

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

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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.

A handwritten signature in blue ink, appearing to read 'X Song', with a horizontal line underneath.

Xiaowei Song

Dedication

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

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Table of Contents

Declaration	i
Dedication	ii
Acknowledgments	iii
Table of Contents	iv
List of Figures	viii
List of Tables.....	x
List of Abbreviations.....	xi
Abstract	xiii
Plate 1 <i>Sminthopsis macroura</i>	xv
Plate 2 <i>Cercartetus nanus</i>	xvi
Chapter 1 General Introduction and Aims of the Thesis.....	1
1.1 Homeothermy in Mammals	1
1.1.1 Homeothermy: Advantages, Achievement, and Adaptations	1
1.1.2 Homeothermy: Disadvantage and Challenges for Small Mammals.....	5
1.2 Hibernation and Daily Torpor in Mammals	6
1.2.1 Heterothermy: A Thermoregulatory Adaptation.....	6
1.2.2 Evolution of Mammalian Torpor.....	8
1.2.3 Relationships between Hibernation and Daily Torpor	9
1.2.4 Thermoregulation and Torpor of Marsupials	13
1.3 Aims of the Thesis.....	16
1.3.1 Significance and General Aims	16
1.3.2 Specific Aims	17
Chapter 2 General Materials and Methods.....	19
2.1 Experimental Animals	19
2.1.1 <i>Sminthopsis macroura</i>	19
2.1.2 <i>Cercartetus nanus</i>	22
2.2 Simultaneous Record of MR, T_b , and T_a	25
2.2.1 MR	25
2.2.2 T_b	28
2.2.3 T_a	29
2.3 Simultaneous Record of T_b and Activity in a Temperature Gradient	29
2.3.1 Set-up of the Temperature Gradient	29
2.3.2 T_b and Activity Measurements.....	31
2.4 Definition and Calculation	31
2.4.1 Washout of Respirometry System and Instantaneous $\dot{V}O_2$	31

2.4.2 RMR, BMR, TNZ, T_{lc}	32
2.4.3 TBD	34
2.4.4 TMR and T_{bl}	35
2.4.5 T_{tc} , TMR_{min} , T_{bmin}	35
2.4.6 Cooling Rate, $C_{overall}$ and Maximum Rewarming Rates	35
2.4.7 $\dot{V}O_{2max}$ and Maximum MRs	36
2.4.8 Mass-specific Apparent Conductance and Q_{10}	36
2.5 Statistics and Computer Software	37
2.5.1 Statistics.....	37
2.5.2 Computer Software.....	38
Chapter 3 Thermoregulation and Metabolic Rate Reduction During Hibernation and Daily Torpor.....	39
3.1 Introduction	39
3.2 Materials and Methods	41
3.2.1 Measurements on <i>S. macroura</i>	41
3.2.2 Measurements on <i>C. nanus</i>	41
3.2.3 Statistical Methods	42
3.3 Results for <i>Sminthopsis macroura</i>	42
3.3.1 General Torpor Pattern	42
3.3.2 Normothermia.....	44
3.3.3 Torpor	44
3.4 Results for <i>Cercartetus nanus</i>	52
3.4.1 General Torpor Pattern	52
3.4.2 Normothermia.....	52
3.4.3 Torpor	54
3.5 Discussion	65
3.5.1 Two Responses of TMR to T_a	65
3.5.2 Thermoregulation during Torpor.....	65
3.5.3 Reduction of MR during Daily Torpor	67
3.5.4 Reduction of MR during Hibernation.....	71
Chapter 4 Interrelations between Metabolic Rate and Body Temperature during Entry into and Arousal from Hibernation and Daily Torpor	76
4.1 Introduction	76
4.2 Materials and Methods	77
4.3 Results for <i>Sminthopsis macroura</i>	78
4.3.1 Time Course of MR and T_b Reduction during Entry into Daily Torpor... ..	78
4.3.2 Cooling Rates during Entry into Daily Torpor	79

