

Utah State University

DigitalCommons@USU

All Graduate Theses and Dissertations

Graduate Studies

5-1997

The Role of Cold Acclimatization on the Biogeography of the Mountain Chickadee (*Parus gambeli*) and the Juniper Titmouse (*Parus ridgwayi*)

Sheldon J. Cooper
Utah State University

Follow this and additional works at: <https://digitalcommons.usu.edu/etd>

 Part of the [Biology Commons](#)

Recommended Citation

Cooper, Sheldon J., "The Role of Cold Acclimatization on the Biogeography of the Mountain Chickadee (*Parus gambeli*) and the Juniper Titmouse (*Parus ridgwayi*)" (1997). *All Graduate Theses and Dissertations*. 4471.

<https://digitalcommons.usu.edu/etd/4471>

This Dissertation is brought to you for free and open access by the Graduate Studies at DigitalCommons@USU. It has been accepted for inclusion in All Graduate Theses and Dissertations by an authorized administrator of DigitalCommons@USU. For more information, please contact digitalcommons@usu.edu.



THE ROLE OF COLD ACCLIMATIZATION ON THE BIOGEOGRAPHY
OF THE MOUNTAIN CHICKADEE (*PARUS GAMBELI*) AND THE
JUNIPER TITMOUSE (*PARUS RIDGWAYI*)

by

Sheldon J. Cooper

A dissertation submitted in partial fulfillment
of the requirements for the degree

of

DOCTOR OF PHILOSOPHY

in

Biology

Approved:

UTAH STATE UNIVERSITY
Logan, Utah

1997

Copyright © Sheldon J. Cooper 1997

All Rights Reserved

ABSTRACT

The Role of Cold Acclimatization on the Biogeography
of the Mountain Chickadee (*Parus gambeli*) and the
Juniper Titmouse (*Parus ridgwayi*)

by

Sheldon J. Cooper, Doctor of Philosophy

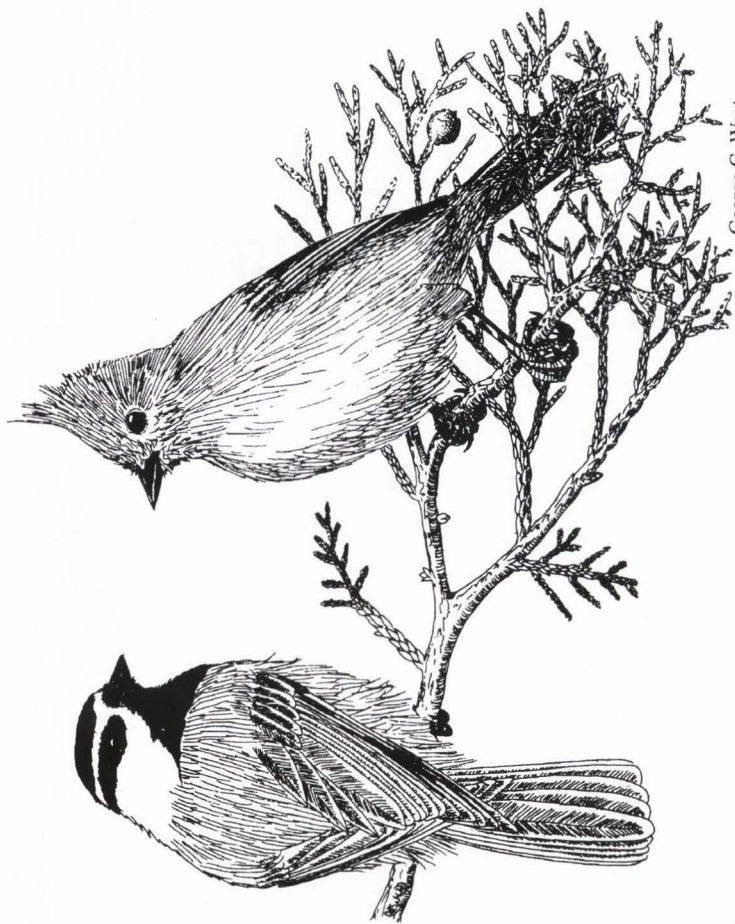
Utah State University, 1997

Major Professor: Dr. James A. Gessaman
Department: Biology

Biogeographic patterns of animals are shaped by biotic interactions, such as competition, and by abiotic factors, such as climate. Mountain Chickadees (*Parus gambeli*) and Juniper Titmice (*Parus ridgwayi*) are permanent residents of regions of western North America and are ecologically similar, but have different northern range limits. I measured several physiological variables, including basal metabolic rate (BMR), peak metabolic rate (PMR = maximal thermogenic capacity), metabolic response to varying environmental temperature (MRT), evaporative water loss (EWL), and daily energy expenditure (DEE) for summer- and winter-acclimatized Mountain Chickadees and Juniper Titmice to determine if seasonal and interspecific variation in cold tolerance and thermogenic ability shape the northern range distribution of these two species. In addition, I examined the ecological consequences of nocturnal hypothermia and cavity

roosting in seasonally acclimatized Mountain Chickadees and Juniper Titmice.

Winter birds tolerated colder test temperatures than summer birds for both species. This improved cold tolerance was associated with a significant increase in PMR in winter chickadees (27.1%) and titmice (11.4%) compared to summer. BMR was significantly higher in winter birds (16.0%) compared to summer birds for both species. BMR and PMR were significantly higher for chickadees compared to titmice in both summer and winter. Winter chickadees were able to withstand colder test temperatures than winter titmice. The Mountain Chickadee's lower critical temperature is lower than the Juniper Titmouse's in summer and in winter. The Mountain Chickadee's upper critical temperature is also lower than the Juniper Titmouse's and chickadees also had significantly higher evaporative water loss rates compared to titmice. Seasonal acclimatization in Mountain Chickadees involves insulatory as well as metabolic changes. For Juniper Titmice winter acclimatization appears to be primarily a metabolic process. The laboratory metabolism data for activity costs associated with DEE revealed that foraging energy requirements were not significantly higher than alert perching energy requirements. DEE was significantly higher ($P < 0.05$) in winter-acclimatized chickadees and titmice compared to their summer counterparts. The marked increase in calculated DEE in winter birds compared to summer contrasts a pattern of increased DEE in the breeding season for several avian species. The data from this study indicate that the northern range limit of small birds can be limited by energetic and water balance demands.



George C. West

ACKNOWLEDGMENTS

James A. Gessaman, my major professor, provided support, encouragement, a generous amount of lab space, and the wide array of research equipment needed to complete my dissertation. Most importantly, he gave me the freedom to pursue an independent research project, which has provided me with valuable skills necessary to continue with research in the future.

I thank members of my graduate committee, LeGrande C. Ellis, Peter C. Ruben, Dana K. Vaughan, and Wayne A. Wurtsbaugh, for their helpful suggestions and revisions of my dissertation.

Keith L. Dixon was instrumental in the completion of my dissertation. He gave me information on study site locations and audio tapes of Mountain Chickadee and Juniper Titmice songs needed to capture these species, and allowed me to band birds as a subpermittee under the jurisdiction of his federal master banding permit. My project benefitted greatly due to Dr. Dixon's expertise of chickadees and titmice.

Valuable field assistance was provided by Brent Cooper, Jaci Cooper, Dan Roberts, and Glenn Wilson. Maintenance of birds while in captivity was made possible by help from Jaci Cooper and Glenn Wilson who fed captive birds numerous mornings, allowing me to go out to the field and mist-net more individuals.

Kim A. Sullivan generously loaned me cup anemometers, a Campbell CR-10 datalogger, air temperature thermometers, and operative temperature thermometers used in this project. In addition, she served as a valuable committee member until June 1996,

when she went on sabbatical leave.

Funding was provided by a Sigma-Xi grants-in-aid of research award, a North American Bluebird Society student research grant, and by funding from the Ecology Center at Utah State University to James A. Gessaman

Lastly, I must thank my wife, Jaci, who in addition to providing me with field and lab assistance, also provided me with encouragement and love necessary for the completion of my dissertation. She demonstrated remarkable patience throughout the time period of my dissertation work, for which I am indebted.

Sheldon J. Cooper

CONTENTS

	Page
ABSTRACT	iii
FRONTISPIECE	v
ACKNOWLEDGMENTS	vi
LIST OF TABLES	xii
LIST OF FIGURES	xiv
CHAPTER	
1. INTRODUCTION	1
LITERATURE CITED	5
2. SEASONAL VARIATION IN COLD TOLERANCE AND MAXIMAL THERMOGENIC CAPACITY MAY INFLUENCE THE NORTHERN RANGE DISTRIBUTION OF THE MOUNTAIN CHICKADEE AND THE JUNIPER TITMOUSE	10
ABSTRACT	10
INTRODUCTION	11
METHODS	15
Study species and sites	15
Experimental animals	15
Helox cold stress	18
Maximal oxygen consumption	20
Basal metabolic rate measurements	21
Statistics	21
RESULTS	22
Body mass	22
Cold tolerance and body temperature	23
Peak metabolic rate	26
Basal metabolic rate	28

DISCUSSION	30
Body mass	30
Cold tolerance and thermal conductance	31
Basal and peak metabolic rates	33
LITERATURE CITED	36
3. SEASONAL THERMOREGULATION IN THE MOUNTAIN CHICKADEE AND THE JUNIPER TITMOUSE: EFFECTS OF ENERGETIC CONSTRAINTS ON RANGE DISTRIBUTION	43
ABSTRACT	43
STUDY AREA AND METHODS	46
Study area	46
Birds	46
Body composition	48
Metabolic response to temperature	48
Statistics	50
RESULTS	51
Body mass and composition	51
Metabolic response to temperature	51
Evaporative water loss	57
DISCUSSION	57
Body mass and composition	57
Metabolic response to temperature below thermoneutrality	61
Metabolic response to temperature above thermoneutrality	62
LITERATURE CITED	64
4. THE ROLE OF DAILY ENERGY EXPENDITURE ON THE BIOGEOGRAPHY OF THE MOUNTAIN CHICKADEE AND JUNIPER TITMOUSE	69
ABSTRACT	69
INTRODUCTION	70
MATERIALS AND METHODS	72

	Study site and species	72
	Time-activity budgets	72
	Meteorology	73
	Laboratory metabolism measurements	74
	Time-activity-laboratory estimate of DEE	76
	RESULTS	78
	Weather	78
	Time-activity budgets	78
	Laboratory metabolic rates	82
	Time-activity laboratory estimate of DEE	86
	DISCUSSION	87
	Activity heat and thermoregulation	87
	Seasonal variation in DEE	88
	Role of DEE on northern range limits	90
	LITERATURE CITED	90
5.	NOCTURNAL HYPOTHERMIA IN SEASONALLY ACCLIMATIZED MOUNTAIN CHICKADEES AND JUNIPER TITMICE	94
	ABSTRACT	94
	INTRODUCTION	95
	MATERIALS AND METHODS	96
	Animals and collection sites	96
	Body temperature measurements	97
	Measurements of metabolism	97
	Statistics	98
	RESULTS	99
	Body temperature	99
	Metabolic rates and thermal conductance	103
	DISCUSSION	105
	Hypothermia	105
	Energy metabolism and thermal conductance	109

	Energetic significance	110
	REFERENCES	111
6.	THE THERMAL AND ENERGETIC SIGNIFICANCE OF CAVITY ROOSTING IN SEASONALLY ACCLIMATIZED MOUNTAIN CHICKADEES AND JUNIPER TITMICE	113
	ABSTRACT	113
	INTRODUCTION	113
	METHODS	115
	Study area	115
	Cavity roosts	115
	Microclimate sampling	116
	Statistics	117
	RESULTS	118
	DISCUSSION	123
	LITERATURE CITED	127
7.	SUMMARY	130
	APPENDICES	134
	APPENDIX A. ANOVA TABLES	135
	APPENDIX B. CONTRIBUTION ACKNOWLEDGMENT FROM COAUTHOR	138
	APPENDIX C. DEE ENERGETIC COST ESTIMATES	140
	CURRICULUM VITAE	145

LIST OF TABLES

Table	Page
2.1 Mass-specific (mW/g) and per-unit metabolic mass ($mW g^{-0.75}$) basal metabolic rates (BMR) and peak metabolic rates (PMR) for seasonally acclimatized Mountain Chickadees (MOCH) and Juniper Titmice (JUTI) from northern Utah. Values for metabolic rates were converted from mL O ₂ /min using an energy equivalent of 20.1 J/mL O ₂ . Metabolic expansibilities (ME) were determined as PMR/BMR. Body masses are means for the treatment group. Sample size is indicated in parentheses	24
2.2 Enhancement of thermal conductance in helox compared to air for passerines	32
3.1 Seasonal values of body mass and composition for Mountain Chickadees (MOCH) and Juniper Titmice (JUTI). All values are for morning birds except evening body mass. Sample size is indicated in parentheses. Mean values are presented with their corresponding standard errors. Adjusted means were determined using ANCOVA using body mass as the covariate. Means were compared using <i>t</i> -tests.	52
3.2 Relationship of mass-specific $\dot{V}O_2$ (mL O ₂ g ⁻¹ h ⁻¹) to standard operative temperature (°C) below thermoneutrality for seasonally acclimatized Mountain Chickadees (MOCH) and Juniper Titmice (JUTI).	55
3.3 Relationship of mass-specific $\dot{V}O_2$ (mL O ₂ g ⁻¹ h ⁻¹) to standard operative temperature (°C) above thermoneutrality for seasonally acclimatized Mountain Chickadees (MOCH) and Juniper Titmice (JUTI)	56
3.4 Relationship of evaporative water loss (mg g ⁻¹ h ⁻¹) to standard operative temperature (°C) for seasonally acclimatized Mountain Chickadees (MOCH) and Juniper Titmice (JUTI)	60
4.1 Percentage of the active day that seasonally acclimatized Mountain Chickadees (MOCH) and Juniper Titmice (JUTI) spent in various activities	81
4.2 Daily energy budget of seasonally acclimatized Mountain Chickadees (MOCH) and Juniper Titmice (JUTI) as calculated by the TAL method	87

