution of the capacity for torpor to avian fitness has been underestimated.

Hypothermic responses have been investigated in approximately 90 avian species, or less than 1% of extant birds. Approximately 50% of these were described as exhibiting torpor. The small size of the available data set makes it difficult to infer phylogenetic patterns or ecological determinants of avian torpor. The objective of this study was to construct a model to generate testable hypotheses concerning the occurrence of torpor in particular species. Specifically, I argue that the occurrence of avian torpor can be predicted by a) phylogeny, b) body mass (M_b) constraints, c) a trade-off between energetic benefits and potential ecological costs, and d) specific ecological factors. Where possible, I test predictions using available data.

Phylogeny

Endothermy evolved independently in mammals and birds (Ruben 1995). Moreover, it is generally believed that early birds were ectothermic, and that endothermy did not become a ubiquitous avian trait until the Cretaceous period (Dawson and Whittow 2000). Malan (1996) has argued that endothermic hibernation and torpor represent a release of an inhibition of the

primitive tendency towards wide-amplitude T_b cycling, which comprised a hypothesized intermediate step in the transition from ectothermy to endothermy. This monophyletic hypothesis has been further developed by Grigg and Beard (2000), who proposed a hypothetical stepwise transition from ectothermy to endothermy. The atypical torpor patterns shown by two species of mousebirds provide circumstantial support for this hypothesis, as they appear to represent an intermediate step in Malan's (1996) hypothesized origin of heterothermy (McKechnie and Lovegrove 2000).

However, Geiser (1998) noted that avian torpor occurs in more modern taxa containing small species which often rely on a fluctuating food supply, rather than ancient orders that typically contain large species. The occurrence of avian torpor may hence be explained by size and diet, rather than phylogeny, and the possibility of a polyphyletic origin of endotherm torpor cannot be excluded (Geiser 1998). Nevertheless, this view of torpor as a functionally advanced adaptation does not necessarily refute the monophyletic hypothesis (Geiser 1998). Furthermore, the occurrence of torpor in older avian orders such as the Galliformes, Piciformes and Upupiformes has not been investigated, and there is insufficient information available to meaningfully assess the phylogenetic distribution of avian torpor.

Malan's (1996) hypothesis of the plesiomorphic nature of heterothermy provides a starting point for a model of the evolutionary determinants of avian torpor. If this hypothesis is correct, then torpor should be more prevalent in phylogenetically older taxa, once other factors are controlled for. Although there are presently insufficient data available to test this prediction, torpor does appear to be more common in phylogenetically older taxa (Chapter 1). In particular, torpor is more common in orders such as the Coliiformes, Trochiliformes and Strigiformes than in the Passeriformes (Chapter 1). Dawson and Whittow (2000) suggested that the shallow hypothermia shown by some species may reflect a phylogenetic constraint on

tolerance of cooling, and this may well explain the absence of torpor in most passerines, even those permanently resident in Arctic and sub-Arctic regions (Chapter 1). *A priori*, the absence of torpor in these species is surprising, as they routinely face low ambient temperatures (T_a) combined with low food availability and short photoperiod.

Body size

The mass-dependent relative cost of re-warming following a hypothermic bout represents a significant constraint on a bird's capacity to use torpor. Prothero and Jürgens (1986) modelled the energy savings an endotherm derives from a torpor bout in terms of bout length and body size. These authors showed that the relationship between M_b and the time in torpor for which the total energy savings during the entry and maintenance phases are equal to the costs of re-warming during the arousal phase is given by the equation:

$$W^{1-b} = \frac{1}{\left(\frac{24s}{1-\alpha}\right)\left(\frac{1}{a}\right) - \left(\frac{1}{2C_o}\right)} \left(\frac{t_{fc}}{T_b - T_a}\right) \quad (\text{A24 in Prothero and Jürgens 1986})$$

where W = weight in kg, s = specific heat in kcal/(kg.°C), C_o = coefficient relating cooling rate during the entry phase to W , t_{fc} = time spent fully cooled i.e duration of maintenance phase (h), $\alpha = 10/[(T_b - T_a).Q_{10}]$, and a and b are the intercept and coefficient respectively of the equation relating resting metabolic rate (RMR) to M_b i.e $\text{RMR} = aW^b$. This equation can then used to calculate the critical M_b (W_c) i.e. the M_b at which the energetic savings during the entry and maintenance phases are equal by setting the right-hand side of equation A24 to Q , such that:

$$W_c^{1-b} = Q \quad (\text{A22 in Prothero and Jürgens 1986})$$

or

$$W_c = 10^{(\log Q)/1-b} \quad (\text{A23 in Prothero and Jürgens 1986})$$

These authors assumed that during torpor $T_b = T_a$. However, Q_{10} values, rather than temperature gradients ($T_b - T_a$), were used to calculate reductions in metabolic rate. The assumption is hence not critical, and the model still operates if T_b is maintained above T_a during torpor. A second assumption was that the decrease in T_b during the entry phase occurred linearly. Although this is not the case, the authors showed, using empirical data for a hummingbird, that the model is nonetheless adequate. Although Prothero and Jürgens (1986) used this model to calculate critical M_b s for varying bout lengths, the model can also be used to calculate critical M_b s for various torpor T_b s for a specific bout length. I assumed $s = 0.932$ kcal/(kg. °C) (specific heat of tissues; Withers 1992), $C_o = -0.583$ (scaling exponent for thermal conductance of non-passerine birds; Aschoff 1981), $Q_{10} = 2.5$, and normothermic $T_b = 38.5^\circ\text{C}$ (mean avian rest-phase T_b ; Prinzinger et al. 1991). For a and b , I used values from a conventional least-squares linear regression of field metabolic rate (FMR) on M_b for 81 bird species (Tieleman and Williams 2000). It should be noted that Prothero and Jürgens's (1986) model requires resting metabolic rate (RMR) to estimate the metabolic costs of remaining normothermic. However, RMR varies substantially depending on T_a , and FMR is probably a more realistic estimate than basal metabolic rate (BMR) of the energy required to remain normothermic under natural conditions. I then used Prothero and Jürgens' (1986) model to calculate critical M_b s for a range of T_b s during torpor (Figure 1).