4.3.3	Time Course of Arousal from Daily Torpor.....	83
4.3.4	Rewarming Rates during Arousal from Daily Torpor.....	83
4.3.5	Maximum MR during Arousal from Daily Torpor.....	84
4.4	Results for <i>Cercartetus nanus</i>	93
4.4.1	Time Course of MR and T_b Reduction during Entry into Hibernation.....	93
4.4.2	Cooling Rates during Entry into Hibernation.....	97
4.4.3	Time Course of Arousal from Hibernation.....	97
4.4.4	Rewarming Rates during Arousal from Hibernation.....	98
4.4.5	Maximum MR during Arousal from Hibernation	100
4.5	Discussion	106
4.5.1	Reduction of MR and T_b during Torpor Entry.....	106
4.5.2	Cooling Rate during Torpor Entry.....	109
4.5.3	Rewarming Rates during Arousal.....	110
4.5.4	Maximum Heat Production during Arousal	112
Chapter 5	Energetics of Hibernation and Daily Torpor	115
5.1	Introduction	115
5.2	Materials and Methods ..	117
5.2.1	Animals.....	117
5.2.2	Data Analysis.....	117
5.3	Results for <i>Sminthopsis macroura</i>	118
5.3.1	Energetics of Daily Torpor as a Function of T_a	118
5.3.2	Energetics in Relation to Duration of Arousal	125
5.3.3	Energetics in Relation to Duration of Torpor	126
5.4	Results for <i>Cercartetus nanus</i>	130
5.4.1	Energetics of Hibernation as a Function of T_a	130
5.4.2	Energetics in Relation to Duration of Arousal	136
5.4.3	Energetics in Relation to Duration of Torpor	137
5.5	Discussion	143
5.5.1	Arousal and Related Energetics.....	143
5.5.2	Torpor Duration and Related Energetics	144
5.5.3	Energy Benefits by the Use of Torpor	147
Chapter 6	Relationships between Torpor and Behavioural Thermoregulation	150
6.1	Introduction	150
6.2	Materials and Methods ..	151
6.2.1	Animals and Experimental Procedure	151
6.2.2	Data Acquisition and Analysis	152
6.3	Results for <i>Sminthopsis macroura</i>	156

6.3.1 Activity.....	156
6.3.2 Torpor.....	156
6.3.3 Body Temperature Fluctuation.....	160
6.3.4 Selection of Ambient Temperature.....	160
6.4 Results for <i>Cercartetus nanus</i>	164
6.4.1 Activity.....	164
6.4.2 Torpor.....	164
6.4.3 Body Temperature Fluctuation.....	167
6.4.4 Selection of Ambient Temperature.....	167
6.5 Discussion.....	171
6.5.1 Temperature Selection.....	171
6.5.2 Torpor and Responses to Food Restriction.....	174
Chapter 7 General Conclusions.....	177
Literature Cited.....	182
Publications Resulting from This Work.....	208

List of Figures

Fig. 2.1 Distribution range of <i>Smintnopsis macroura</i>	20
Fig. 2.2 Distribution range of <i>Cercartetus nanus</i>	23
Fig. 2.3 Details of system A of the respirometry equipment.....	26
Fig. 2.4 Details of system B of the respirometry equipment.....	26
Fig. 2.5 Longitudinal view of the set-up of the T_a gradient.....	30
Fig. 3.1 Patterns of $\dot{V}O_2$ and T_b fluctuation of <i>S. macroura</i>	43
Fig. 3.2 Effect of T_a on MR, T_b , ΔT and C during daily torpor.....	46
Fig. 3.3 TMR as a function of T_b at T_a s above the T_{tc} during daily torpor.....	48
Fig. 3.4 TMR as a function of ΔT at T_a s above the T_{tc} during daily torpor.....	49
Fig. 3.5 TMR as a function of T_b at T_a s below the T_{tc} during daily torpor:.....	50
Fig. 3.6 TMR below T_{tc} and RMR below T_{lc} as function of T_a for <i>S.</i> <i>macroura</i>	51
Fig. 3.7 Patterns of $\dot{V}O_2$ and T_b fluctuation of <i>C. nanus</i>	53
Fig. 3.8 Effect of T_a on MR, T_b , ΔT and C during hibernation.....	57
Fig. 3.9 TMR as a function of T_b at T_a s above the T_{tc} during hibernation.....	59
Fig. 3.10 TMR as a function of ΔT at T_a s above the T_{tc} during hibernation.....	61
Fig. 3.11 TMR below T_{tc} and RMR below T_{lc} as function of T_a of <i>C. nanus</i>	63
Fig. 3.12 Illustration of Q_{10} s for MR reduction during daily torpor in <i>S.</i> <i>macroura</i>	68
Fig. 3.13 Comparison between TMR and the RMR predicted by ΔT in <i>C.</i> <i>nanus</i>	73
Fig. 4.1 Patterns of reduction of MR and T_b during torpor entry in <i>S.</i> <i>macroura</i>	80
Fig. 4.2 Q_{10} s for MR reduction during torpor entry in <i>S. macroura</i>	81
Fig. 4.3 Cooling rates during torpor entry in <i>S. macroura</i>	82
Fig. 4.4 Patterns of increase of MR and T_b during arousal in <i>S. macroura</i>	85
Fig. 4.5 Duration of rewarming of <i>S. macroura</i>	86
Fig. 4.6 Overall and maximum rewarming rates of <i>S. macroura</i> at different T_a s.....	87
Fig. 4.7 Overall rewarming rate of <i>S. macroura</i> as a function of the T_b before arousal.....	88
Fig. 4.8 Maximum rewarming rate of <i>S. macroura</i> as a function of the T_b at which the maximum rewarming rate was reached.....	89
Fig. 4.9 Maximum MR of <i>S. macroura</i> during arousal as a function of T_b	90
Fig. 4.10 Maximum MR during arousal and $\dot{V}O_{2max}$ of <i>S. macroura</i> at different T_a s.....	91