6.1	Average overnight micrometeorological variables and predicted energy expenditure (means \pm SE) at open sites compared to cavity roosts for Mountain Chickadees (MOCH) and Juniper Titmice (JUTI) for summer roost periods	123
6.2	Average overnight micrometeorological variables and predicted energy expenditure (means \pm SE) at open sites compared to cavity roosts for Mountain Chickadees (MOCH) and Juniper Titmice (JUTI) for winter roost periods	124
A1	Analysis of variance of the effect of helox test temperature ($^{\circ}$ C) on the mass-specific $\dot{V}O_2$ ($\text{mL O}_2\text{g}^{-1}\text{h}^{-1}$) of summer-acclimatized Mountain Chickadees	136
A2	Analysis of variance of the effect of helox test temperature ($^{\circ}$ C) on the mass-specific $\dot{V}O_2$ ($\text{mL O}_2\text{g}^{-1}\text{h}^{-1}$) of summer-acclimatized Juniper Titmice	136
A3	Analysis of variance of the effect of helox test temperature ($^{\circ}$ C) on the mass-specific $\dot{V}O_2$ ($\text{mL O}_2\text{g}^{-1}\text{h}^{-1}$) of winter-acclimatized Juniper Titmice	137
A4	Analysis of variance of the effect of helox test temperature ($^{\circ}$ C) on the mass-specific $\dot{V}O_2$ ($\text{mL O}_2\text{g}^{-1}\text{h}^{-1}$) of winter-acclimatized Mountain Chickadees	137

LIST OF FIGURES

Figure	Page
2.1 Range distributions of the Mountain Chickadee (a) and the Juniper Titmouse (b) in North America.	14
2.2 Study site locations of Mountain Chickadees (MOCH) and Juniper Titmice (JUTI) from northern Utah. Chickadees were captured at Tony Grove (TG), Beaver Mountain Ski Area (BM) and Sunrise Campground (SR) within the Cache National Forest. Titmice were captured near Rosette (RT), Utah	16
2.3 Annual temperature profiles for Mountain Chickadee (MOCH) (a) and Juniper Titmouse (JUTI) (b) study sites in northern Utah. Weather data from Utah Climate Center, Utah State University	17
2.4 Cold tolerance for seasonally acclimatized Mountain Chickadees (a) and Juniper Titmice (b) over the 65-min test period. Bars represent percent of individuals that became hypothermic. Numbers above bars indicate sample size	25
2.5 Thermal conductance in helox on a per-unit metabolic mass basis ($\text{mW}\cdot\text{g}^{-0.75}\cdot\text{C}^{-1}$) for seasonally acclimatized Mountain Chickadees (MOCH) and Juniper Titmice (JUTI). Error bars represent standard deviations of means for each group	27
2.6 Metabolism (mW/g) at various helox chamber temperatures for summer (a) and winter (b) acclimatized Mountain Chickadees (MOCH) and Juniper Titmice (JUTI). Means and 95% confidence intervals are shown at each temperature	29
3.1 Annual temperature profiles for Mountain Chickadee (MOCH) and Juniper Titmouse (JUTI) study sites in northern Utah. Mean daily maximum (A), mean daily (B), and mean daily minimum (C) plotted for each month	47
3.2 Relationship between metabolism ($\dot{V}\text{O}_2$) and standard operative temperature (T_{so}) for summer-acclimatized (A) and winter-acclimatized (B) Mountain Chickadees (MOCH) and Juniper Titmice (JUTI). Horizontal lines represent mean BMR	54

3.3	Relationship between evaporative water loss and standard operative temperature for summer (A) and winter (B) acclimatized Mountain Chickadees (MOCH) and Juniper Titmice (JUTI)	58
3.4	Relationship between natural log of evaporative water loss and standard operative temperature in summer (A) and winter (B) acclimatized Mountain Chickadees (MOCH) and Juniper Titmice (JUTI)	59
4.1	Temperature and wind speed for Mountain Chickadees (A) and Juniper Titmice (B) during the summer study period, August 1996	79
4.2	Temperature and wind speed for Mountain Chickadees (A) and Juniper Titmice (B) during the winter study period, February 1996	80
4.3	Relationship between oxygen consumption and standard operative temperature for summer-acclimatized Mountain Chickadees (A) and Juniper Titmice (B) during the active phase of their daily cycle. Dots represent active birds under lit conditions and open circles represent resting birds under dark conditions	84
4.4	Relationship between oxygen consumption and standard operative temperature for winter-acclimatized Mountain Chickadees (A) and Juniper Titmice (B) during the active phase of their daily cycle. Dots represent active birds under lit conditions and open circles represent resting birds under dark conditions	85
5.1	Daily body temperature rhythm of summer (A) and winter (B) acclimatized mountain chickadees (MOCH) and juniper titmice (JUTI) from northern Utah	100
5.2	Relationship between nocturnal body temperature and standard operative temperature for summer (A) and winter (B) acclimatized mountain chickadees (MOCH) and juniper titmice (JUTI) from northern Utah	102
5.3	Relationship of thermal conductance to standard operative temperature in summer (A) and winter (B) acclimatized mountain chickadees (MOCH) and juniper titmice (JUTI). LOWESS regression lines are shown for summer (A) birds and linear regression lines are plotted for winter (B) birds as slopes in winter are near zero	104

5.4	Relationship of oxygen consumption to the difference between T_b and T_{es} for summer (A) and winter (B) acclimatized mountain chickadees (MOCH) and juniper titmice (JUTI) from northern Utah	106
5.5	Energy savings associated with nocturnal hypothermia in summer (A) and winter (B) acclimatized mountain chickadees (MOCH) and juniper titmice (JUTI). Energy savings are % reduction in metabolism compared to predicted euthermic rates	107
6.1	Micrometeorological measurements at open sites (°) and at cavity roosts (•) for Mountain Chickadees on 31 July-1 August. Variables measured were averaged over 2-h periods	119
6.2	Micrometeorological measurements at open sites (°) and at cavity roosts (•) for Juniper Titmice 2 August-3 August. Variables measured were averaged over 2-h periods	120
6.3	Micrometeorological measurements at open sites (°) and at cavity roosts (•) for Mountain Chickadees on 6 February-7 February. Variables measured were averaged over 2-h periods	121
6.4	Micrometeorological measurements at open sites (°) and at cavity roosts (•) for Juniper Titmice 27 February-28 February. Variables measured were averaged over 2-h periods	122

CHAPTER 1

INTRODUCTION

Two long-standing hypotheses address the question of what factors shape biogeographic patterns of animals. One hypothesis states that biotic factors, such as competition or predation, exert the primary forces determining the distribution of species (MacArthur 1958). The other hypothesis states that abiotic factors, such as climate, are the primary forces determining the distributional patterns of animals (Andrewartha and Birch 1954). In general, most ecological studies have concluded that biotic interactions appear to control the biogeographic patterns of species (Connell 1961, Terborgh and Weske 1975, Moulton and Pimm 1983). However, most ecological studies have examined range boundaries within fairly small, localized areas (Kareiva and Andersen 1988) and details from these local studies may have obscured other factors involved with biogeography (Root 1988a). A good example of this is temperature, which is considered by some as one of the main factors determining the distribution and abundance of animals (Cox and Moore 1980, Brown and Gibson 1983, Krebs 1985). Climate or temperature may influence an animal's range physiologically through its impact on energy or water balance, and/or ecologically through its influence on food availability and vegetation (Weathers and van Riper 1982).

In avian ecology, interspecific competition has been commonly used to explain biogeography of individual species (Terborgh and Weske 1975, Moulton and Pimm 1983). For desert birds, it has been proposed that climate affects biogeography primarily through its effect on vegetation and resulting habitat requirements and that physiology is

unimportant in limiting the occurrence of desert species (Bartholomew and Dawson 1953, 1958, Bartholomew and Cade 1963). In addition, because birds are highly mobile endotherms, climate has been cited to affect distribution patterns indirectly through ecological consequences (Dawson and Bartholomew 1968). However, physiological comparisons of closely related species have indicated that minor but significant differences in water or energy balance can be interpreted as adaptive for living in specific environments (Dawson 1954, Rising 1969, Hinds and Calder 1973, Hinsley et al. 1993). In addition, thermoregulatory differences in similar bird species from dissimilar climates appear to be linked with species distributions (Weathers and van Riper 1982, Hayworth and Weathers 1984).

For wintering North American birds, average minimum January temperature is strongly associated with the northern range limit of 60.2% of 113 species examined (Root 1988b). Root (1988a) calculated the metabolic rate at the northern range boundary of the distribution for 14 passerines known to have range boundaries associated with a particular average minimum January temperature isotherm. These calculated metabolic rates, based on physiological measurements taken from the literature, provide strong correlative evidence that physiological demands restrict the northern boundaries of these wintering passerine birds (Root 1988a). Thus, biogeographical patterns, especially northern range limits of small birds, may be directly affected by climate.

The conclusions drawn from these studies may be limited because physiological variables measured included only basal metabolic rate, metabolic rates in response to varying air temperatures, and in some, evaporative water loss rates. In addition, the

physiological measurements in these studies were taken during only one season (summer or winter), thus ignoring the possible importance of seasonal changes in physiological tolerances on biogeography in birds.

For small birds that overwinter in cold temperate regions, the onset of winter creates energetically challenging conditions. These conditions include low air temperatures and decreased foraging time due to shorter days, which can be further restricted by snow or ice cover. Small birds meet this energetic challenge primarily through metabolic adjustments (reviews: Marsh and Dawson 1989a, b; Dawson and Marsh 1989, Dawson and O'Connor 1996). These metabolic adjustments generally include tolerance of colder temperatures in winter-acclimatized birds relative to summer birds (Hart 1962, Barnett 1970, Pohl and West 1973), increased thermogenic endurance in winter birds (Dawson and Carey 1976, Dawson et al. 1983, Swanson 1990, O'Connor 1995), and increased summit metabolism in winter birds (Hart 1962, Dawson and Smith 1986, Swanson 1990, Cooper and Swanson 1994, O'Connor 1995, Liknes and Swanson 1996). In addition to the above metabolic adjustments, small birds can also acclimatize to cold physiologically by adjusting fat storage and undergoing regulated hypothermia; physically by insulatory adjustments; and behaviorally by utilizing less stressful microclimates (Mayer et al. 1982). Thus, in order to determine how extensive the influence of physiology is on biogeographic patterns, seasonal acclimatization to cold needs to be examined in closely related species with differing northern range limits.

The Mountain Chickadee (*Parus gambeli*) and the Juniper Titmouse (*Parus ridgwayi*) are small, largely nonmigratory passerine birds that occupy regions of western

North America. Recently, the Plain Titmouse (*Parus inornatus*) has been split into the Juniper Titmouse and the Oak Titmouse (*Parus inornatus*) (Cicero 1996). The Mountain Chickadee's distributional range extends to northern British Columbia (60° north latitude), whereas the Juniper Titmouse's range extends to portions of southern Oregon and Idaho (44° north latitude) (Godfrey 1986, Cicero 1996). Mountain Chickadees co-occur with Juniper Titmice throughout the titmouse's range. Where Mountain Chickadees and Juniper Titmice co-occur, they both occupy juniper woodlands (Bent 1946). These two species overlap during the breeding season without aggressive interactions and they do not respond to heterospecific song during territory establishment or during the breeding season (pers. obs.). Thus, it does not appear that interspecific competition shapes the biogeography of these two species. Vegetation appears to be the primary factor associated with the Juniper Titmouse's northern range distribution. The northern range of Mountain Chickadees is not associated with any of six environmental variables examined by (Root 1988b). However, the Mountain Chickadee's northern range limit does not extend beyond a -23°C average minimum January temperature isotherm, whereas the Juniper Titmouse's northern range limit does not extend past a -12°C isotherm of minimum January temperature (Root 1988c). Therefore, the direct effect of climate on the physiology of these two species may be important in determining their northern range distribution.

The objective of this study was to determine the role of seasonal acclimatization of thermoregulation on the northern range limits of the Mountain Chickadee and Juniper Titmouse. Specifically, I compared seasonal variation in physiological, physical, and

behavioral adjustments to cold in these species in order to determine the importance of climate's direct effect on the biogeographic patterns of small passerine birds.

LITERATURE CITED

- Andrewartha, H. G., and L. C. Birch. 1954. The distribution and abundance of animals. University of Chicago Press, Chicago, Illinois, USA.
- Barnett, L. B. 1970. Seasonal changes in temperature acclimatization of the House Sparrow, *Passer domesticus*. Comparative Biochemistry and Physiology **33**:559-578.
- Bartholomew, G. A., and T. J. Cade. 1963. The water economy of land birds. Auk **80**:504-539.
- Bartholomew, G. A., and W. R. Dawson. 1953. Respiratory water loss in some birds of the southwestern United States. Physiological Zoology **26**:162-166.
- Bartholomew, G. A., and W. R. Dawson. 1958. Body temperatures in California and Gambel's quail. Auk **75**:150-156.
- Bent, A. C. 1946. Life histories of North American jays, crows, and titmice. United States National Museum Bulletin **191**.
- Brown, J. H., and A. C. Gibson. 1983. Biogeography. Mosby, St. Louis, Missouri, USA.
- Cicero, C. 1996. Sibling species of titmice in the *Parus inornatus* complex (Aves: Paridae). University of California Publications in Zoology **128**:1-217.
- Connell, J. H. 1961. The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*. Ecology **42**:710-723.