The duration of avian torpor bouts is typically between 8 and 12 hours (Geiser and Ruf 1995). Hence, I used Prothero and Jürgens' (1986) model to predict critical M_b s for torpor

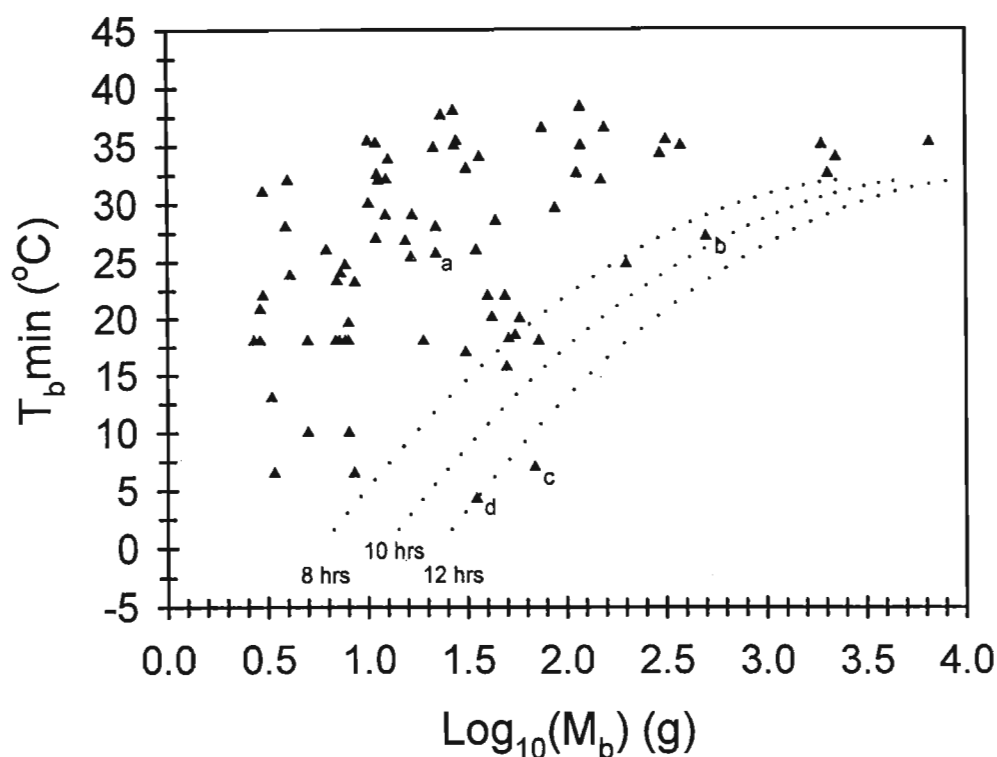


Figure 1. Relationship between minimum body temperature during avian facultative hypothermia ($T_{b,min}$) and \log_{10} body mass (M_b) for 77 species. The dotted lines indicate the minimum T_b at which a facultative hypothermic response will result in a net energy saving, and were calculated using Prothero and Jürgens' (1986) energetic model for daily torpor. Data for (a) *Delichon urbica* (Prinzinger and Siedle 1988), (b) *Podargus strigoides* (Körtner et al. 2000), (c) *Caprimulgus europaeus* (Peiponen 1966) and (d) *Phalaenoptilus nuttallii* (Brigham 1992) are indicated by lower case letters. Although *P. nuttallii* is a hibernator, datum (d) was recorded during a bout of 8-10 hrs (R.M. Brigham pers. comm.), and may hence be considered to be a minimum torpor T_b .

bouts lasting 8 hours and 12 hours respectively. The model predicts that torpor $T_b = 30^\circ\text{C}$ should occur in species with $M_b < 630\text{g}$ (bout length = 8 hours) and $M_b < 2800\text{g}$ (bout length = 12 hours). Torpor $T_b = 20^\circ\text{C}$ should occur in species smaller than 70g (bout length = 8 hours) and 250g (bout length = 12 hours). Finally, torpor $T_b = 10^\circ\text{C}$ should occur in species smaller than 18g (bout length = 8 hours) and 66g (bout length = 12 hours).

A comparison of the plots generated by Prothero and Jürgens' (1986) model with the

observed relationship between avian M_b and minimum hypothermic T_b in 77 species (Figure 1) suggests that the lower boundary of this relationship is determined by M_b -dependent constraints on rewarming. Moreover, the model can be used to predict critical T_b s for avian heterotherms of various body masses. The only data that lie outside the theoretical boundaries plotted in Figure 1 are those for *Phalaenoptilus nuttallii* and *Caprimulgus europaeus*. In *C. europaeus*, a minimum T_b of ca. 7°C was recorded during a bout lasting approximately 16 hours (Fig 6 in Peiponen 1966). In *P. nuttallii*, a minimum T_b of 4.3°C occurred during a bout of 8-10 hours (R.M. Brigham pers. comm.). The latter datum is the only minimum torpor T_b not accounted for by Prothero and Jürgens' (1986) model.

Figure 1 also reveals that a large component of variation in observed torpor T_b cannot be attributed to body size alone. Much of this variation may reflect phylogenetic variation in the capacity for torpor. Also, torpor T_b may be determined by the prevailing T_a . Body temperature during torpor in four hummingbird species was correlated with minimum environmental T_a , rather than with M_b (Wolf and Hainsworth 1972), leading these authors to suggest that minimum torpor T_b may show adaptive variance correlated with the prevailing T_a .

Prothero and Jürgens' (1986) model allows observed minimum torpor T_b to be compared with the critical value expected on the basis of M_b and bout length. By predicting critical T_b , and thus the maximum extent of T_b depression that will result in a net energy saving, the model provides an objective basis for incorporating M_b -related constraints into a description of the extent of hypothermic responses in a particular species. For instance, a minimum T_b of 27°C in a 500g tawny frogmouth *Podargus strigoides* (Körtner et al. 2000) is close to the critical T_b for a species of this size (datum "b" in Figure 1). In contrast, a minimum T_b of 25.7°C in a 22g House martin *Delichon urbica* (Prinzinger and Siedle 1988) is considerably higher than the critical T_b (datum "a" in Figure 1). This comparison suggests

that when the constraints of M_b are taken into account, torpor is more pronounced in *P. strigoides* than in *D. urbica*. The extent of T_b depression as a percentage of the predicted maximum may be useful when comparing the extent to which facultative hypothermia has evolved as an energy-saving mechanism in closely related species.

Trade-off between energetic benefits and ecological costs

Species which possess the capacity for torpor by virtue of their phylogenetic position and M_b are likely to use torpor only if it confers direct fitness benefits. Presumably, the use of torpor is adaptive when the energetic benefits exceed the potential ecological costs. An understanding of the factors that determine these costs and benefits will hence facilitate the identification of species likely to use torpor. A comparison of the relative costs and benefits of torpor is similar to the approach taken by Pravosudov and Lucas (2000), who proposed a mathematical model for the use of nocturnal hypothermia by small food-caching species overwintering in temperate regions. Pravosudov and Lucas' (2000) model was based on trade-offs between risk of starvation, risk of diurnal predation, risk of nocturnal predation, hypothermia and energy reserves. The model predicted that a) the use of hypothermia is favoured by low energy reserves, low T_a and high variability in foraging success, and b) the risk of nocturnal predation is an important determinant of the use of hypothermia (Pravosudov and Lucas 2000).

