THERMAL AND METABOLIC STRATEGIES OF TWO MARSUPIALS, *Sminthopsis macroura* AND *Cercartetus nanus*: A PHYSIOLOGICAL COMPARISON BETWEEN DAILY TORPOR AND HIBERNATION

By **Xiaowei Song**

(B. Sci. Biol. TNU; M. Sci. Zool. Academia Sinica)

A THESIS SUBMITTED FOR THE DEGREE OF DOCTOR OF PHILOSOPHY

OF THE UNIVERSITY OF NEW ENGLAND

May 1997

Declaration

I certify that the substance of this thesis has not already been submitted for any degree and is not currently being submitted for any other degree or qualification.

I certify that any help received in preparing this thesis, and all sources used, have been acknowledged in this thesis.

Xiaowei Song

Dedication

This thesis is dedicated to the memory of my dad, Song Kai (May 1924 - May 1995).

Acknowledgments

First of all, I would like to sincerely thank my supervisor, Dr. Fritz Geiser, for his constant enthusiasm, encouragement, and effort, and for his support, advice, and help in all aspects of this research project, especially in preparation of this thesis.

I would like to sincerely thank John de Bavay, Gerhard Körtner, Bronwyn McAllan, and Jo Holloway for their valuable comments and help with revising various drafts of this manuscript, Bronwyn McAllan for proof reading the whole thesis.

I would like to thank Gerhard Körtner for his untiring assistance with numerous and many kinds of problems, in particular, with the equipment and computer programs. I would like to thank Stuart Cairns for his invaluable advice and assistance with statistics.

I thank Barry Lovegrove and Thomas Ruf for providing some of the computer software, Lynn Selwood for supplying some of the experimental animals, and Keith Cornish for constructing a part of the equipment. Jo Holloway, Tracy Maddocks, Frank Falkenstein, Sandy Hamdorf looked after my animals on several occasions, this is much appreciated. I thank Mark Brigham, David Woodland, Paul Whitington, Gordon White, Steve Trémont and many others for discussing aspects of my thesis. All members of the academic, technical, secretarial and administration staff of the Zoology Department are thanked for their assistance and help. Thanks go also to Jo, Tracy, Frank, Wendy, Chris, Dionne, Darren and all other friends of mine for companionship, friendship, and help with my everyday English language.

I thank my family for consistent understanding, encouragement, and support over years of my education, especially over the years of my PhD.

Last but not least, I would like to thank my cute little furry friends for making my days more enjoyable and for providing all the data for the sake of this project.

This project was financially supported by a John Crawford PhD scholarship from Australian government.

Table of Contents

List of Figures

List of Tables

List of Abbreviations

AD_aMR	: Average arousal energy cost
AD_tMR	: Average torpor energy cost
ATBDMR	: Average torpor bout energy cost
ANOVA	: Analysis of variance
BAT	: Brown adipose tissue
BM	: Body mass
BMR	: Basal metabolic rate
C	: Apparent thermal conductance
°C	: Degrees Celsius
cm	: centimetres
D_a	: Arousal duration
D_t	: Torpor duration
D_t'	: Torpor duration threshold
g	: grams
h	: hours
$He\text{-}O_2$	: Helium-oxygen
L	: Litres
L : D	: Light phase : dark phase
Maximum MR	: Maximum metabolic rate during a physiological state
$mL\ g^{-1}\ h^{-1}$	: Millilitres per gram hour
$mL\ min^{-1}$	: Millilitres per minute
min	: minute
mm	: Millimetres
MR	: Metabolic rate
n	: Number of observations
N	: Number of individuals