- Cooper, S. J., and D. L. Swanson. 1994. Seasonal acclimatization of thermoregulation in the Black-capped Chickadee. *Condor* **96**:638-646.
- Cox, B. C., and P. D. Moore. 1980. *Biogeography: an ecological and evolutionary approach*. John Wiley and Sons, New York, New York, USA.
- Dawson, W. R. 1954. Temperature regulation and water requirements of the brown and Abert Towhees, *Pipilo fuscus* and *Pipilo aberti*. University of California Publications in Zoology **59**:81-124.
- Dawson, W. R., and G. A. Bartholomew. 1968. Temperature regulation and water economy of desert birds. Pages 357-394 in G. W. Brown, Jr., editor. *Desert biology*. Academic Press, New York, New York, USA
- Dawson, W. R., and C. Carey. 1976. Seasonal acclimatization to temperature in cardueline finches. I. Insulative and metabolic adjustments. *Journal of Comparative Physiology* **112**:317-333.
- Dawson, W. R., and R. L. Marsh. 1989. Seasonal acclimatization to cold and season in birds. Pages 83-94 in C. Bech and R. E. Reinertsen, editors. *Physiology of cold adaptation in birds*. Plenum Press, New York, New York, USA.
- Dawson, W. R., R. L. Marsh, W. A. Buttemer, and C. Carey. 1983. Seasonal and geographic variation of cold resistance in House Finches (*Carpodacus mexicanus*). *Physiological Zoology* **56**:353-369.
- Dawson, W. R., and T. P. O'Connor. 1996. Energetic features of avian thermoregulatory responses. Pages 85-124 in C. Carey, editor. *Avian energetics and nutritional ecology*. Chapman and Hall, New York, New York, USA.

- Dawson, W. R., and B. K. Smith. 1986. Metabolic acclimatization in the American Goldfinch (*Carduelis tristis*). Pages 427-434 in H. C. Heller, X. J. Musacchia, and L. C. H. Wang, editors. Living in the cold: physiological and biochemical adaptations. Elsevier, New York, New York, USA.
- Godfrey, W. E. 1986. The birds of Canada. National Museums of Canada, Ottawa, Ontario, Canada.
- Hart, J. S. 1962. Seasonal acclimatization in four species of small wild birds. *Physiological Zoology* 35:224-236.
- Hayworth, A. M., and W. W. Weathers. 1984. Temperature regulation and climatic adaptation in Black-billed and Yellow-billed Magpies. *Condor* 86:19-26.
- Hinds, D. S., and W. A. Calder. 1973. Temperature regulation of the Pyrrhuloxia and the Arizona Cardinal. *Physiological Zoology* 46:55-71.
- Hinsley, S. A., P. N. Ferns, D. H. Thomas, and B. Pinshow. 1993. Black-bellied Sandgrouse (*Pterocles orientalis*) and Pin-tailed Sandgrouse (*Pterocles alchata*): closely related species with differing bioenergetic adaptations to arid zones. *Physiological Zoology* 66:20-42.
- Kareiva, P., and M. Andersen. 1988. Spatial aspects of species interactions. Pages 35-50 in A. Hastings, editor. Community ecology, Springer-Verlag, New York, New York, USA.
- Krebs, C. J. 1985. Ecology. Harper and Row, New York, New York, USA.

- Liknes, E. T., and D. L. Swanson. 1996. Seasonal variation in cold tolerance, basal metabolic rate, and maximal capacity for thermogenesis in White-breasted Nuthatches *Sitta carolinensis* and Downy Woodpeckers *Picoides pubescens*, two unrelated arboreal temperate residents. *Journal of Avian Biology* **27**:279-288.
- MacArthur, R. H. 1958. Population ecology of some warblers of northeastern coniferous forests. *Ecology* **39**:599-619.
- Marsh, R. L., and W. R. Dawson. 1989a. Avian adjustments to cold. Pages 205-253 in L. C. H. Wang, editor. *Advances in comparative and environmental physiology*. Springer, Berlin, Germany.
- Marsh, R. L., and W. R. Dawson. 1989b. Energy substrates and metabolic acclimatization in small birds. Pages 105-114 in C. Bech and R. E. Reinertsen, editors. *Physiology of cold adaptation in birds*. Plenum Press, New York, New York, USA.
- Mayer, L., S. Lustick, and B. Battersby. 1982. The importance of cavity roosting and hypothermia to energy balance of winter acclimatized Carolina Chickadee. *International Journal of Biometeorology* **26**:231-238.
- Moulton, M. P., and S. L. Pimm. 1983. The introduced Hawaiian avifauna: biogeographic evidence for competition. *American Naturalist* **121**:669-690.
- O'Connor, T. P. 1995. Metabolic characteristics and body composition in house finches: effects of seasonal acclimatization. *Journal of Comparative Physiology B* **165**:298-305.

- Pohl, H., and G. C. West. 1973. Daily and seasonal variation in metabolic response to cold and forced exercise in the Common Redpoll. *Comparative Biochemistry and Physiology* **45A**:851-867.
- Rising, J. D. 1969. A comparison of metabolism and evaporative water loss of Baltimore and Bullock orioles. *Comparative Biochemistry and Physiology* **31**:915-925.
- Root, T. 1988a. Energy constraints on avian distributions and abundance. *Ecology* **69**:330-339.
- . 1988b. Environmental factors associated with avian distributional boundaries. *Journal of Biogeography* **15**:489-505.
- . 1988c. Atlas of wintering North American birds. University of Chicago Press, Chicago, Illinois, USA.
- Swanson, D. L. 1990. Seasonal variation in cold hardiness and peak rates of cold-induced thermogenesis in the Dark-eyed Junco (*Junco hyemalis*). *Auk* **107**:561-566.
- Terborgh, J., and J. S. Weske. 1975. The role of competition in the distribution of Andean birds. *Ecology* **56**:562-576.
- Weathers, W. W., and C. van Riper. 1982. Temperature regulation in two endangered Hawaiian honeycreepers: the Palila (*Psittirostra bailleui*) and the Laysan Finch (*Psittirostra cantans*). *Auk* **99**:667-674.

CHAPTER 2

SEASONAL VARIATION IN COLD TOLERANCE AND MAXIMAL
THERMOGENIC CAPACITY MAY INFLUENCE THE NORTHERN
RANGE DISTRIBUTION OF THE MOUNTAIN CHICKADEE
AND THE JUNIPER TITMOUSE

Abstract. Biogeographic patterns of animals are shaped by biotic interactions, such as competition, and by abiotic factors, such as climate. Mountain Chickadees (*Parus gambeli*) and Juniper Titmice (*Parus ridgwayi*) are permanent residents of regions of western North America and are ecologically similar, but have different northern range limits. I measured basal metabolic rate (BMR) and peak metabolic rate (PMR = maximal thermogenic capacity) for summer- and winter-acclimatized Mountain Chickadees and Juniper Titmice to determine if seasonal and interspecific variation in cold tolerance and thermogenic ability shape the northern range distribution of these two species.

Winter birds tolerated colder test temperatures than summer birds for both species. This improved cold tolerance was associated with a significant increase in PMR in winter chickadees (27.1%) and titmice (11.4%) compared to summer. Both species had significantly lower thermal conductance in winter than in summer, which also improved cold tolerance. BMR was significantly higher in winter birds (16%) compared to summer birds for both species. BMR and PMR were significantly higher for chickadees compared to titmice in both summer and winter. Winter chickadees were able to withstand colder test temperatures than winter titmice.

The seasonal metabolic acclimatization of Mountain Chickadees and Juniper Titmice is similar to other temperate wintering passerines. For Mountain Chickadees, these metabolic adjustments are greater than many other passerines and likely enable Mountain Chickadees to survive in colder, more northern habitats than occupied by Juniper Titmice.

INTRODUCTION

Biogeographic patterns of animals are shaped by biotic interactions, such as competition, and by abiotic factors, such as climate. Climate may influence a species' range physiologically through its impact on thermoregulation, and/or ecologically through its influence on food availability and vegetation (Weathers and van Riper 1982). In avian ecology, interspecific competition has been widely used to explain biogeographic patterns of species (Terborgh and Weske 1975, Moulton and Pimm 1983). In addition, because birds are extremely mobile endotherms, climate is generally assumed to affect their distribution patterns indirectly through its ecological consequences (Dawson and Bartholomew 1968). However, for wintering North American birds, average minimum January temperature is associated with the northern range limit of 60.2% of 113 species (Root 1988a). In addition, Root (1988b) presents data that links the winter distribution patterns of several species of North American birds with physiological demands of thermoregulation. Thus, geographical distribution in small birds may be directly affected by climate.

In addition to data from Root (1988a, b), some other studies have shown

thermoregulatory differences in similar bird species from dissimilar climates that appear to be linked with species distribution (Weathers and van Riper 1982, Hayworth and Weathers 1984). Comparisons of other closely related species have indicated that minor but significant differences in energy or water balance can be interpreted as being adaptive for living in specific environments (Dawson 1954, Rising 1969, Hinds and Calder 1973, Hinsley et al. 1993). These studies measured only basal metabolic rate and metabolic response to varying air temperatures during only one season (summer or winter). For small birds that overwinter in cold temperate regions the onset of winter creates energetically challenging conditions. These conditions include low air temperatures and decreased foraging time due to shorter days, which can be further restricted by snow or ice cover. Small birds meet this energetic challenge primarily through metabolic adjustments (reviews: Marsh and Dawson 1989a, b; Dawson and Marsh 1989, Dawson and O'Connor 1996). These metabolic adjustments generally include tolerance of colder temperatures in winter-acclimatized birds relative to summer birds (Hart 1962, Barnett 1970, Pohl and West 1973), increased thermogenic endurance in winter birds (Dawson and Carey 1976, Dawson et al. 1983, Swanson 1990, O'Connor 1995), and increased summit metabolism in winter birds (Hart 1962, Dawson and Smith 1986, Swanson 1990, Cooper and Swanson 1994, O'Connor 1995, Liknes and Swanson 1996). Thus, in order to determine how extensive the influence of physiology is on biogeographic patterns, seasonal acclimatization to cold needs to be examined in closely related species with differing northern range limits.

The Mountain Chickadee (*Parus gambeli*) and the Juniper Titmouse (*Parus*

ridgwayi) are small, largely nonmigratory passerine birds that occupy regions of western North America. Recently, the Plain Titmouse (*Parus inornatus*) has been split into the Juniper Titmouse and the Oak Titmouse (*Parus inornatus*) (Cicero 1996). The Mountain Chickadee's distributional range extends to northern British Columbia (60° north latitude) whereas the Juniper Titmouse's range extends to portions of southern Oregon and Idaho (44° north latitude) (Godfrey 1986, Cicero 1996) (Fig. 2.1). Vegetation appears to be the primary factor associated with the Juniper Titmouse's northern range distribution. The northern range of Mountain Chickadees is not associated with any of six environmental variables examined by (Root 1988a). However, the Mountain Chickadee's northern range limit does not extend beyond a -23°C average minimum January temperature isotherm, whereas the Juniper Titmouse's northern range limit does not extend past a -12°C isotherm of minimum January temperature (Root 1988c). Therefore, the direct effect of climate on the physiology of these two species may be important in determining their northern range distribution.

In this study I compare seasonal variation in basal metabolic rate, cold tolerance, cold endurance, and maximal thermogenic capacity (PMR) in Mountain Chickadees and Juniper Titmice from northern Utah in order to determine the role of seasonal metabolic adjustments on the biogeography of these two species.

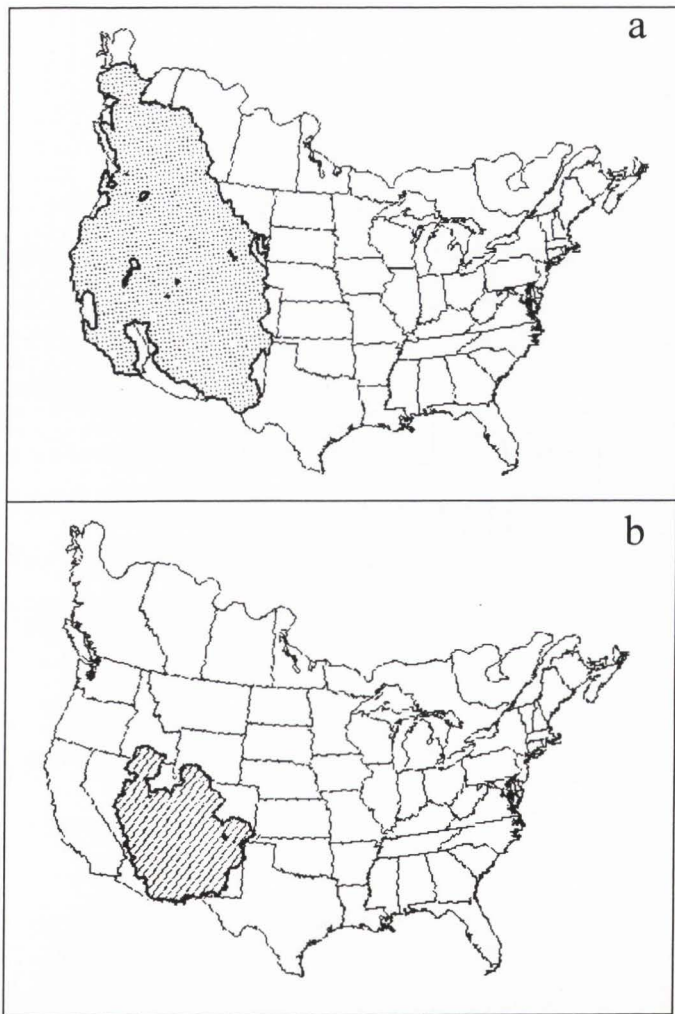


FIG. 2.1 Range distribution of the Mountain Chickadee (a) and the Juniper Titmouse (b) in North America.