The major energetic benefit of torpor is a reduction in rest-phase energy expenditure (Reinertsen 1996). The relative benefits of torpor are hence likely to be correlated with other energetic traits that determine a bird's energy requirements. Moreover, adaptive variance in such traits may be useful in identifying species in which the energetic benefits of torpor are relatively high. One such energetic trait which exhibits adaptive variance is basal metabolic

rate (BMR). Gradients of resource predictability comprise a major source of selection pressure underlying the slow-fast BMR continuum in both mammals (Lovegrove 2000) and birds (Chapter 6). Birds inhabiting habitats characterized by erratic rainfall and primary production typically possess lower BMRs than species living in more predictable environments (Tieleman and Williams 2000; Chapter 6).

The adaptive variance in avian BMR implies that species near the lower end of the metabolic continuum (i.e. those with low relative BMR) have experienced strong selection for reduced energy requirements. Hence, the capacity for reductions in energy requirements by means of torpor is likely to be similarly adaptive for these species. Data for mammalian heterotherms supports this hypothesized association between low BMR and torpor. Lovegrove (1996) found that in Afrotropical and Australasian mammals, the BMR of species which employ hibernation or daily torpor was significantly lower than those that do not, and argued that this co-incidence of low BMR and torpor reflects strong selection for energy conservation. An association between avian torpor and low BMR has previously been noted by McNab (1988), who argued that the use of torpor is a consequence of small M_b and low metabolic rate.

In contrast, species at the upper end of the metabolic continuum possess high relative BMRs and elevated energy requirements. In these species, the capacity for torpor is likely to be adaptive when the ability to meet metabolic requirements is limited by intake rates. For instance, McWhorter and Martinez del Rio (2000) found that intake rates of broad-tailed hummingbirds (*Selasphorus platycerus*) were limited by their digestive physiology. Hummingbirds acclimated to $T_a = 22^\circ\text{C}$ did not respond to a proximate increase in energy requirements, namely a rapid decrease in T_a , by increasing energy intake (McWhorter and Martinez del Rio 2000). An analysis of intestinal sucrose hydrolysis rates suggested that this

lack of response was due to a physiological limitation. Moreover, the frequency of torpor appeared to increase following the decrease in T_a (McWhorter and Martinez del Rio 2000).

The observations suggest that the energetic benefits of torpor are greatest at the extremes of the avian metabolic continuum. On the other hand, the potential ecological costs of torpor are presumed to be determined primarily by the increased risk of predation (Reinertsen 1996). Hence, the potential ecological costs are independent of relative metabolic rate, and are constant across the metabolic continuum. A model of the relative energetic benefits and potential ecological costs of torpor (Figure 2), predicts that torpor should be more prevalent at the extremes of the metabolic continuum. In these species, the likelihood that the energetic benefits of torpor exceed the potential ecological costs is highest (Figure 2). The model also predicts that this effect should be more pronounced in species for which the potential ecological costs of torpor are high. For instance, if we assume that the small size of hummingbirds makes them difficult to detect by nocturnal predators, the model predicts that hummingbird species across the entire metabolic continuum should exhibit torpor. In contrast, larger, more conspicuous species probably exhibit torpor only if their metabolic rates lie near the outer limits of the metabolic continuum.

To test the prediction that torpor should be more prevalent at the extremes of the avian metabolic continuum, I obtained measures of BMR for ca. 420 avian species from the literature. I calculated a conventional least-squares linear regression of $\log_{10}\text{BMR}$ on $\log_{10}M_b$ ($\log_{10}\text{BMR} = 0.667 \cdot \log_{10}M_b + 0.838$) and then calculated a $\log_{10}\text{BMR}$ residual for each species. The residuals were approximately normally distributed (Figure 3a) and ranged from -0.591 in the red-billed woodhoopoe *Phoeniculus purpureus* to +0.441 in the white-necked jacobin *Florisuga mellivora*. Of these species, 35 are known to exhibit torpor (Appendix 1; for the purposes of this analysis, I follow Reinertsen (1996) and assume that $T_b < 30^\circ\text{C}$ is

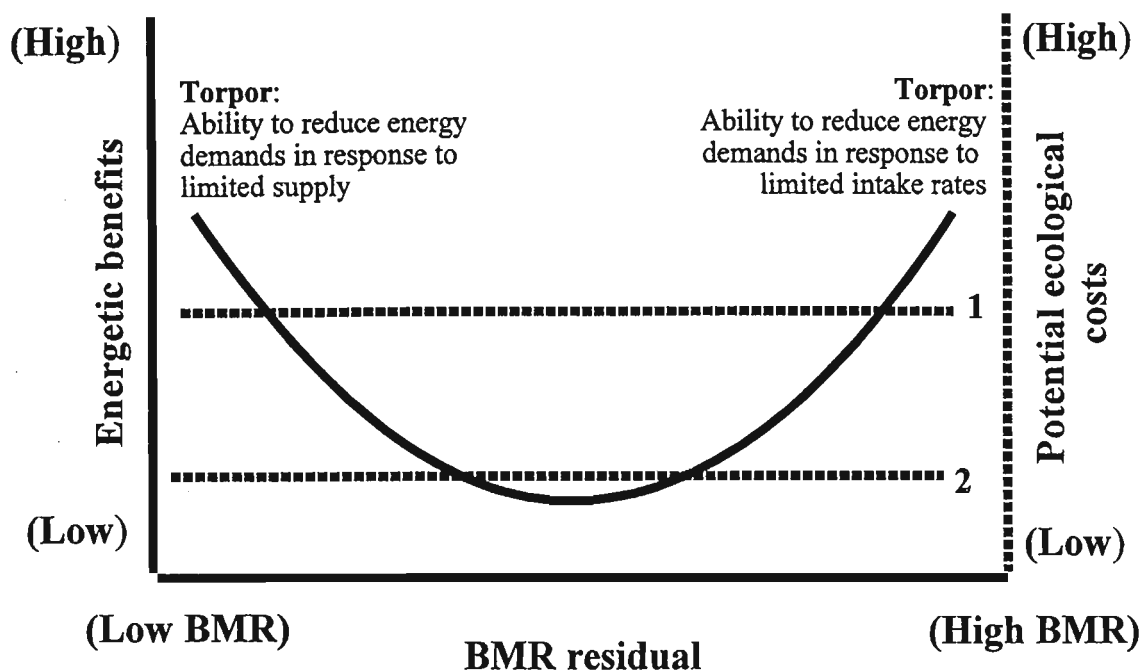


Figure 2. A simple model of the relative energetic benefits and potential ecological costs of avian torpor. The energetic benefits of torpor (solid line) are greatest at the extremes of the metabolic continuum. In contrast, the potential costs of torpor (dotted lines) are determined by ecological factors such as relative conspicuousness while at the roost, and are hence independent of relative BMR. Dotted line 1 indicates a taxon in which the potential ecological costs of torpor are high (e.g. large, non-cryptic species easily located by predators). Dotted line 2 indicates a taxon in which the potential ecological costs of torpor are low (e.g. small, cryptic species). The capacity for torpor should be adaptive when the energetic benefits are greater than the potential ecological costs i.e. when the solid line is above the dotted line. Note that for taxa with low potential costs of torpor (dotted line 2), torpor is adaptive over a greater proportion of the metabolic continuum than for species with relatively high ecological costs (dotted line 1).

indicative of torpor). The frequency distribution of the \log_{10} BMR residuals of these 35 species (Figure 3b) differed significantly ($\chi^2 = 68.934$; $df = 24$; $P \ll 0.05$) from the expected null distribution. A frequency distribution of the proportion of species known to exhibit torpor (Figure 3c) suggests that torpor is indeed more prevalent in species near the extremes of the avian metabolic continuum. In addition, the association between torpor and low relative BMR appears to be stronger in larger species. An examination of Appendix 1 reveals that with the exception of *Apus apus*, all species with a $M_b > 30g$ known to use torpor have relatively large

negative \log_{10} BMR residuals (< -0.170). Hence, whereas torpor in small species occurs over the entire BMR continuum, torpor in larger species is restricted to species with relatively low BMR.