PIR : Passive infrared detector

POH : Preoptic and hypothalamic

Q_{10} : Temperature quotient

r^2 : Coefficient of determination

RMR : Resting metabolic rate

RQ : Respiratory quotient

SD : Standard deviation

ΔT : Differential between body temperature and air temperature

T_a : Air temperature

T_b : Body temperature

T_{bl} : Lowest body temperature during a torpor bout

T_{bmax} : Daily body temperature maximum

T_{bmean} : Daily mean body temperature

T_{bmin} : Minimum body temperature during torpor

T_{lc} : Lower critical temperature

T_{uc} : Upper critical temperature

T_{tc} : Critical air temperature during torpor

T_{set} : Set-point of body temperature

TBD : Torpor bout duration

TMR : Metabolic rate during torpor

TMR_{min} : Minimum metabolic rate during torpor

TNZ : Thermoneutral zone

UMR : Undershoot of metabolic rate

V : Volts

$\dot{V}o_2$: Rate of oxygen consumption

$\dot{V}o_{2max}$: Maximum rate of oxygen consumption

W : Watts

Z : Correction factor for washout of the respiratory equipment

Abstract

Many small mammals employ hibernation or daily torpor to reduce energy expenditure by lowing metabolic rate and body temperature. Although it is known that the reduction of metabolic rate is more pronounced during hibernation than during daily torpor, it is unclear whether different physiological processes contribute to metabolic rate reduction during the two patterns of torpor. In addition, differences in relation to behaviour and energy expenditure between hibernation and daily torpor are not well understood.

To determine physiological differences between hibernation and daily torpor, a detailed investigation was conducted by using two similar-sized small marsupials, *Cercartetus nanus*, a hibernator, and *Sminthopsis macroura*, a daily heterotherm. Thermophysiological variables, including metabolic rate, body temperature, thermal differential between body temperature and ambient temperature, and conductance of the two species were measured under the same experimental conditions. Interrelations between these variables during both normothermia and torpor were analysed over a wide temperature range. Torpor entry, steady-state torpor, and arousal were distinguished in the analyses. In addition, temperature selection and locomotor activity in relation to the use of torpor were investigated. Energy expenditure in response to duration of torpor and arousal was also compared.

During steady-state torpor in both *S. macroura* and *C. nanus*, two physiological processes are responsible for the changes of metabolic rate at ambient temperatures below and above a critical temperature. Below the critical temperature, torpid animals defended body temperature at or above a set-point by proportional thermoregulation. In contrast, above the critical temperature, torpid animals allowed body temperature and metabolic rate to decline. Thus, metabolic rate in this temperature range was a function of body temperature, and not the thermal differential between the animal and its environment. During daily torpor in *S. macroura*, the reduction of metabolic rate appears to be well explained by temperature effects. However, during hibernation in

C. nanus, metabolic inhibition also appears to contribute to metabolic rate reduction. This metabolic inhibition during hibernation was clearly evident because metabolic rate of *C. nanus* decreased by about 50% during torpor within the thermoneutral zone. The greater extent of the initial drop of metabolic rate observed during entry into hibernation than that observed during daily torpor entry provides further evidence for the involvement of metabolic inhibition in *C. nanus*. This is the first *in vivo* experiment that clearly demonstrates largely temperature-independent metabolic inhibition in endotherms. Due to the substantial reduction of metabolic rate during torpor, energy expenditure was reduced from normothermic levels by up to 98% in *C. nanus*, and up to 70% in *S. macroura*. The overall energy expenditure during hibernation was low at low temperatures above the critical temperature. In contrast, daily torpor was cheaper at higher temperatures, because torpor bouts were relatively short and thus arousal costs, which increased at low temperatures, were relatively high. Therefore, selection of high temperature as observed in *S. macroura* results in low energy expenditure. Nevertheless, *C. nanus* also preferred high temperatures for torpor despite a relatively high energy expenditure. It appears that they select a high temperature so they have sufficient time for foraging, and that they employ short bouts of torpor opportunistically. Torpor bout length was related to metabolic rate during both hibernation and daily torpor. However, since arousal occurred at a particular time of day, bout length also appears to be influenced by a circadian rhythm. During arousal, *S. macroura* employed its maximum thermogenic capacity. In contrast, *C. nanus*, which possessed a higher thermogenic capacity and exhibited higher rewarming rates than *S. macroura*, did not use its full thermogenic capacity during arousal. A short arousal process was frequently associated with a low energy cost and appears to be energetically more favourable. The thermal and metabolic characteristics of *C. nanus* and *S. macroura* indicate that different physiological adjustments are involved in hibernation and daily torpor to achieve energy conservation.

Plate 1 *Sminthopsis macroura* (Dasyuridae: Marsupialia)

Plate 2 *Cercartetus nanus* (Burramyidae: Marsupialia)