METHODS

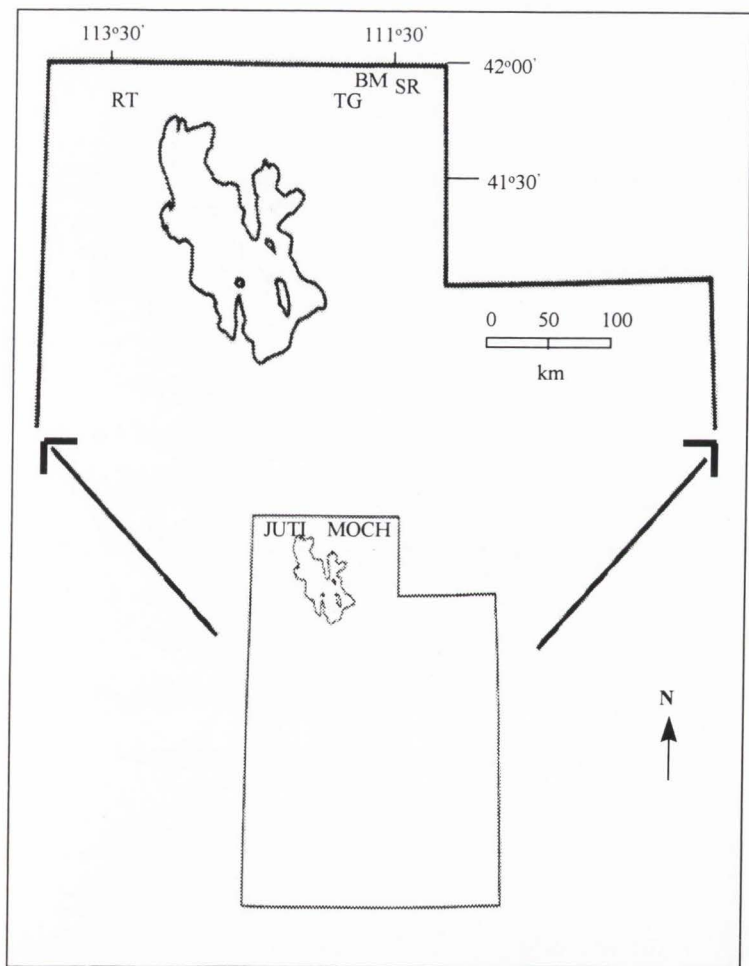
Study species and sites

Mountain Chickadees were captured in several locations within the Cache National Forest, Cache County, in northeastern Utah (41° 52'N 111° 30'W) (Fig. 2.2). Elevation ranges from 2180 to 2250 m and vegetation at these sites consists of Lodgepole pine (*Pinus contorta*), quaking aspen (*Populus tremuloides*), subalpine fir (*Abies lasiocarpa*), Englemann spruce (*Picea engelmannii*), limber pine (*Pinus flexilis*), and Douglas fir (*Pseudotsuga menziesii*). Juniper Titmice were captured near Rosette, Box Elder County, in northwestern Utah (41° 50'N 113° 25'W) (Fig. 2.2). The elevation is 1700 m and vegetation of the pygmy forest is comprised of mostly Utah Juniper (*Juniperus osteosperma*) and some singleleaf pinyon pine (*Pinus monophylla*). Although the study site locations differed for the two species, both the Mountain Chickadee and Juniper Titmouse were captured at similar latitudes, altitudes, and annual temperature profiles (Fig. 2.3). Because of the relative uniformity of these variables, I do not believe that any differences in metabolism measured in these two species are due to local climate conditions.

Experimental animals

Mountain Chickadees and Juniper Titmice were captured in summer and winter by mist net in 1994, 1995, and 1996. Body mass to the nearest 0.1 g was measured upon capture with an Ohaus model CT-1200 portable electronic balance. Following capture,

FIG. 2.2 Study site locations of Mountain Chickadees (MOCH) and Juniper Titmice (JUTI) from northern Utah. Chickadees were captured at Tony Grove (TG), Beaver Mountain Ski Area (BM), and Sunrise Campground (SR) within the Cache National Forest. Titmice were captured near Rosette (RT), Utah.



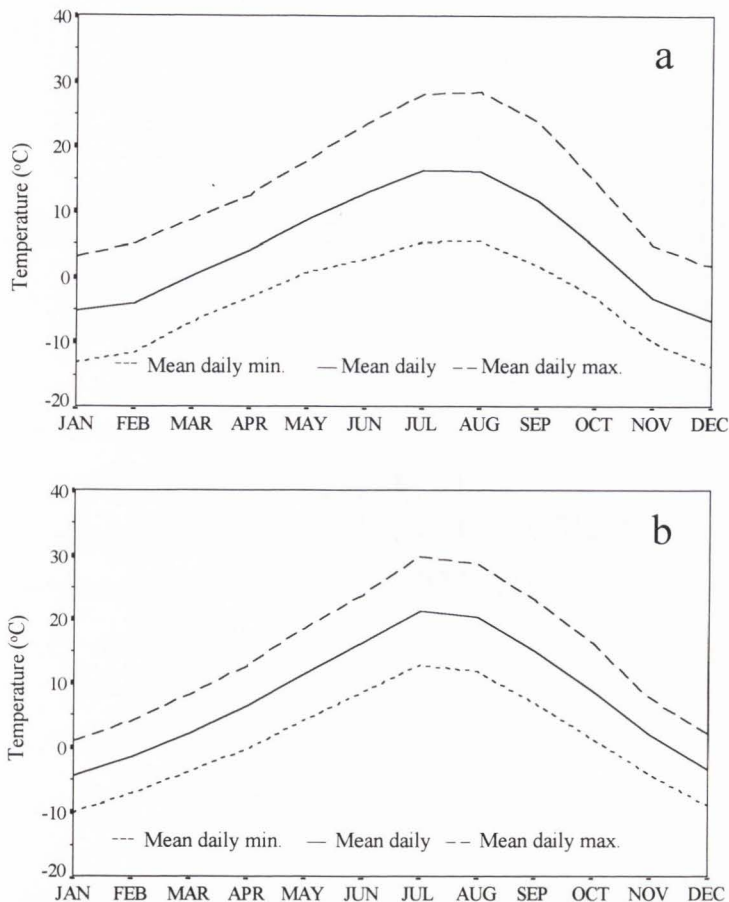


FIG. 2.3. Annual temperature profiles for Mountain Chickadee (a) and Juniper Titmouse (b) study sites in northern Utah. Weather data from Utah Climate Center, Utah State University.

birds were transported to the laboratory, where they were housed individually in 0.3-m³ cages in a 3-m³ temperature-controlled environmental chamber. The chamber temperature and photoperiod followed a cycle that approximated the season and study site to which the bird had been accustomed. While caged, birds were provided water, grit, and food (*Tenebrio* larvae and wild bird seed) *ad libitum*. All birds maintained mass while in captivity. Birds tested from 11 May to 21 August were designated "summer birds," and those tested from 25 November to 28 February were designated "winter birds."

Helox cold stress

Cold stress tests were conducted using a gas mixture of approximately 79% helium and 21% oxygen (helox). Helium is approximately four times more conductive than nitrogen. The high thermal conductivity of helox facilitates heat loss without impairing oxygen uptake and thereby allows maximal cold-induced thermogenesis or peak metabolic rate (PMR) at relatively moderate temperatures (Rosenmann and Morrison 1974). Cold stress tests were conducted by placing individual birds into a metabolic chamber constructed from a 3.8-L paint can filled approximately one-third full with solid paraffin with the inner surface painted black to provide an emissivity near 1.0. The effective volume of the metabolic chamber was calculated according to Bartholomew et al. (1981) and was 2,660 mL in the absence of a bird. Helox was then passed through the chamber at metered rates and oxygen consumption ($\dot{V}O_2$) measured (see below). The metabolic chamber was placed inside an environmental chamber capable of regulating temperature $\pm 0.5^\circ\text{C}$. Metabolic chamber temperature was monitored continuously throughout cold

stress tests with an Omega thermocouple thermometer (Model Omni IIB, previously calibrated to a thermometer traceable to the U.S. Bureau of Standards) attached to a 30-gauge copper-constantan thermocouple inserted into the inlet port of the metabolic chamber and approximately 5 cm above the bird's head.

Temperatures for cold stress were 6, 3, and 0°C in summer, and 0, -3, -6, -9, and -12°C in winter. The lower temperatures at each season caused a majority of individuals to become hypothermic. Previous studies documenting PMR in passerines indicate that helox temperatures resulting in hypothermia in a majority of individuals before 60 min elicit maximal thermogenesis and colder helox temperatures cause these birds to become rapidly hypothermic with depressed metabolic rates (Dawson and Smith 1986, Swanson 1990, 1993). Individual birds were exposed to a single temperature within the series for 65 min, or until they became hypothermic (indicated by a steady decline in $\dot{V}O_2$ over 3 min). Some individuals were tested at a second temperature within the series approximately 24 hr after their first cold stress test. At the termination of each cold stress test, birds were removed from the chamber and body temperature (T_b) ($\pm 0.1^\circ\text{C}$) was recorded with a 30-gauge copper-constantan thermocouple attached to an Omega Model HH25-TC thermometer (previously calibrated to a thermometer traceable to the U.S. Bureau of Standards). The thermocouple was inserted into the cloaca to a depth where further insertion did not alter temperature reading (approximately 10-12 mm). Birds with a cloacal temperature $< 37^\circ$ were considered hypothermic.

Maximal oxygen consumption

Prior to placing individuals in the metabolic chamber, the chamber was flushed with helox until the efflux oxygen concentration was stable. After placing a bird in the chamber, I measured the rate of oxygen consumption ($\dot{V}O_2$) during helox cold stress using open-circuit respirometry. Dry, CO₂-free helox from compressed gas cylinders was drawn through the metabolic chamber using a diaphragm pump. Outlet flow rates of 1096-1118 mL/min were maintained by a Matheson precision rotameter (Model 604) calibrated to $\pm 1\%$ volumetrically (Brooks vol-u-meter, Brooks Instrument Division, Hatfield, Pennsylvania) located downstream from the metabolic chamber. These flow rates yielded changes in oxygen content between influx and efflux gas of 0.3% to 0.7% and maintained oxygen content of efflux gas above 20.2%. In addition, these flow rates allowed the gas mixture within the metabolic chamber to reach 99% equilibrium in ≈ 11 min, as calculated using the equation of Lasiewski et al. (1966). Fractional concentration of oxygen in dry, CO₂-free efflux gas was determined from a 100 mL/min subsample using an Ametek Model S-3A oxygen analyzer (Pittsburgh, Pennsylvania). Measurements of dry, CO₂-free efflux gas were recorded every 10 s on a computer using Datacan 5.0 data collection and analysis software (Sable Systems International, Henderson, Nevada). Oxygen consumption values were calculated using Eq. 4a of Withers (1977). I analyzed PMR data according to Dawson and Smith (1986) by averaging $\dot{V}O_2$ over consecutive 10-min intervals (1-10, 2-11, etc.). The highest 10-min mean $\dot{V}O_2$ was considered PMR at the test temperature. The first 15 min of $\dot{V}O_2$ measurements were omitted from calculations

in order for efflux oxygen concentrations readings to stabilize. Tests were conducted on the day of capture or on the day after capture from 1100 to 1700 h (MST).

Basal metabolic rate measurements

Procedures utilized to measure basal metabolic rate (BMR) were similar to those for PMR except air was used rather than helox. For BMR, chamber temperature ranged from 20-30°C, which is within the thermal neutral zone for both the Mountain Chickadee and Juniper Titmouse (Cooper unpubl. data). BMR was measured from 2200 to 0300 h in summer and from 2100 hr to 0400 h (MST) in the winter. Birds were fasted for at least 4 h before testing to insure post-absorptive conditions. Dry, CO₂-free air was drawn through the metabolic chamber at outlet flow rates of 442-450 mL/min. After a 1-h equilibration period, metabolic rates were determined as the mean $\dot{V}O_2$ over a 60-min period. Oxygen consumption was calculated as steady state $\dot{V}O_2$ using Eq. 4a of Withers (1977). All values for $\dot{V}O_2$ were corrected for STP.

Statistics

All means are presented with their corresponding standard deviations. In order to determine PMR, I compared $\dot{V}O_2$ of more than two groups using one-way analysis of variance (ANOVA). Seasonal means of cold endurance, PMR, and BMR were compared using two-tailed Student's *t*-tests as variances were not significantly different (*F*-tests for equality of variances). Due to the substantial mass differences between the two species, all values of BMR and PMR were computed as mass-specific values. In addition, means

for BMR and PMR are expressed as per-unit metabolic mass (i.e., body mass raised to the $3/4$ power) in order to remove the confounding effect of mass. The effect of helox T_a on T_b was analyzed by least squares regression. Birds that became hypothermic in <25 min had substantially lower PMR than birds that remained normothermic for longer periods and were omitted from calculations of mean PMR. Statistical significance was accepted at $P < 0.05$. All statistics were computed with SPSS 6.1 (SPSS Inc., Chicago, Illinois).

This study has one inherent limitation. I cannot conclude that observed differences are adaptive evolved responses because I compare only two species (Garland and Adolph 1994). However, the purpose of this study was not to examine the process of evolutionary adaptation, but rather to examine the ecological consequences of physiological differences between two species.