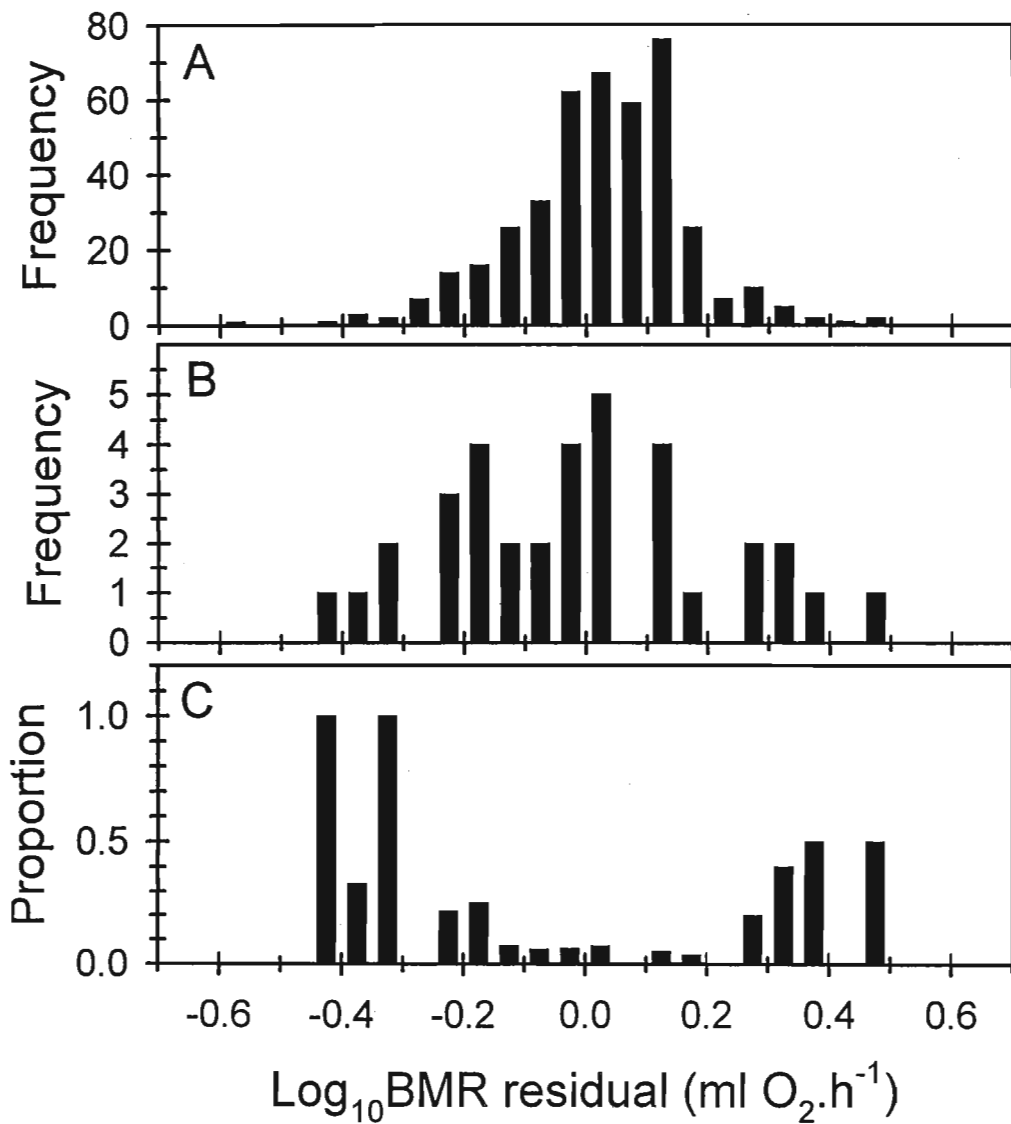


Figure 3. Frequency distributions of (A) \log_{10} BMR residuals of ca. 420 avian species, (B) \log_{10} BMR residuals of 35 avian species in which torpor has been reported, and (C) proportion of species known to use torpor.

This analysis provides, at best, circumstantial support for the predictions of the above model. Although it suggests that torpor is more prevalent in species with relatively low and high BMRs respectively, it does not necessarily show a correlation between the occurrence of torpor and adaptive variance in avian BMR. Statistical procedures exist whereby phylogenetically-independent prediction limits can be generated based on a particular species' phylogenetic position (Garland and Ives 2000). However, it is not, to the best of my knowledge, currently possible to calculate a phylogenetically-independent residual which takes a particular species' phylogenetic position into account. Nevertheless, the observation that torpor is more prevalent in species at the extremes of the metabolic continuum does suggest that an understanding of selection pressures underlying variance in energetic parameters such as BMR may be useful in identifying species likely to exhibit torpor.

Ecological factors

I have argued that generalised factors, namely phylogeny, body size, and energetic traits such as BMR, can be used to generate hypotheses concerning the occurrence of avian torpor. However, both the relative energetic benefits a bird derives and the potential ecological costs it incurs by using torpor are determined by a suite of ecological factors. Any attempt to predict the occurrence of torpor in a particular species needs to take into account specific aspects of its ecology and behaviour. Ecological correlates of torpor have been discussed elsewhere (Reinertsen 1996). Here, I discuss specific examples and attempt to identify ecological factors determining the relative costs and benefits of torpor.