Fig. 4.11 Patterns of MR and T_b reduction during torpor entry in <i>C. nanus</i>	95
Fig. 4.12 Cooling rates during torpor entry in <i>C. nanus</i>	96
Fig. 4.13 Patterns of increase of MR and T_b during arousal in <i>C. nanus</i>	98
Fig. 4.14 Duration of rewarming of <i>C. nanus</i>	99
Fig. 4.15 Overall and maximum rewarming rates of <i>C. nanus</i> at different T_{as}	101
Fig. 4.16 Overall rewarming rate of <i>C. nanus</i> as a function of the T_b before arousal	102
Fig. 4.17 Maximum rewarming rate of <i>C. nanus</i> as a function of the T_b at which the maximum rewarming rate was reached.....	103
Fig. 4.18 Maximum MR of <i>C. nanus</i> during arousal as a function of T_b	104
Fig. 4.19 Maximum MR during arousal and $\dot{V}O_{2max}$ of <i>C. nanus</i> at different T_{as}	105
Fig. 5.1 Calculations of torpor duration, arousal duration, total torpor MR, total arousal MR, and the equivalent RMR in <i>S. macroura</i>	119
Fig. 5.2 Average torpor MR of <i>S. macroura</i> as a function of T_a	121
Fig. 5.3 Average arousal MR of <i>S. macroura</i> as a function of T_a	122
Fig. 5.4 Average torpor bout MR of <i>S. macroura</i> as a function of T_a	123
Fig. 5.5 Ratio of average torpor bout MR to RMR of <i>S. macroura</i> as a function of T_a	124
Fig. 5.6 Interrelations between total arousal MR and arousal duration of <i>S.</i> <i>macroura</i>	125
Fig. 5.7 Torpor duration of <i>S. macroura</i> as a function of T_a	127
Fig. 5.8 Interrelations between torpor duration and average torpor MR of <i>S.</i> <i>macroura</i>	128
Fig. 5.9 Torpor duration threshold as a function of T_a in <i>S. macroura</i>	129
Fig. 5.10 Calculations of torpor duration, arousal duration, total torpor MR, total arousal MR, and the equivalent RMR in <i>C. nanus</i>	130
Fig. 5.11 Average torpor MR of <i>C. nanus</i> as a function of T_a	132
Fig. 5.12 Average arousal MR of <i>C. nanus</i> as a function of T_a	133
Fig. 5.13 Average torpor bout MR of <i>C. nanus</i> as a function of T_a	134
Fig. 5.14 Ratio of average torpor bout MR to RMR of <i>C. nanus</i> as a function of T_a	135
Fig. 5.15 Interrelations between total arousal MR and arousal duration of <i>C.</i> <i>nanus</i>	136
Fig. 5.16 Torpor duration of <i>C. nanus</i> as a function of T_a	139
Fig. 5.17 Torpor duration of <i>C. nanus</i> as a function of average torpor MR.....	140
Fig. 5.18 Torpor duration threshold of <i>C. nanus</i> as a function of T_a	142
Fig. 6.1 Locomotor activity of <i>S. macroura</i> in a T_a gradient.....	157

Fig. 6.2 Torpor frequency of <i>S. macroura</i> in a T_a gradient	158
Fig. 6.3 Torpor bout duration of <i>S. macroura</i> in a T_a gradient.....	159
Fig. 6.4 Average daily T_{bs} of <i>S. macroura</i> in a T_a gradient.....	161
Fig. 6.5 Location of <i>S. macroura</i> in a T_a gradient	163
Fig. 6.6 Locomotor activity of <i>C. nanus</i> in a T_a gradient	165
Fig. 6.7 Torpor bout duration of <i>C. nanus</i> in a T_a gradient.....	166
Fig. 6.8 T_{bs} of <i>C. nanus</i> that displayed torpor in a T_a gradient.....	168
Fig. 6.9 Location of <i>C. nanus</i> in the T_t gradient.....	169
Fig. 6.10 Location of torpid <i>C. nanus</i> in a T_a gradient	170

List of Tables

Table 2.1.....	33
Table 3.1.....	56
Table 6.1.....	154
Table 6.2.....	155

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
$^{\circ}C$: Degrees Celsius
cm	: centimetres
D_a	: Arousal duration
D_t	: Torpor duration
D_t'	: Torpor duration threshold
g	: grams
h	: hours
He-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 lowering 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 favorable. 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)