RESULTS

Body mass

Mean mass at capture for summer chickadees was 11.4 ± 0.7 g ($n = 25$), which was significantly greater than winter chickadees (10.9 ± 0.8 g, $n = 26$, $t = 2.310$, $P = 0.025$). Mean mass at capture for summer titmice was 16.9 ± 1.2 g ($n = 14$), which did not differ significantly from winter titmice (16.9 ± 1.1 g, $n = 9$, $t = -0.080$, $P = 0.941$). Titmice had significantly greater body mass than chickadees in summer ($t = -18.94$, $P < 0.001$) and in winter ($t = -17.69$, $P < 0.001$). Seasonal trends for body mass at

capture paralleled those for mean body mass during metabolic tests in both species (Table 2.1).

Cold tolerance and body temperature

Both species were tolerant of colder helox temperatures in winter than in summer (Fig. 2.4). For example, greater than 50% of summer chickadees and titmice became hypothermic from 0 to 6°C while in winter it took temperatures from -6 to -12°C to induce hypothermia in greater than 50% of individuals tested. In winter, titmice were unable to tolerate helox cold stress at -12°C ($n = 4$) for more than 25 min and were omitted from PMR calculations. The average time it took for summer birds to become hypothermic in helox was 38.0 min for chickadees ($n = 19$) and 42.0 min for titmice ($n = 13$), which was not significantly different ($t = -0.790$, $P = 0.438$). In winter, the average time it took to become hypothermic in helox was 44.8 min for chickadees ($n = 17$) and 37.5 min for titmice ($n = 13$), which was not significantly different ($t = 1.350$, $P = 0.189$). For chickadees, the increased time to hypothermia in winter relative to summer was not significant ($t = -1.340$, $P = 0.189$).

Mean T_b of normothermic birds after helox cold stress in summer birds was $37.7 \pm 0.6^\circ\text{C}$ ($n = 7$) for chickadees and $38.3 \pm 1.1^\circ\text{C}$ ($n = 10$) for titmice. For winter birds, mean T_b of normothermic birds after helox cold stress was $37.9 \pm 1.1^\circ\text{C}$ ($n = 3$) for chickadees and $37.7 \pm 0.5^\circ\text{C}$ ($n = 3$) for titmice. For birds remaining normothermic throughout helox cold stress tests, T_b was independent of T_a in helox (summer: chickadees, $r^2 = 0.003$, $F = 0.015$, $P = 0.906$; titmice, $r^2 = 0.245$, $F = 2.600$, $P = 0.145$;

TABLE 2.1. Mass-specific (mW/g) and per-unit metabolic mass ($mW \cdot g^{-0.75}$) basal metabolic rates (BMR) and peak metabolic rates (PMR) for seasonally acclimatized Mountain Chickadees (MOCH) and Juniper Titmice (JUTI) from northern Utah. Values for metabolic rates were converted from mL O₂/min using an energy equivalent of 20.1 J/mL O₂. Metabolic expansibilities (ME) were determined as PMR/BMR. Body masses are means for the treatment group. Sample size is indicated in parentheses.

Species*	Body mass (g)	BMR	Body mass (g)	PMR	ME
Mass-specific					
sMOCH	11.1 ± 1.1 ^b	20.92 ± 4.32 (14) ^b	11.4 ± 0.9 ^b	125.09 ± 22.43 (26) ^b	6.0
wMOCH	11.1 ± 1.1 ^b	24.31 ± 4.18 (17) ^{a,b}	11.0 ± 0.9 ^b	159.45 ± 18.89 (9) ^{a,b}	6.6
sJUTI	16.1 ± 0.8	16.82 ± 1.81 (16)	16.2 ± 1.2	99.84 ± 11.67 (23)	5.9
wJUTI	17.2 ± 1.1 ^a	19.15 ± 2.26 (12) ^a	17.0 ± 1.1 ^a	109.61 ± 14.28 (16) ^a	5.7
Per-unit metabolic mass					
sMOCH	11.1 ± 1.1 ^b	38.12 ± 7.70 (14) ^b	11.4 ± 0.9 ^b	229.78 ± 40.65 (26) ^b	6.0
wMOCH	11.1 ± 1.1 ^b	44.35 ± 7.88 (17) ^{a,b}	11.0 ± 0.9 ^b	292.05 ± 35.49 (9) ^{a,b}	6.6
sJUTI	16.1 ± 0.8	33.63 ± 3.50 (16)	16.2 ± 1.2	200.04 ± 21.89 (16)	5.9
wJUTI	17.2 ± 1.1 ^a	39.03 ± 4.95 (12) ^a	17.0 ± 1.1 ^a	222.82 ± 32.24 (16) ^a	5.7

*Species and prefixes: s = summer, w = winter. ^a Indicates significant difference in seasonal intraspecific comparisons ($P < 0.05$). ^b Indicates significant difference in seasonal interspecific comparisons ($P < 0.05$).

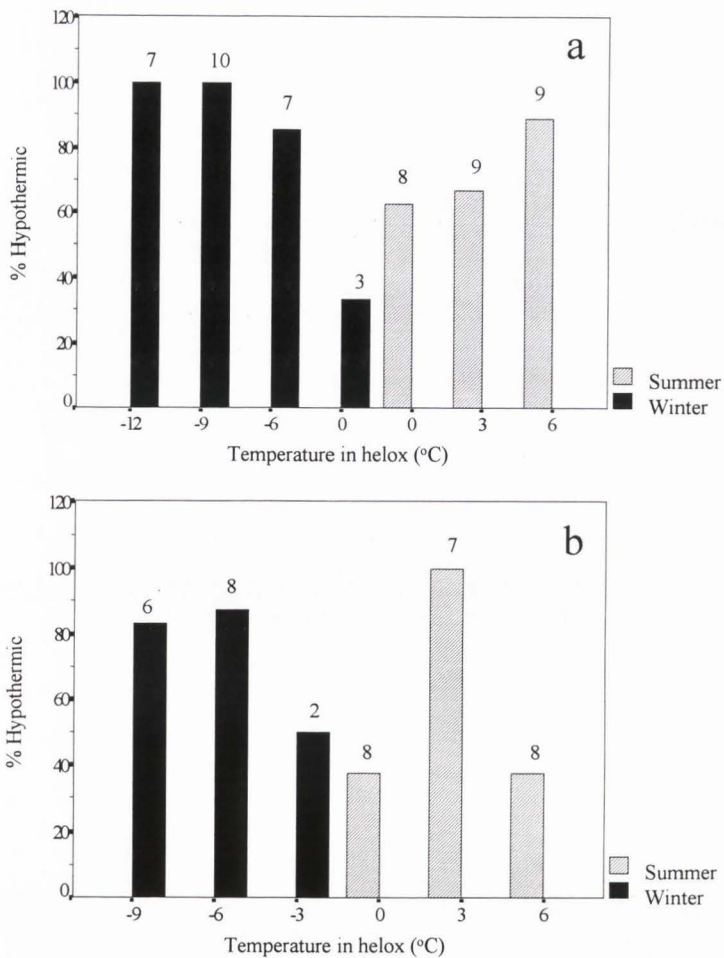


FIG. 2.4. Cold tolerance for seasonally acclimatized Mountain Chickadees (a) and Juniper Titmice (b) over the 65-min test period. Bars represent percent of individuals that became hypothermic. Numbers above bars indicate sample size.

winter: chickadees, $r^2 = 0.212$, $F = 0.270$, $P = 0.695$; titmice, $r^2 = 0.429$, $F = 0.750$, $P = 0.546$).

Cold tolerance may be influenced by seasonal variation in thermal conductance; therefore, mass-specific thermal conductance was calculated for individual birds using the equation: $C = \text{PMR} / (T_b - T_a)$ (Scholander et al. 1950). Thermal conductance for chickadees varied significantly between summer ($3.89 \pm 0.71 \text{ mWg}^{-1} \cdot ^\circ\text{C}^{-1}$, $n = 25$) and winter ($3.40 \pm 0.61 \text{ mWg}^{-1} \cdot ^\circ\text{C}^{-1}$, $n = 26$, $t = 2.67$, $P = 0.010$). Conductance for titmice also varied significantly between summer ($2.96 \pm 0.34 \text{ mWg}^{-1} \cdot ^\circ\text{C}^{-1}$, $n = 23$) and winter ($2.72 \pm 0.37 \text{ mWg}^{-1} \cdot ^\circ\text{C}^{-1}$, $n = 15$, $t = 2.03$, $P = 0.050$). Thermal conductance expressed per-unit metabolic mass was significantly lower in summer titmice ($5.93 \pm 0.64 \text{ mWg}^{-0.75} \cdot ^\circ\text{C}^{-1}$) relative to summer chickadees ($7.15 \pm 1.3 \text{ mWg}^{-0.75} \cdot ^\circ\text{C}^{-1}$, $t = 4.11$, $P < 0.001$). In winter, conductance expressed per-unit metabolic mass was not significantly different in titmice ($5.54 \pm 0.82 \text{ mWg}^{-0.75} \cdot ^\circ\text{C}^{-1}$) and chickadees ($6.17 \pm 1.13 \text{ mWg}^{-0.75} \cdot ^\circ\text{C}^{-1}$, $t = 1.91$, $P = 0.063$; Fig. 2.5).

Peak metabolic rate

Both mass-specific (mWg^{-1}) and per-unit metabolic mass ($\text{mWg}^{-0.75}$) PMR varied seasonally in chickadees and titmice, with maximum values occurring in winter (Table 2.1). For chickadees, $\dot{V}\text{O}_2$ did not vary with helox temperatures during summer, and PMR represents pooled values over the 0 to 6°C range tested ($F_{(2, 23)} = 0.165$, $P = 0.849$; Appendix Table A1; Fig. 2.6a). For summer titmice, $\dot{V}\text{O}_2$ did vary with helox temperatures ($F_{(2, 20)} = 4.835$, $P = 0.0194$; Appendix Table A2). Pairwise mean

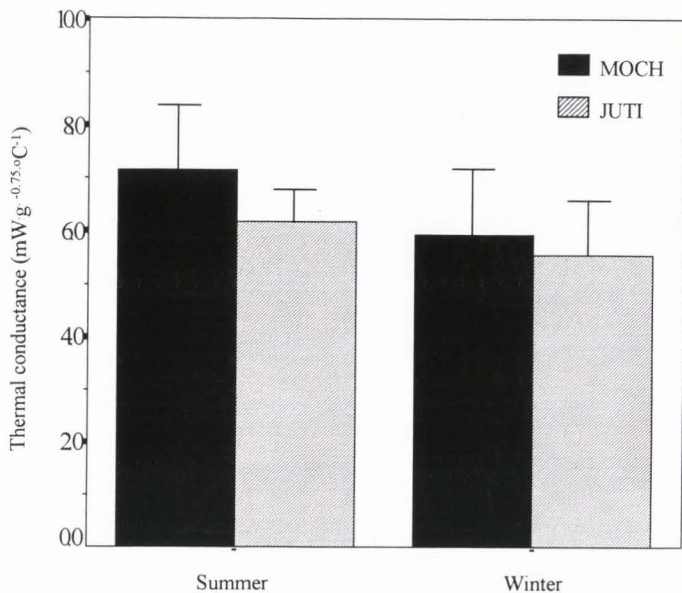


FIG. 2.5. Thermal conductance in helox on a per-unit metabolic mass basis ($\text{mW} \cdot \text{g}^{-0.75} \cdot \text{C}^{-1}$) for seasonally acclimatized Mountain Chickadees (MOCH) and Juniper Titmice (JUTI). Error bars represent standard deviations of means for each group.

comparisons were made using Fisher's *LSD* and birds at 0°C had significantly higher PMR than at 6°C. However, birds at 0°C were not different than 3°C and at 3°C were not significantly different than 6°C. Therefore, I pooled PMR over the helox temperature range for summer titmice (Fig. 2.6a). In winter titmice, $\dot{V}O_2$ did not vary with helox temperatures and PMR represents pooled values over the -3 to -9°C temperature range ($F_{(2, 13)}$, $P = 0.324$; Appendix Table A3). For winter chickadees, $\dot{V}O_2$ varied significantly with helox temperature (Appendix Table A4). Pairwise mean comparisons using Fisher's *LSD* showed that $\dot{V}O_2$ was significantly higher at -9°C compared with other test temperatures and this rate was used as the PMR ($F_{(3, 23)}$, $P = 0.007$; Fig. 2.6b).

Winter chickadees had higher mass-specific PMR ($t = 4.11$, $P < 0.001$) and per-unit metabolic mass PMR ($t = 3.71$, $P = 0.001$) than summer chickadees. Winter titmice also showed higher PMR relative to summer titmice on both a mass-specific and per-unit metabolic mass basis (mass-specific; $t = 2.35$, $P = 0.024$, per unit metabolic mass; $t = 3.05$, $P = 0.004$; Table 2.1). Summer chickadees had higher mass-specific PMR than summer titmice ($t = 4.85$, $P < 0.001$) and per-unit metabolic mass PMR also differed between species ($t = 3.24$, $P = 0.003$; Fig. 2.6a). Winter chickadees had higher mass-specific PMR ($t = 7.46$, $P < 0.001$) and per-unit metabolic mass PMR ($t = 4.97$, $P < 0.001$) than winter titmice (Fig. 2.6b).