Schleucher (1994; in press) investigated hypothermic responses in two small (< 40g) doves, *Geopelia cuneata* and *Oena capensis*, and the relatively large (200g) fruit-dove *Drepanoptila holosericea*. Both *G. cuneata* and *O. capensis* exhibited shallow hypothermia in

response to food deprivation, with minimum T_b s of 35.3°C and 34.4°C respectively (Schleucher 1994; in press). However, *D. holosericea* exhibited torpor (minimum T_b = 24.8°C) during ad libitum feeding at T_a s between 12°C and 27°C (Schleucher in press). *A priori*, the two small, xeric, granivores might seem more likely candidates for torpor than a larger, rainforest frugivore. However, *O. capensis* and *G. cuneata* are continental species, occurring in the African and Australian arid zones respectively (Baptista et al. 1997). They are both nomadic species (Baptista et al. 1997), and are presumably able to avoid areas of low food availability. Moreover, both these species have several potential nocturnal mammalian predators (Kingdon 1997; Strahan 2001). In contrast, *D. holosericea* is a non-migratory species restricted to the island of New Caledonia (Baptista et al. 1997). In the Australasian zoogeographical region, the El Niño Southern Oscillation (ENSO) causes unpredictable, severe droughts (Philander 1983; Stone et al. 1996). A frugivorous species such as *D. holosericea* is likely to experience large fluctuations in fruit availability associated with ENSO events (Van Schaik 1986; Ashton et al. 1988; Wright et al. 1999). Moreover, selection for reduced energy expenditure is likely to be stronger in island species than their mainland counterparts (Lovegrove 2000). Importantly, there are no mammalian predators on New Caledonia, and *D. holosericea* presumably experiences virtually zero risk of nocturnal predation (Nowak and Paradiso 1983).

An important ecological determinant of torpor may be the degree to which the roost site is exposed to fluctuations in T_a . For instance, Calder's (1994) and Calder and Booser's (1973) findings that the use of torpor by broad-tailed hummingbirds *Selasphorus platycercus* is dependent on energy intake are in contrast to Carpenter's (1974) observation that the use of torpor in the Andean hillstar *Oreotrochilus estella* was apparently independent of food availability, particularly during winter. The birds in the former studies appeared to roost in

tree canopies (Calder 1994), whereas *O. estella* roosts in caves at high altitudes in the Andes (Carpenter 1974). The latter site is more favourable for the use of torpor, since birds roosting in a cave are presumably buffered from rapid fluctuations in external T_a , as well as from other factors which could rapidly alter avenues of heat loss, such as rain and wind. Whereas the use of torpor in *O. estella* appears to be determined largely by a seasonal cycle, torpor in *S. platycerus* appears to represent a proximate response to short-term fluctuations in energy balance. This difference may well result from species-specific roost site characteristics.

The mousebirds (Coliiformes) are one of the best-known groups of avian heterotherms (Prinzinger et al. 1991; Reinertsen 1996). However, mousebirds exhibit well-developed communal roosting (clustering) in the wild, and I have argued (Chapters 2-4) that published descriptions of torpor in mousebirds frequently represent proximate responses to artificial conditions. Under natural conditions, mousebirds probably use torpor rarely, for example if separated from a flock (Chapters 2-4). These observations suggest that whereas the capacity for torpor may occur in communally roosting species, communal roosting obviates the need to use torpor under most conditions. Mousebirds, and possibly other communally roosting species in which the capacity for torpor occurs, represent an exception to the observation that laboratory studies tend to underestimate the frequency, duration and depth of torpor under natural conditions (Geiser et al. 2000).

One of the most striking disparities in the phylogenetic distribution of avian torpor occurs in the order Strigiformes. Whereas torpor has been reported in the Caprimulgidae, Eurostopodidae, Aegothelidae, and Podargidae, it is unknown in the owls (Tytonidae and Strigidae) (Chapter 1). Moreover, an apparent absence of hypothermic responses was observed in Tengmalm's owls *Aegolius funereus* exposed to low T_a and restricted feeding (Hohtola et al. 1994). The use of torpor by the nightjars and their relatives is presumably

facilitated by their cryptic plumage. In addition, the vertebrate prey populations of many owl species show a lower degree of temporal and spatial fluctuation than the insect prey of nightjars and relatives (R.M. Brigham, pers. comm.). However, torpor may well occur in some small, insectivorous owls. For instance, 75% of the genus *Otus* prey predominantly on insects, and several of these species are highly cryptic (Marks et al. 1991).

Literature cited

- Aschoff, J. 1981. Thermal conductance in mammals and birds: its dependence on body size and circadian phase. *Comp. Biochem. Physiol.* 69A: 611 - 619.
- Ashton, P. S., Givnish, T. J., and Appanah, S. 1988. Staggered flowering in the Dipterocarpaceae: new insights into floral induction and the evolution of mast fruiting in the aseasonal tropics. *Am. Nat.* 132: 44 - 66.
- Baptista, L. F., Trail, P. W., and Horblit, H. M. 1997. Family Columbidae (pigeons and doves). In: del Hoyo, J., Elliot, A., and Sargatal, J. (Eds.) Handbook of the birds of the world. Vol. 4. Sandgrouse to cuckoos. Lynx Edicions, Barcelona.
- Bartholomew, G. A. and Trost, C. H. 1970. Temperature regulation in the speckled mousebird, *Colius striatus*. *Condor* 72: 141 - 146.
- Bartholomew, G. A., Vleck, C. M., and Bucher, T. L. 1983. Energy metabolism and nocturnal hypothermia in two tropical passerine frugivores, *Manacus vitellinus* and *Pipra mentalis*. *Physiol. Zool.* 56: 370 - 379.
- Bech, C. and Nicol, S. C. 1999. Thermoregulation and ventilation in the tawny frogmouth, *Podargus strigoides*: a low-metabolic avian species. *Aust. J. Zool.* 47: 143 - 153.
- Bennett, P. M. and Harvey, P. H. 1987. Active and resting metabolism in birds: allometry, phylogeny and ecology. *J. Zool., Lond.* 213: 327 - 363.
- Bligh, J. and Johnson, K. G. 1973. Glossary of terms for thermal physiology. *J. Appl. Physiol.* 35: 941 - 961.

- Brigham, R. M. 1992. Daily torpor in a free-ranging goatsucker, the common poorwill (*Phalaenoptilus nuttallii*). *Physiol. Zool.* 65: 457 - 472.
- Brigham, R. M. and Firman, M. C. 1990. Activity periods and use of torpor by two goatsuckers, the poorwill, *Phalaenoptilus nuttallii*, and the common nighthawk, *Chordeiles minor*. *Bat Research News* Winter 1990: 72 - 73.
- Calder, W. A. 1994. When do hummingbirds use torpor in nature? *Physiol. Zool.* 67: 1051 - 1076.
- Calder, W. A. and Booser, J. 1973. Hypothermia of broad-tailed hummingbirds during incubation in nature with ecological correlations. *Science* 180: 751 - 753.
- Carpenter, F. L. 1974. Torpor in an Andean hummingbird: its ecological significance. *Science* 183: 545 - 547.
- Cheke, R. A. 1971. Temperature rhythms in African montane sunbirds. *Ibis* 113: 500 - 506.
- Dawson, W. R. and Fisher, C. D. 1969. Responses to temperature by the spotted nightjar (*Eurostopodus guttatus*). *Condor* 71: 49 - 53.
- Dawson, W. R. and Whittow, G. C. 2000. Regulation of body temperature. In: Sturkie, P. D. (Ed.) *Avian Physiology*. Academic Press, New York.
- Garland, T. and Ives, A. R. 2000. Using the past to predict the present: confidence intervals for regression equations in phylogenetic comparative methods. *Am. Nat.* 155: 346 - 364.
- Geiser, F. 1998. Evolution of daily torpor and hibernation in birds and mammals: importance

of body size. *Clin. Exp. Pharmacol. Physiol.* 25: 736 - 740.