Basal metabolic rate

Summer chickadees ($n = 14$) had significantly higher mass-specific BMR ($n = 16$, $t = 3.46$, $P = 0.002$) and per-unit metabolic mass BMR than summer titmice ($t = 2.10$,

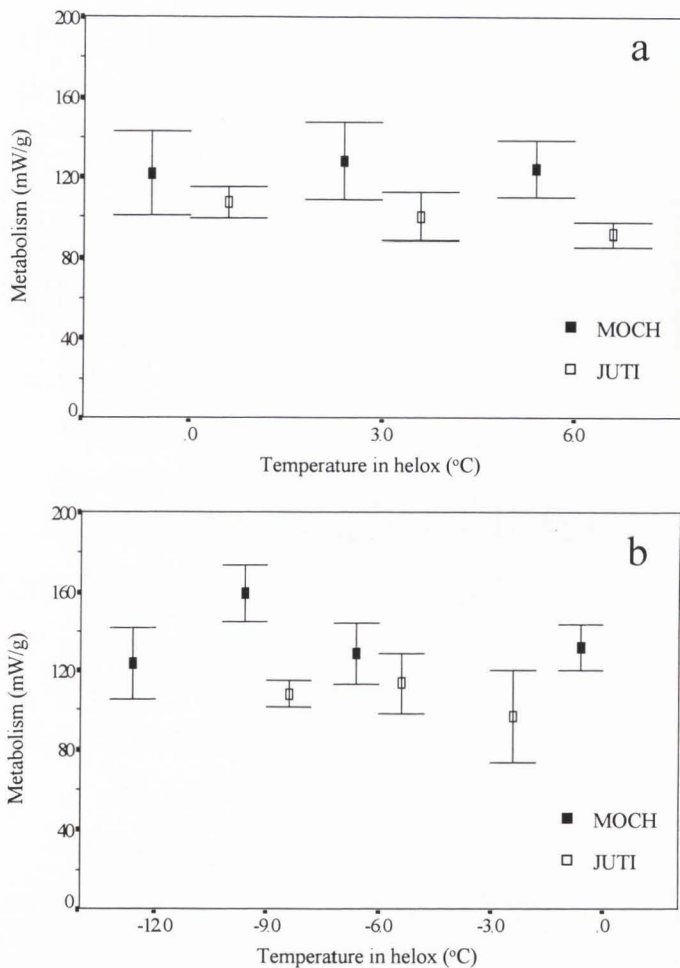


FIG. 2.6. Metabolism (mW/g) at various helox chamber temperatures for summer (a) and winter (b) acclimatized Mountain Chickadees (MOCH) and Juniper Titmice (JUTI). Means and 95% confidence intervals are shown at each temperature.

$P = 0.045$). Winter chickadees also showed a higher mass-specific BMR ($t = 3.89$, $P = 0.001$) and per-unit metabolic mass BMR in winter ($t = 2.07$, $P = 0.049$) than winter titmice (Table 2.1). Both species had significantly greater BMR in winter than in summer. BMR for winter chickadees ($n = 17$) was significantly higher on both a mass-specific and per-unit metabolic mass basis relative to summer chickadees ($t = 2.21$, $P = 0.035$). The mass-specific BMR ($t = 3.03$, $P = 0.006$) and per-unit metabolic mass BMR ($t = 3.38$, $P = 0.002$) for winter titmice ($n = 14$) were higher than for summer titmice (Table 2.1).

DISCUSSION

Body mass

The body mass of Juniper Titmice in this study did not vary seasonally, whereas Mountain Chickadees had lower body mass upon capture in winter relative to summer. Evening body masses during BMR tests were equivalent in summer and winter chickadees (Table 2.1). Increased body mass and fat stores are a common pattern of many cold-temperate wintering passerines, enabling these birds to meet thermoregulatory demands and buffer against temporary foraging restriction due to inclement weather (King 1972, Dawson and Marsh 1986, Waite 1992, O'Connor 1995). However, the body mass and fat scores of tree-foraging birds typically change little compared to ground-foraging birds (Rogers 1987). This is associated with more predictable food supplies in tree foraging birds compared to ground foraging birds (Rogers 1987, Rogers and Smith 1993). In addition, chickadees and titmice cache food in the fall for use in the winter (Bent 1946,

Haftorn 1974). Therefore, minor seasonal changes in body mass in chickadees and titmice in this study agree with the findings of Rogers (1987).

Cold tolerance and thermal conductance

The cold tolerance of both species improved in winter (Fig.2.4). Improved cold tolerance in winter-acclimatized birds is widespread in cold-temperate wintering species and is generally associated with increased thermogenic capacity (Marsh and Dawson 1986, Dawson and Marsh 1989, Swanson 1990, Cooper and Swanson 1994, O'Connor 1995, Liknes and Swanson 1996). Although cold exposure endurance did not increase significantly in these two species, increased cold tolerance is likely attributable to increased shivering endurance, which is closely linked to increased PMR (Marsh and Dawson 1989b, Bennett 1991). I estimated air temperature equivalents for helox test temperatures by inserting PMR into equations relating $\dot{V}O_2$ to T_a below thermoneutrality (Cooper unpubl. data) and solving for T_a . Estimated air temperatures ranged from -35.6 to -69.3°C for summer birds and from -63.1 to -92.6°C for winter birds. This illustrates that both species are capable of tolerating acute cold exposure well below temperatures experienced under natural conditions.

In summer, minimal thermal conductance in helox was 14.4% higher in chickadees and 8.8% higher in titmice than in winter. This indicates that winter birds are better insulated. Minimal thermal conductance was significantly lower in summer titmice compared to summer chickadees, indicating that chickadees were equally cold tolerant in summer in spite of less plumage insulation. Minimal thermal conductance in helox

exceeded minimal thermal conductance in air (Cooper unpubl. data) in summer by 2.46 times in chickadees and by 2.90 times in titmice and in winter by 2.66 times in chickadees and by 2.47 times in titmice. These values are similar to factorial increments in minimal thermal conductance induced by helox cold stress in other temperate-wintering passerines (Table 2.2). High factorial increments in minimal thermal conductance by helox cold stress indicate that heat loss in small birds is limited mainly by plumage insulation rather than body tissues such as subcutaneous fat (Dawson and Smith 1986). In addition, these values indicate that the importance of plumage insulation in chickadees and titmice is not markedly increased relative to other temperate-wintering birds.

TABLE 2.2 Enhancement of thermal conductance in helox compared to air for passerines.

Species	$C_{\text{helox}}/C_{\text{Air}}$	Reference
Common Redpoll <i>Carduelis flammea</i>	2.6	Rosenmann and Morrison (1974)
American Goldfinch <i>Carduelis tristis</i>	2.7	Dawson and Smith (1986)
House Sparrow <i>Passer domesticus</i>	1.72	Koteja (1986)
Dark-eyed Junco <i>Junco hyemalis</i>	3.0	Swanson (1990)
Black-capped Chickadee <i>Parus atricapillus</i>	2.84	Cooper and Swanson (1994)
Mountain Chickadee <i>Parus gambeli</i>	2.50 ^a	This study
Juniper Titmouse <i>Parus ridgwayi</i>	2.69 ^a	This study

^aAverage of summer and winter $C_{\text{helox}}/C_{\text{Air}}$ values.

Basal and peak metabolic rates

Both species had significantly elevated BMR and PMR in winter compared to summer. Increased BMR and PMR in winter for both chickadees and titmice demonstrate that metabolic adaptations are important components of winter acclimatization in these species. BMR varies seasonally in some passerines (Pohl and West 1973, Weathers and Caccamise 1978, Swanson 1991a, Cooper and Swanson 1994, Liknes and Swanson 1996), but not in others (Dawson and Carey 1976, Dawson et al. 1985, O'Connor 1995). Factorial increment in BMR per-unit metabolic mass was 1.16 in winter for chickadees and titmice. BMR exceeded allometrically predicted values by 9.6% for summer chickadees and 27.4% for winter chickadees. For summer titmice, BMR was 2.4% lower than allometric predictions, and for winter titmice, BMR was 13.1% higher than predicted (Aschoff and Pohl 1970). Elevated BMR in winter chickadees and titmice is possibly related to morphological and/or metabolic adjustments needed to meet the extra thermoregulatory demands of winter. For example, Dark-eyed Juncos have significantly increased pectoralis muscle and liver mass in winter compared to summer, which is associated with winter acclimatization and variation in BMR (Swanson 1991b). However, for House Finches, pectoralis mass increases in winter without a concomitant increase in BMR (O'Connor 1995). The possible adaptive significance and mechanistic basis of increased winter BMR in birds is not certain. In this study chickadees had higher BMR than titmice in both summer and winter. This increased BMR is associated with increased PMR in chickadees relative to titmice. Thus, increased BMR may likely be due to

maintenance of the increased metabolic machinery needed for increased thermogenic capacity (Swanson 1991b).

Winter PMR on a per-unit metabolic mass basis exceeds summer PMR by 27.1% in chickadees and by 11.4% in titmice. These values are within the range of winter increases in PMR in other passerines, which range from 0 to 52% greater than summer values (Marsh and Dawson 1989a, Liknes and Swanson 1996). The winter elevation of PMR for Mountain Chickadees is similar to the 36% increase in PMR recorded for winter Black-capped Chickadees (Cooper and Swanson 1994). PMR in summer was 5.0% lower for chickadees and 16.2% lower for titmice than allometrically predicted values. PMR in winter, was 19.9% higher for chickadees and 6.7% lower for titmice than predicted using the allometric equation of Dutenhoffer and Swanson (1996), which was derived using PMR values for spring, summer, and winter-acclimatized passerines. These allometric comparisons of PMR demonstrate that winter chickadees are capable of markedly increased PMR compared to other passerines. Metabolic expansibilities (PMR/BMR; Dawson and Carey 1976) for chickadees and titmice (Table 2.1) are similar to those recorded for Black-capped Chickadees in summer (6.7 x) and winter (7.9 x) and are among the highest recorded for birds, which range from 3.3 to 8.1 times (Marsh and Dawson 1986, Saarela et al. 1989, Dutenhoffer and Swanson 1996, Liknes and Swanson 1996). These metabolic expansibilities demonstrate that chickadees and titmice are capable of elevating metabolism to a substantial degree to compensate for high rates of heat loss at cold winter temperatures. In addition, these metabolic expansibilities demonstrate that chickadees and titmice are able to elevate metabolism under cold stress

to a greater degree than many passerines in spite of behavioral adaptations such as food caching and using regulated nocturnal hypothermia (Cooper unpubl. data).

Maximal thermogenic capacity may not be a precise indicator of cold tolerance in some species, because intraspecific geographic variation in cold resistance is not always related to variation in PMR but may be influenced more by differences in thermal conductance and body size (Dawson et al. 1983, Swanson 1993). Although chickadees are smaller in body size and have higher thermal conductance than titmice, they are able to withstand equal helox temperatures in summer and colder helox temperatures in winter than titmice. In addition, Marsh and Dawson (1989b) suggested that increased thermogenic endurance during cold exposure in winter involves an increased ability to sustain higher fractions of PMR compared to summer-acclimatized individuals. For species with marked winter increment of PMR, even maintaining a constant fraction of PMR would increase heat production for a given fraction of thermogenic capacity, and therefore increase cold tolerance. Therefore, PMR appears to be a good indicator of cold tolerance in chickadees and titmice.

Clearly, winter acclimatization in Mountain Chickadees and Juniper Titmice involves increased basal metabolism, maximal thermogenic capacity, and cold tolerance. Mountain Chickadees have significantly higher basal metabolism and peak metabolism compared to Juniper Titmice, which likely shape the northern range boundaries of these two species.

LITERATURE CITED

- Aschoff, J., and H. Pohl. 1970. Rhythmic variations in energy metabolism. Federation Proceedings **29**:1541-1552.
- Barnett, L. B. 1970. Seasonal changes in temperature acclimatization of the House Sparrow, *Passer domesticus*. Comparative Biochemistry and Physiology **33**:559-578.
- Bartholomew, G. A., D. Vleck, and C. M. Vleck. 1981. Instantaneous measurements of oxygen consumption during pre-flight warm-up and post-flight cooling in Sphingid and Saturnid moths. Journal of Experimental Biology **90**:17-32.
- Bent, A. C. 1946. Life histories of North American jays, crows, and titmice. United States National Museum Bulletin **191**.
- Cicero, C. 1996. Sibling species of titmice in the *Parus inornatus* complex (Aves: Paridae). University of California Publications in Zoology **128**:1-217.
- Cooper, S. J., and D. L. Swanson. 1994. Seasonal acclimatization of thermoregulation in the Black-capped Chickadee. Condor **96**:638-646.
- Dawson, W. R. 1954. Temperature regulation and water requirements of the brown and Abert Towhees, *Pipilo fuscus* and *Pipilo aberti*. University of California Publications in Zoology **59**:81-124.
- Dawson, W. R., and G. A. Bartholomew. 1968. Temperature regulation and water economy of desert birds. Pages 357-394 in G. W. Brown, Jr., editor. Desert biology. Academic Press, New York, New York, USA.

- Dawson, W. R., W. A. Buttemer, and C. Carey. 1985. A reexamination of the metabolic response of House Finches to temperature. *Condor* **87**:424-427.
- Dawson, W. R., and C. Carey. 1976. Seasonal acclimatization to temperature in cardueline finches. I. Insulative and metabolic adjustments. *Journal of Comparative Physiology* **112**:317-333.
- Dawson, W. R., and R. L. Marsh. 1986. Winter fattening in the American Goldfinch and the possible role of temperature in its regulation. *Physiological Zoology* **59**:353-369.
- Dawson, W. R., and R. L. Marsh. 1989. Seasonal acclimatization to cold and season in birds. Pages 83-94 in C. Bech and R. E. Reinertsen, editors. *Physiology of cold adaptation in birds*. Plenum Press, New York, New York, USA.
- Dawson, W. R., R. L. Marsh, W. A. Buttemer, and C. Carey. 1983. Seasonal and geographic variation of cold resistance in House Finches (*Carpodacus mexicanus*). *Physiological Zoology* **56**:353-369.
- Dawson, W. R., and T. P. O'Connor. 1996. Energetic features of avian thermoregulatory responses. Pages 85-124 in C. Carey, editor. *Avian energetics and nutritional ecology*. Chapman and Hall, New York, New York, USA.
- Dawson, W. R., and B. K. Smith. 1986. Metabolic acclimatization in the American Goldfinch (*Carduelis tristis*). Pages 427-434 in H. C. Heller, X. J. Musacchia, and L. C. H. Wang, editors. *Living in the cold: physiological and biochemical adaptations*. Elsevier, New York, New York, USA.

- Dutenhoffer, M., and D. L. Swanson. 1996. Relationship of basal to summit metabolic rate in passerine birds and the aerobic capacity model for the evolution of endothermy. *Physiological Zoology* **69**:1232-1254.
- Garland, T., Jr., and S. C. Adolph. 1994. Why not do two species comparative studies: limitations on inferring adaptation. *Physiological Zoology* **67**:797-828.
- Godfrey, W. E. 1986. The birds of Canada. National Museums of Canada, Ottawa, Canada.
- Haftorn, S. 1974. Storage of surplus food by the Boreal Chickadee *Parus hudsonicus* in Alaska, with some records on the Mountain Chickadee *Parus gambeli* in Colorado. *Ornis Scandinavica* **5**:145-161.
- Hart, J. S. 1962. Seasonal acclimatization in four species of small wild birds. *Physiological Zoology* **35**:224-236.
- Hayworth, A. M., and W. W. Weathers. 1984. Temperature regulation and climatic adaptation in Black-billed and Yellow-billed Magpies. *Condor* **86**:19-26.
- Hinds, D. S., and W. A. Calder. 1973. Temperature regulation of the Pyrrhuloxia and the Arizona Cardinal. *Physiological Zoology* **46**:55-71.
- Hinsley, S. A., P. N. Ferns, D. H. Thomas, and B. Pinshow. 1993. Black-bellied Sandgrouse (*Pterocles orientalis*) and Pin-tailed Sandgrouse (*Pterocles alchata*): closely related species with differing bioenergetic adaptations to arid zones. *Physiological Zoology* **66**:20-42.
- King, J. R. 1972. Adaptive periodic fat storage by birds. Pages 200-217 in *Proceedings of the XV Ornithological Congress*. Leiden, The Netherlands.

- Koteja, P. 1986. Maximum cold-induced oxygen consumption in the House Sparrow *Passer domesticus* L. *Physiological Zoology* 59:43-48.
- Lasiewski, R. C., A. L. Acosta, and M. H. Bernstein. 1966. Evaporative water loss in birds—I. Characteristics of the open flow method of determination, and their relation to estimates of thermoregulatory ability. *Comparative Biochemistry and Physiology* 19:445-457.
- Liknes, E. T., and D. L. Swanson. 1996. Seasonal variation in cold tolerance, basal metabolic rate, and maximal capacity for thermogenesis in White-breasted Nuthatches *Sitta carolinensis* and Downy Woodpeckers *Picoides pubescens*, two unrelated arboreal temperate residents. *Journal of Avian Biology* 27:279-288.
- Marsh, R. L., and W. R. Dawson. 1986. Role of metabolic adjustments in avian survival of cold winters. *Proceedings of the International Ornithological Congress* 29:2690-2701.
- Marsh, R. L., and W. R. Dawson. 1989a. Avian adjustments to cold. Pages 205-253 *in* L. C. H. Wang, editor. *Advances in comparative and environmental physiology*. Springer, Berlin, Germany.
- Marsh, R. L., and W. R. Dawson. 1989b. Energy substrates and metabolic acclimatization in small birds. Pages 105-114 *in* C. Bech and R. E. Reinertsen, editors. *Physiology of cold adaptation in birds*. Plenum Press, New York, New York, USA.
- Moulton, M. P., and S. L. Pimm. 1983. The introduced Hawaiian avifauna: biogeographic evidence for competition. *American Naturalist* 121:669-690.

- O'Connor, T. P. 1995. Metabolic characteristics and body composition in house finches: effects of seasonal acclimatization. *Journal of Comparative Physiology B* **165**:298-305.
- Pohl, H., and G. C. West. 1973. Daily and seasonal variation in metabolic response to cold and forced exercise in the Common Redpoll. *Comparative Biochemistry and Physiology* **45A**:851-867.
- Rising, J. D. 1969. A comparison of metabolism and evaporative water loss of Baltimore and Bullock orioles. *Comparative Biochemistry and Physiology* **31**:915-925.
- Rogers, C. M. 1987. Predation risk and fasting capacity: do wintering birds maintain optimal body mass? *Ecology* **68**:1051-1061.
- Rogers, C. M., and J. N. M. Smith. 1993. Life-history theory in the nonbreeding period: trade-offs in avian fat reserves. *Ecology* **74**:419-426.
- Root, T. 1988a. Environmental factors associated with avian distributional boundaries. *Journal of Biogeography* **15**:489-505.
- . 1988b. Energy constraints on avian distributions and abundance. *Ecology* **69**:330-339.
- . 1988c. Atlas of wintering North American birds. University of Chicago Press, Chicago, Illinois, USA.
- Rosenmann, M., and P. Morrison. 1974. Maximum oxygen consumption and heat loss facilitation in small homeotherms by HeO_2 . *American Journal of Physiology* **226**:490-495.

- Saarela, S., B. Klapper, and G. Heldmaier. 1989. Thermogenic capacity of Greenfinches and Siskins in winter and summer. Pages 115-112 in C. Bech and R. E. Reinertsen, editors. Physiology of cold adaptation in birds. Plenum Press, New York, New York, USA.
- Scholander, P. R., R. Hock, V. Walters, F. Johnson, and L. Irving. 1950. Heat regulation in some arctic and tropical mammals and birds. *Biological Bulletin* **99**:237-258.
- Swanson, D. L. 1990. Seasonal variation in cold hardiness and peak rates of cold-induced thermogenesis in the Dark-eyed Junco (*Junco hyemalis*). *Auk* **107**:561-566.
- . 1991a. Seasonal adjustments in metabolism and insulation in the Dark-eyed Junco. *Condor* **93**:538-545.
- . 1991b. Substrate metabolism under cold stress in seasonally acclimatized Dark-eyed Juncos. *Physiological Zoology* **64**:1578-1592.
- . 1993. Cold tolerance and thermogenic capacity in Dark-eyed Juncos in winter: geographic variation and comparison with American Tree Sparrows. *Journal of Thermal Biology* **18**:275-281.
- Terborgh, J., and J. S. Weske. 1975. The role of competition in the distribution of Andean birds. *Ecology* **56**:562-576.
- Waite, T. A. 1992. Winter fattening in Gray Jays: seasonal, diurnal, and climatic correlates. *Ornis Scandinavica* **23**:499-503.
- Weathers, W. W., and D. F. Caccamise. 1978. Seasonal acclimatization to temperature in Monk Parakeets. *Oecologia* **35**:173-183.

- Weathers, W. W., and C. van Riper. 1982. Temperature regulation in two endangered Hawaiian honeycreepers: the Palila (*Psittirostra bailleui*) and the Laysan Finch (*Psittirostra cantans*). *Auk* **99**:667-674.
- Withers, P. C. 1977. Measurement of $\dot{V}O_2$, $\dot{V}CO_2$, and evaporative water loss with a flow-through mask. *Journal of Applied Physiology* **42**:120-123.

CHAPTER 3

SEASONAL THERMOREGULATION IN THE MOUNTAIN CHICKADEE
AND THE JUNIPER TITMOUSE: EFFECTS OF ENERGETIC
CONSTRAINTS ON RANGE DISTRIBUTION¹

ABSTRACT.--The Mountain Chickadee (*Parus gambeli*) and the Juniper Titmouse (*Parus ridgwayi*) are closely related, ecologically similar passerines, that are year-round residents of regions of western North America with different northern range distributions. I measured oxygen consumption, evaporative water loss, body temperature, and body composition on seasonally acclimatized individuals in order to determine patterns of cold acclimatization in these species and to determine if cold acclimatization shapes the northern range distribution of these two species.

Pectoralis muscle mass increased 33% in chickadees and 24% in titmice in winter and paralleled increased basal and peak metabolic rates. Dry mass of contour plumage increased in winter for both species and was associated with decreased thermal conductance in winter chickadees compared to summer chickadees. The Mountain Chickadee's lower critical temperature is 4.2°C lower than the Juniper Titmouse's in summer and 2.4°C lower in winter. The Mountain Chickadee's upper critical temperature is 4.2°C lower than the Juniper Titmouse's and chickadees also had significantly higher evaporative water loss rates compared to titmice.

¹This chapter when submitted to the Auk will be coauthored with Dr. J. A. Gessaman.

Calculated northern boundary metabolic rates of winter chickadees are 2.47 times their basal metabolic rate and 2.80 times basal metabolic rate for titmice. This is in close agreement with a proposed 2.45 times basal metabolic rate as a limit to northern range distributions in passerines. In addition, the data for cold tolerance and heat tolerance suggest that climate acts directly to shape the biogeographic patterns of the Mountain Chickadee and Juniper Titmouse.

Climate may influence the biogeography of birds physiologically through its impact on energy and water balance, and/or ecologically through its impact on food availability and vegetation (Weathers and van Riper 1982). For birds, the general viewpoint is that climate limits range distribution through its ecological and behavioral factors rather than by physiological factors (Bartholomew 1958, Dawson and Bartholomew 1968). However, significant energetic differences are apparent in similar bird species from dissimilar climates (Dawson 1954, Rising 1969, Hinds and Calder 1973, Weathers and van Riper 1982, Hayworth and Weathers 1984, Hinsley et al. 1993). In spite of these data, generalizations regarding the association between biogeography and physiology for birds are not clear. Root (1988a) provides data for 14 species of passerines that have northern winter range limits restricted to areas where the energy required for maintenance and thermoregulation does not exceed ≈ 2.5 times basal metabolic rate (BMR). These data indicate that biogeography in small birds may be directly affected by climate. In order to determine how pervasive physiology may be on range distributions, seasonal acclimatization of thermoregulation needs to be examined in closely related species that

have different northern range boundaries.

The Mountain Chickadee (*Parus gambeli*) and the Juniper Titmouse (*Parus ridgwayi*) are small, mostly nonmigratory members of the Paridae family that occupy regions of western North America. The Plain Titmouse (*Parus inornatus*) has recently been split into the Oak Titmouse (*Parus inornatus*) and the Juniper Titmouse (*Parus ridgwayi*) (Cicero 1996). The Juniper Titmouse's northern range extends to portions of southern Oregon and Idaho (44° N), whereas the Mountain Chickadee's northern range extends to northern British Columbia (60° N) (Godfrey 1986, Cicero 1996). The primary environmental factor associated with the northern range distribution of the Juniper Titmouse is vegetation. The northern range boundary of Mountain Chickadees is not associated with any of six environmental variables examined by Root (1988b). However, the northern range of the Mountain Chickadee does not extend past a -23°C average minimum January temperature isotherm, whereas the Juniper Titmouse's northern range does not extend beyond a -12°C isotherm of mean minimum January temperature (Root 1988c). Therefore, I studied seasonal variation in body mass and composition, metabolic response to temperature, and evaporative water loss in Mountain Chickadees and Plain Titmouse to determine patterns of metabolic and insulatory cold acclimatization and determine if metabolic and insulatory acclimatization may shape the biogeography of these two species. In addition, using the data from this study, I calculated northern boundary metabolic rate (NBMR) for these two species in order to determine if it was less than 2.5 times BMR as predicted by Root (1988a).

STUDY AREA AND METHODS

Study area.--Mountain Chickadees were captured in several locations within the Cache National Forest, Cache County, in northeastern Utah at elevations of 2180 to 2250 m. Juniper Titmice were captured near Rosette, Box Elder County, in northwestern Utah at an elevation of 1700 m (see Fig. 2.2). Although the two species were collected at different study sites, both Mountain Chickadees and Juniper Titmice were captured at similar latitudes, altitudes, and annual temperature profiles (Fig. 3.1). Therefore, I do not believe that any differences in metabolism measured in these two species are due to local climate conditions.