Geiser, F., Holloway, J. C., Körtner, G., Maddocks, T. A., Turbill, C., and Brigham, R. M.

2000. Do patterns of torpor differ between free-ranging and captive mammals and birds? In: Heldmaier, G. and Klingenspor, M. (Eds.) *Life in the cold: 11th International Hibernation Symposium*. Springer, Berlin.

Geiser, F. and Ruf, T. 1995. Hibernation versus daily torpor in mammals and birds:

physiological variables and classification of torpor patterns. *Physiol. Zool.* 68: 935 - 966.

Grigg, G. and Beard, L. 2000. Hibernation by echidnas in mild climates: hints about the

evolution of endothermy. In: Heldmaier, G. and Klingenspor, M. (Eds.) *Life in the cold: 11th International Hibernation Symposium*. Springer, Berlin.

Hainsworth, F. R. and Wolf, L. L. 1970. Regulation of oxygen consumption and body

temperature during torpor in a hummingbird, *Eulampis jugularis*. *Science* 168: 368 - 369.

Hiebert, S. M. 1991. Seasonal differences in the response of rufous hummingbirds to food

restriction: body mass and the use of torpor. *Condor* 93: 526 - 537.

Hoffmann, R. and Prinzinger, R. 1984. Torpor und Nahrungsausnutzung bei 4

Mausvogelarten (Coliiformes). *J. Ornithol.* 125: 225 - 237.

Hohtola, E., Pyörmilä, A., and Rintamäki, H. 1994. Fasting endurance and cold resistance

without hypothermia in a small predatory bird: the metabolic strategy of Tengmalm's owl, *Aegolius funereus*. *J. Comp. Physiol.* 164: 130 - 437.

- Kingdon, J. 1997. The Kingdon field guide to African mammals. Academic Press, San Diego.
- Koskimies, J. 1948. On temperature regulation and metabolism in the swift, *Micropus a. apus* L. during fasting. *Experimentia* 4: 274 - 276.
- Körtner, G., Brigham, R. M., and Geiser, F. 2000. Winter torpor in a large bird. *Nature* 407: 318.
- Krüger, K., Prinzinger, R., and Schuchmann, K. L. 1982. Torpor and metabolism in hummingbirds. *Comp. Biochem. Physiol.* 73A: 679 - 689.
- Lasiewski, R. C. 1963. Oxygen consumption of torpid, resting, and flying hummingbirds. *Physiol. Zool.* 36: 122 - 140.
- Lasiewski, R. C. and Dawson, W. R. 1964. Physiological responses to temperature in the common nighthawk. *Condor* 66: 477 - 490.
- Leon, B. and Nicolson, S. W. 1997. Metabolic rate and body temperature of an African sunbird, *Nectarinia chalybea*: daily rhythm and the effect of ambient temperature. *S. Afr. J. Zool.* 32: 31 - 36.
- Lovegrove, B. G. 1996. The low basal metabolic rates of marsupials: the influence of torpor and zoogeography. In: Geiser, F., Hulbert, A. J., and Nicol, S. C. (Eds.) Adaptations to the cold: Tenth International Hibernation Symposium. University of New England Press, Armidale.
- Lovegrove, B. G. 2000. The zoogeography of mammalian basal metabolic rate. *Am. Nat.* 156: 201 - 219.

- Lyman, C. P., Willis, J. S., Malan, A., and Wang, L. C. H. 1982. Hibernation and torpor in mammals and birds. Academic Press, New York.
- MacMillen, R. E. and Trost, C. H. 1967. Nocturnal hypothermia in the inca dove *Scardafella inca*. *Comp. Biochem. Physiol.* 23: 243 - 253.
- Malan, A. 1996. The origins of hibernation: a reappraisal. In: Geiser, F., Hulbert, A. J., and Nicol, S. C. (Eds.) Adaptations to the cold: Tenth International Hibernation Symposium. University of New England Press, Armidale.
- Marks, J. S., Cannings, R. J., and Mikkola, H. 1991. Family Strigidae (typical owls). In: del Hoyo, J., Elliot, A., and Sargatal, J. (Eds.) Handbook of the birds of the world. Vol. 5. Barn-owls to hummingbirds. Lynx Edicions, Barcelona.
- McKechnie, A. E. and Lovegrove, B. G. 2000. Heterothermy in mousebirds: evidence of avian proto-torpor? In: Heldmaier, G. and Klingenspor, M. (Eds.) Life in the cold: 11th International Hibernation Symposium. Springer, Berlin.
- McKechnie, A. E. and Lovegrove, B. G. 2001. Thermoregulation and the energetic significance of clustering behavior in the white-backed mousebird (*Colius colius*). *Physiol. Biochem. Zool.* 74: 238 - 249.
- McNab, B. K. 1988. Body mass, food habits, and the use of torpor in birds. In: Bech, C. and Reinertsen, R. E. (Eds.) Physiology of cold adaptation in birds. Plenum Press, New York.
- McWhorter, T. J. and Martinez del Rio, C. 2000. Does gut function limit hummingbird food intake? *Physiol. Biochem. Zool.* 73: 313 - 324.

- Merola-Zwartjes, M. and Ligon, J. D. 2000. Ecological energetics of the Puerto Rican tody: heterothermy, torpor and intra-island variation. *Ecology* 81: 990 - 1002.
- Nowak, R. M. and Paradiso, J. L. 1983. Walker's mammals of the world. John Hopkins University Press, Baltimore.
- Peiponen, V. A. 1966. The diurnal heterothermy of the nightjar (*Caprimulgus europaeus* L.). *Ann. Acad. Sci. Fennicae (A IV)* 101: 1 - 35.
- Philander, S. G. H. 1983. El Niño Southern Oscillation phenomena. *Nature* 302: 295 - 301.
- Pravosudov, V. V. and Lucas, J. R. 2000. The costs of being cool: a dynamic model of nocturnal hypothermia by small food-caching birds in winter. *J. Avian. Biol.* 31: 463 - 472.
- Prinzinger, R., Göppel, R., Lorenz, A., and Kulzer, E. 1981. Body temperature and metabolism in the red-backed mousebird (*Colius castanotus*) during fasting and torpor. *Comp. Biochem. Physiol.* 69A: 689 - 692.
- Prinzinger, R., Preßmar, A., and Schleucher, E. 1991. Body temperature in birds. *Comp. Biochem. Physiol.* 99A: 499 - 506.
- Prinzinger, R. and Siedle, K. 1988. Ontogeny of metabolism, thermoregulation and torpor in the house martin *Delichon u. urbica* (L.) and its ecological significance. *Oecologia* 76: 307 - 312.
- Prothero, J. and Jürgens, K. D. 1986. An energetic model of daily torpor in endotherms. *J. Theor. Biol.* 121: 403 - 415.
- Reinertsen, R. E. 1985. Hypothermia in northern passerine birds. In: Heller, H. C., Musacchia, X. J., and Wang, L. C. H. (Eds.) *Living in the cold: physiological and biochemical adaptations*. Elsevier, New York.
- Reinertsen, R. E. 1996. Physiological and ecological aspects of hypothermia. In: Carey, C.

(Ed.) Avian energetics and nutritional ecology. Chapman & Hall, New York.

Ruben, J. 1995. The evolution of endothermy in mammals and birds: from physiology to fossils. *Ann. Rev. Physiol.* 57: 69 - 95.

Schaub, R., Prinzinger, R., and Schleucher, E. 1999. Energy metabolism and body temperature in the Blue-naped mousebird (*Urocolius macrourus*) during torpor. *Ornis Fennica* 76: 211 - 219.

Schleucher, E. 1994. Untersuchungen zur Ökophysiologie von Taubenarten aus extremen Biotopen am Beispiel des australischen Diamanttäubchens *Geopelia cuneata* und des afrikanischen Kaptäubchens *Oena capensis*. Ph.D. Thesis, University of Frankfurt.

Schleucher, E. (in press). Heterothermia in pigeons and doves reduces energetic costs. *J. Therm. Biol.*

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

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

Strahan, R. 1991. Complete book of Australian mammals. Cornstalk, Sydney.

Tieleman, B. I. and Williams, J. B. 2000. The adjustment of avian metabolic rates and water fluxes to desert environments. *Physiol. Biochem. Zool.* 73: 461 - 479.

Van Schaik, C. P. 1986. Phenological changes in a Sumatran rain forest. *J. Trop. Ecol.* 2: 327 - 347.

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

Wolf, L. L. and Hainsworth, F. R. 1972. Environmental influence on regulated body temperature in torpid hummingbirds. *Comp. Biochem. Physiol.* 41A: 167 - 173.

Wright, S. J., Carrasco, C., Calderón, O., and Paton, S. 1999. The El Niño Southern Oscillation, variable fruit production, and famine in a tropical forest. *Ecology* 80: 1632 - 1647.

Appendix 1. Avian species known to depress body temperature (T_b) to below 30°C during facultative hypothermic responses and for which measures of basal metabolic rate (BMR) are available.

Species	M_b (g)	$T_{b,hypo}$ (°C)	BMR (ml O ₂ ·h ⁻¹)	log ₁₀ BMR residual (ml O ₂ ·h ⁻¹)	Source
Coraciiformes					
<i>Todus mexicanus</i>	6.2	26	20.1	-0.063	1
Coliiformes					
<i>Colius colius</i> ^a	35.1	26	31.8	-0.368	2
<i>Colius striatus</i>	51	18.2	42.4	-0.349	3
<i>Colius castanotus</i>	58	20	69.3	-0.172	4,5
<i>Urocolius macrourus</i>	49	22	38.6	-0.378	6,5
Apodiformes					
<i>Apus apus</i>	42	20.1	72.5	-0.060	7,8
Trochiliformes					
<i>Agleactis cupripennis</i>	7.2	18	44.8	+0.242	9
<i>Anthracocorax nigricollis</i>	7.7	18	54.2	+0.306	9
<i>Calypte anna</i>	3.4	8.8	13.1	-0.075	10
<i>Chlorostilbon mellisugus</i>	2.9	18	25.8	+0.267	9
<i>Chrysuronia oenone</i>	5	18	43.0	+0.330	9
<i>Eugenes fulgens</i>	8	10	21.9	-0.099	11
<i>Eulampis jugularis</i>	8	18	26.2	-0.021	12
<i>Florisuga mellivora</i>	6.9	18	68.8	+0.441	9
<i>Lampornis clemenciae</i>	8	19.6	18.3	+0.177	9
<i>Ocreatus underwoodii</i>	2.7	18	26.7	+0.301	9

<i>Oreotrochilus estella</i>	8.5	6.5	34.8	+0.085	13,9
<i>Orthorhynchus cristatus</i>	2.9	20.8	17.4	+0.096	9
<i>Patagona gigas</i>	19	18	50.6	+0.014	9
<i>Selasphorus rufus</i>	3.3	13	11.1	-0.140	10
<i>Selasphorus sasin</i>	3	22	11.4	-0.099	9
<i>Urosticte benjamini</i>	3.9	28	23.2	+0.135	9
Strigiformes					
<i>Phalaenoptilus nuttallii</i>	35	4.3	27.6	-0.427	14,8
<i>Chordeiles minor</i>	72.5	18	78.9	-0.181	15
<i>Eurostopodus argus^b</i>	88	29.6	73.04	-0.272	16
<i>Podargus strigoides</i>	500	27.2	243.8	-0.250	17,18
Columbiformes					
<i>Scardafella inca</i>	44	28.5	48.7	-0.246	19
<i>Drepanoptila holosericea</i>	200	24.8	144.4	-0.212	20
Passeriformes					
<i>Pipra mentalis</i>	12.3	29	34.9	-0.021	21
<i>Manacus vitellinus</i>	15.5	26.8	24.7	-0.011	21
<i>Delichon urbica</i>	22	25.7	67.4	+0.096	22
<i>Parus major</i>	16.8	29	53.7	+0.076	23
<i>Nectarinia chalybea</i>	7	23.3	22.6	-0.047	24,25
<i>Nectarinia tacazze</i>	11	27	35.8	+0.023	26,8
<i>Nectarinia famosa</i>	16.5	25.4	28.0	-0.202	27

a. McKechnie and Lovegrove (2001) considered the low T_b s exhibited by single *Colius colius* when not clustering with conspecifics at low T_a to represent normothermic T_b cycles, rather than facultative T_b depression.

b. Formerly *Eurostopodus guttatus*

Sources (where two sources are listed, T_h hypo was obtained from the first source, and BMR from the second source): 1. Merola-Zwartjes and Ligon (2000); 2. McKechnie and Lovegrove (2001); 3. Chapter 2; 4. Prinzing et al. (1981); 5. Hoffmann and Prinzing (1984); 6. Schaub et al. (1999); 7. Koskimies (1948); 8. Bennett and Harvey (1987); 9. Krüger et al. (1982); 10. Lasiewski (1963); 11. Wolf and Hainsworth (1972); 12. Hainsworth and Wolf (1970); 13. Carpenter (1974); 14. Brigham (1992); 15. Lasiewski and Dawson (1964); 16. Dawson and Fisher (1969); 17. Körtner et al. (2000); 18. Bech and Nicol (1999); 19. MacMillen and Trost (1967); 20. Schleucher (in press); 21. Bartholomew et al. (1983); 22. Prinzing and Siedle (1988); 23. Reinertsen (1985); 24. J.R.B. Lighton and B. Leon (unpublished data); 25. Leon and Nicolson (1997); 26. Cheke (1971); 27. C.T. Downs and M. Brown (unpublished data)

Conclusions

The distinction between rest-phase hypothermia and torpor

The question of whether rest-phase hypothermia and torpor can be distinguished on the basis of T_b is important, since the identification of various physiological states is a prerequisite for understanding the ecological significance of avian facultative hypothermia. The continuous frequency distributions of avian minimum hypothermic T_b (Chapter 1), and ρT_b in speckled mousebirds *Colius striatus* (Chapter 2) suggest that normothermia, rest-phase hypothermia and torpor are not necessarily distinguishable on the basis of T_b . Moreover, there is evidence that the ranges of T_b associated with different physiological states may overlap, further questioning the notion of specific T_b limits for different categories of avian hypothermic responses.

The question, thus, of whether rest-phase hypothermia and torpor represent discrete physiological states or components of a hypothermic response continuum, remains unresolved. If rest-phase hypothermia and daily torpor do indeed represent totally different physiological states, and possibly different levels of responsiveness to external stimuli, the distinction between these responses is an important consideration in studies of thermoregulation in free-ranging birds. Data from Puerto Rican todies (*Todus mexicanus*) (Merola-Zwartjes and Ligon 2000) suggest that torpor and rest-phase hypothermia may indeed represent totally different physiological states. To understand the ecological significance of various avian hypothermic states, experiments need to investigate the relationship between metabolic suppression, T_b suppression, and the ability to respond to external stimuli.

The interaction between facultative hypothermia and communal roosting

The mousebirds (Coliiformes) exhibit a pronounced capacity for heterothermy as well as well-developed social thermoregulation and offer insights into the interaction between these two mechanisms of reducing energy expenditure. My data indicate that clustering behaviour moderates the use of heterothermic responses and suggest that, under natural conditions, the use of torpor by clustering mousebirds is probably rare. The mousebirds appear to represent an exception to the observation made by Geiser et al. (2000) that laboratory studies tend to underestimate the depth, frequency and duration of heterothermy. The fact that mousebirds are one of the best known groups of avian heterotherms appears to stem from the fact that thermoregulation has often been investigated in single birds under laboratory conditions.

The patterns of normothermic and hypothermic thermoregulation exhibited by *C. striatus* (Chapter 2,3) and *C. colius* (McKechnie and Lovegrove 2001; Chapter 4) also offer insights into the evolution of heterothermy. Whereas the physiological mechanisms required for the transition from a low T_b to a high T_b are evident in both species, the mechanisms required for metabolic down-regulation i.e. a transition from a high T_b to a low T_b , are apparently absent. The ability to rapidly increase T_b by means of endogenous heat production would presumably constitute the first step in Malan's (1996) proposed transition from reptilian circadian heterothermy to the homeostatic pattern of high T_b characteristic of endotherms. Such a thermogenic capacity would logically be a prerequisite for the development of mechanisms for the metabolic down-regulation associated with entry into typical endothermic torpor. Hence, I suggest that the patterns shown by *C. striatus* and *C. colius* may be indicative of "proto-torpor", an intermediate stage between Malan's (1996) proposed primitive, wide-amplitude T_b cycling, and modern patterns of torpor.

Why should *C. striatus* and *C. colius* exhibit characteristics intermediate between

hypothesized plesiomorphic thermoregulation and modern patterns of heterothermy? The answer may involve the obligatory nature of clustering behaviour in thermoregulation in these species. Aviary data for *C. striatus* and laboratory (McKechnie and Lovegrove 2001) and field data for *C. colius* clearly indicate the importance of clustering behaviour in the maintenance of a constant rest-phase setpoint T_b , and in the case of *C. colius*, for the avoidance of pathological hypothermia at low T_a s. If we assume that clustering behaviour represents a plesiomorphic trait that developed early in the mousebird lineage, and that Malan's (1996) hypothesis is correct, then it is manifest that the development of typical endothermic torpor was arrested in the phylogenetically ancient Coliiformes by the development of sociality and clustering behaviour. The energy savings associated with clustering probably reduced the selective pressures acting on the development of other mechanisms for reducing energy expenditure, such as torpor. The patterns of thermoregulation I observed in *C. striatus* and those reported for *C. colius* may hence represent a "snapshot" in the evolution of avian torpor.

Evolutionary and ecological determinants of avian facultative hypothermia

Phylogeny is an important determinant of the capacity for facultative hypothermia. Whereas hypothermia occurs throughout the avian phylogeny, the extent of T_b depression appears to be dependent on phylogenetic position. For instance a depression of $T_b > 20^\circ\text{C}$ is restricted to a few families. There are currently too few data to attempt an analysis of the evolution of avian hypothermia. In particular, data on hypothermic responses are absent for older Neoaves. The available data suggest that the capacity for pronounced hypothermia increases with the relative age of a taxon. Passerines possess a limited capacity for facultative hypothermia and with few exceptions, depress $T_b < 10^\circ\text{C}$.

Once phylogeny is considered, body mass (M_b) constrains the maximum extent of T_b

depression during a hypothermic response. The calculation of a predicted minimum hypothermic T_b provides an objective basis for incorporating M_b -related constraints into the description of the extent of hypothermic responses in a particular species.

Phylogenetic position and M_b are important evolutionary determinants of torpor. However, selection acting on the capacity for torpor is likely to be determined by the relative energetic benefits and potential ecological costs. The relative energetic benefits of torpor are presumably high in species which experience strong selection for reduced energy requirements. At a global scale, selection for reduced energy requirements is correlated with climatic predictability. Species inhabiting relatively unpredictable zoogeographical zones exhibit lower basal metabolism rate (BMR) than species in relatively predictable, seasonal zones, presumably reflecting selection associated with unpredictable periods of energy shortage. The adaptive variance in avian BMR means that the avian metabolic continuum is useful in identifying species in which the capacity for torpor is likely to be under strong selection.

At an ecological scale, the use of torpor is determined by a variety of factors, such as vulnerability to predation, relative mobility, temporal fluctuations in food availability, endocrine determinants, and roosting behaviour.

Literature cited

- Geiser, F., Holloway, J. C., Körtner, G., Maddocks, T. A., Turbill, C., and Brigham, R. M. 2000. Do patterns of torpor differ between free-ranging and captive mammals and birds? In: Heldmaier, G. and Klingenspor, M. (Eds.) Life in the cold: 11th International Hibernation Symposium. Springer, Berlin.
- McKechnie, A. E. and Lovegrove, B. G. 2001. Thermoregulation and the energetic significance of clustering behavior in the white-backed mousebird (*Colius colius*). *Physiol. Biochem. Zool.* 74: 238 - 249.
- Merola-Zwartjes, M. and Ligon, J. D. 2000. Ecological energetics of the Puerto Rican tody: heterothermy, torpor and intra-island variation. *Ecology* 81: 990 - 1002.