Birds.--Mountain Chickadees and Juniper Titmice were captured by mist net in summer and winter of 1994, 1995, and 1996 (Scientific collecting permits: UT 2COLL1401, USFWS PRT-779300). Mass at capture was measured to the nearest 0.1 g with an Ohaus model CT-1200 portable electronic balance. Visible fat depots in abdominal and furcular regions were also scored upon capture using a scale of 0-5 (Helms and Drury 1960). Following capture, birds were transported to Logan, Utah, where they were housed individually in 0.3 x 0.3 x 0.3 m cages placed in a 3 x 3 x 2.5 m temperature-controlled environmental chamber. The environmental chamber was reprogrammed weekly to simulate the current photocycle and thermal regime of the study site to which the bird was accustomed. While in captivity, birds were provided free access to water, grit, and food (*Tenebrio* larvae and wild bird seed). All birds maintained mass while caged. Birds tested from 17 May to 1 September were designated "summer birds," and

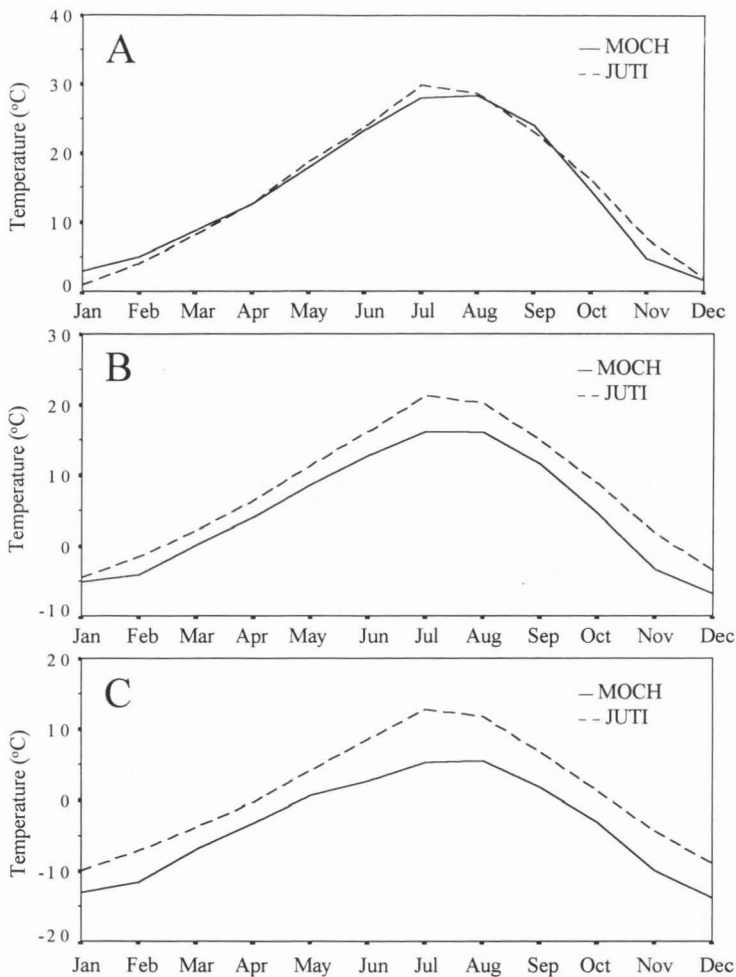


FIG. 3.1. Annual temperature profiles for Mountain Chickadee (MOCH) and Juniper Titmouse (JUTI) study sites in northern Utah. Mean daily maximum (A), mean daily (B), and mean daily minimum (C) plotted for each month.

those tested from 20 November to 1 March were designated "winter birds."

Body composition.--Body composition was determined for birds captured before 0800 h in summer and 0900 h (MST) in winter. Birds were killed by cervical dislocation after body mass and fat scores were determined. The carcasses were then sealed in plastic bags, placed in an ice cooler in the field, and then stored in a freezer at -20°C upon return to the laboratory. Plumage mass was determined by plucking and drying contour feathers in an open-ended vial at $50\text{-}60^{\circ}\text{C}$. The right pectoralis muscle was dissected out of each carcass and wet mass measured. Carcass (including right pectoralis muscle), remiges, and retrices were minced and dried at $50\text{-}60^{\circ}\text{C}$ to a constant mass. Neutral lipid was extracted from the dry carcass by Soxhlet extraction for 8 h in petroleum ether (Dobush et al. 1985). Following the ether extraction, the lean carcass was air dried for 6 h, and then oven dried at $50\text{-}60^{\circ}\text{C}$ to constant mass. The difference between body mass at capture and dry mass equals the total body water. The difference between dry body mass and lean dry mass equals the extractable neutral lipid.

Metabolic response to temperature.-- Nighttime metabolic rate and evaporative water loss (EWL) were measured for Mountain Chickadees and Juniper Titmice in both summer and winter. Measurements were made on individual birds using a 3.8-L metabolic chamber fashioned from a paint can. The inside of the metabolic chamber was painted flat black to provide an emissivity near 1.0. Metabolic chamber temperature was regulated within $\pm 0.5^{\circ}\text{C}$ by placing it in a temperature-controlled environmental chamber. Metabolic chamber temperature was monitored continuously throughout each test with an Omega thermocouple thermometer (Model Omni IIB, previously calibrated to a thermometer

traceable to the U.S. Bureau of Standards) attached to a 30-gauge copper-constantan thermocouple inserted into the inlet port of the metabolic chamber. Metabolic response to temperature (MRT) was measured from 2200 to 0300 h in summer and from 2100 to 0400 h (MST) in winter. Birds were fasted for at least 4 h prior to metabolic tests to insure post-absorptive conditions. Individuals were weighed and then placed inside the metabolic chamber where they perched on 1.0-cm wire mesh placed 3.0 cm above a 1-cm layer of paraffin oil used for the collection of fecal material. Oxygen consumption ($\dot{V}O_2$) was then measured using open-circuit respirometry with an Ametek Model S-3A oxygen analyzer. Dry, CO₂-free air was drawn through the metabolic chamber using a diaphragm pump. Outlet flow rates of dry, CO₂-free air were maintained by a Matheson precision rotameter (Model 604) calibrated to $\pm 1.0\%$ volumetrically (Brooks vol-u-meter) and located downstream from the metabolic chamber. These flow rates yielded changes in oxygen content between influx and efflux gas of 0.3 to 0.6% and maintained oxygen content of efflux gas above 20.3%. Fractional concentration of oxygen in efflux gas was determined from a 100 mL/min subsample passed through the oxygen analyzer. This subsample of efflux gas was recorded every 15 sec using the Datacan 5.0 data acquisition and analysis program (Sable Systems International). Evaporative water loss (EWL) was determined over a 60-min timed interval by measuring the increase in mass of a downstream absorbant train containing Drierite. All weighings were made on an analytical balance (Mettler H51AR).

MRT and EWL were measured on individual birds exposed to a single temperature within a temperature range of -10 to 44°C. The order of temperatures selected was

randomized. Each bird was used only once during a 24-h period and was tested no more than twice total. If an individual was tested twice, it was tested at a $T_a \leq 30^\circ$ and a $T_a \geq 30^\circ\text{C}$. All individuals were tested within 1 week of capture. Flow rates were maintained at 442-450 mL/min for temperatures below 30°C and 1096-1118 mL/min for temperatures above 30°C . These flow rates maintained chamber dew point temperature below 12°C (Lasiewski et al. 1966). Individual birds were placed in the metabolic chamber for a total of 2 h for temperatures $\leq 30^\circ\text{C}$. The first hour was an equilibration time and $\dot{V}\text{O}_2$ was measured over the last 60 min of the trial. For metabolic trials at temperatures $> 30^\circ\text{C}$, individuals were in the chamber for 60 min. The first 10 min was equilibration (time needed for chamber to reach 99% equilibrium using equation of Lasiewski et al. 1966) and $\dot{V}\text{O}_2$ was measured over the last 50 min of the trial. Oxygen consumption was calculated as steady state $\dot{V}\text{O}_2$ using Eq. 4a of Withers (1977). All values were corrected for STP.

Statistics.--Data are reported as means \pm SE. Mean values of neutral lipid, lean dry mass, body water mass, pectoralis mass, and plumage mass were adjusted by analysis of covariance (ANCOVA) using body mass as a covariate. Differences between means were determined by initially testing the *F*-ratio for group variances and then applying a *t*-test for either equal or unequal variances as appropriate. Regression lines were fit by the method of least squares. Homogeneity of slopes of regression lines were compared using *t*-tests, following the protocol of Zar (1984). Intercepts of regression lines were compared by ANCOVA. Statistical significance was accepted at $P < 0.05$.

RESULTS

Body mass and composition.--Mean morning mass at capture for chickadees was significantly lower in winter than summer ($t = 2.660$, $P = 0.009$; Table 3.1) Chickadees that were captured in the evening were significantly heavier than those captured in the morning ($t = -3.390$, $P = 0.001$; Table 3.1). Mean morning mass at capture for titmice did not vary seasonally ($t = 0.380$, $P = 0.707$; Table 3.1). Evening body mass in titmice was not significantly different than mean morning mass (summer, $t = -1.280$, $P = 0.218$; winter, $t = -1.110$, $P = 0.298$; Table 3.1). Titmice had significantly greater body mass than chickadees in summer ($t = -18.530$, $P < 0.001$) and in winter ($t = -20.290$, $P < 0.001$; Table 3.1).

Visible fat depots in furcular and abdominal regions did not vary seasonally in titmice (furcular, $t = 0.380$, $P = 0.707$; abdominal, $t = -0.410$, $P = 0.683$; Table 3.1). Winter chickadees had significantly higher furcular fat scores than in summer ($t = -2.41$, $P = 0.015$), but did not vary seasonally in abdominal fat scores ($t = -1.58$, $P = 0.111$; Table 3.1). Visible fat depots was not significantly different between summer chickadees and titmice (furcular, $t = -0.910$, $P = 0.376$; abdominal, $t = 1.83$, $P = 0.074$; Table 3.1). Fat content did not vary seasonally in chickadees ($t = 0.080$, $P = 0.940$) or titmice ($t = 0.250$, $P = 0.814$). Fat content was not significantly different between summer birds ($t = 1.970$, $P = 0.08$) or winter birds ($t = 0.55$, $P = 0.958$; Table 3.1).

Metabolic response to temperature.--BMR was 3.75 ± 0.21 ml $O_2 \cdot g^{-1} \cdot h^{-1}$ ($n = 14$) in summer chickadees and 3.01 ± 0.08 ml $O_2 \cdot g^{-1} \cdot h^{-1}$ ($n = 16$) in summer titmice. BMR was

TABLE 3.1. Seasonal values of body mass and composition for Mountain Chickadees (MOCH) and Juniper Titmice (JUTI). All values are for morning birds except evening body mass. Sample size is indicated in parentheses. Mean values are presented with their corresponding standard errors. Adjusted means were determined by ANCOVA using body mass as the covariate. Means were compared using *t*-tests.

Measurement	Summer		Winter	
	MOCH	JUTI	MOCH	JUTI
Total body mass (g)				
morning	11.2 ± 0.1 (50)	16.9 ± 0.3 (20) ^b	10.8 ± 0.1 (46) ^a	16.8 ± 0.3 (13) ^b
evening	12.6 ± 0.2 (3) ^c	17.8 ± 0.6 (4)	—	17.6 ± 0.9 (3)
Fat content (g)	0.36 ± 0.03 (8)	0.77 ± 0.09 (4)	0.36 ± 0.05 (7)	0.72 ± 0.17 (4)
Adjusted means	0.54 ± 0.06	0.60 ± 0.05	0.56 ± 0.06	0.56 ± 0.09
Visible fat -furcular	0.06 ± 0.03 (50)	0.19 ± 0.14 (16)	0.29 ± 0.09 (46) ^a	0.11 ± 0.11 (9)
-abdominal	0.22 ± 0.06 (50)	0.06 ± 0.06 (16)	0.39 ± 0.09 (46)	0.11 ± 0.11 (9)
Lean dry mass (g)	2.84 ± 0.08 (8)	4.88 ± 0.19 (4)	2.79 ± 0.14 (7)	4.41 ± 0.20 (4)
Adjusted means	3.41 ± 0.05	4.31 ± 0.15 ^b	3.38 ± 0.13	4.00 ± 0.18 ^b
Plumage mass (g)	0.28 ± 0.03 (7)	0.46 ± 0.04 (6)	0.57 ± 0.03 (7) ^a	0.67 ± 0.03 (4) ^a
Adjusted means	0.36 ± 0.02	0.38 ± 0.02	0.52 ± 0.02	0.73 ± 0.04
Pectoralis mass (g)	0.78 ± 0.05 (8)	0.79 ± 0.05 (6)	1.04 ± 0.05 (7) ^a	0.98 ± 0.07 (4)
Adjusted means	1.03 ± 0.03	0.55 ± 0.04 ^b	1.11 ± 0.06	0.91 ± 0.05

^aIndicates significant difference in seasonal intraspecific comparisons ($P < 0.05$). ^bIndicates significant differences in seasonal interspecific comparisons ($P < 0.05$). ^cIndicates significant differences in intraspecific comparisons ($P < 0.05$) within a season.

significantly higher in summer chickadees compared to titmice ($t = 3.300, P = 0.004$). In winter, BMR was $4.36 \pm 0.18 \text{ ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$ in chickadees ($n = 17$) and $3.43 \pm 0.12 \text{ ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$ in titmice ($n = 12$). BMR was significantly higher in winter chickadees compared to titmice ($t = 3.890, P = 0.001$). Intraspecific comparisons show that winter birds had significantly higher BMR compared to summer birds (chickadees, $t = 2.21, P = 0.035$; titmice, $t = 3.03, P = 0.006$).

Below thermoneutrality, the relationship between mass-specific $\dot{V}\text{O}_2$ ($\text{ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$) and standard operative temperature for summer birds (Fig. 3.2A) and winter birds (Fig. 3.2B) was best described by least squares regression equations in Table 3.2. For interspecific comparisons of summer birds, the slopes of the two regression lines were significantly different ($t = -6.621, P < 0.001$) and the intercepts were significantly different ($F_{(1,29)} = 24.300, P < 0.001$). Interspecific comparisons of regression equations for winter birds were significantly different in slopes ($t = -6.754, P < 0.001$) and intercepts ($F_{(1,16)} = 9.920, P = 0.006$). For chickadees, slopes were significantly different between seasons ($t = -6.091, P < 0.001$) and intercepts were also significantly different between seasons ($F_{(1,21)} = 12.060, P = 0.002$). For titmice, however, neither slopes ($t = 1.520, P = 0.082$) nor intercepts ($F_{(1,24)} = 3.230, P = 0.085$) were significantly different between seasons. Lower critical temperature (LCT) was calculated as the intersection of the regression line below thermoneutrality with a horizontal line through mean BMR for each species and season, respectively. LCT was 18.7°C in summer chickadees, 22.9°C in summer titmice, 14.7°C in winter chickadees, and 17.1°C in winter titmice.

Overall thermal conductance below thermoneutrality is equivalent to the slope of

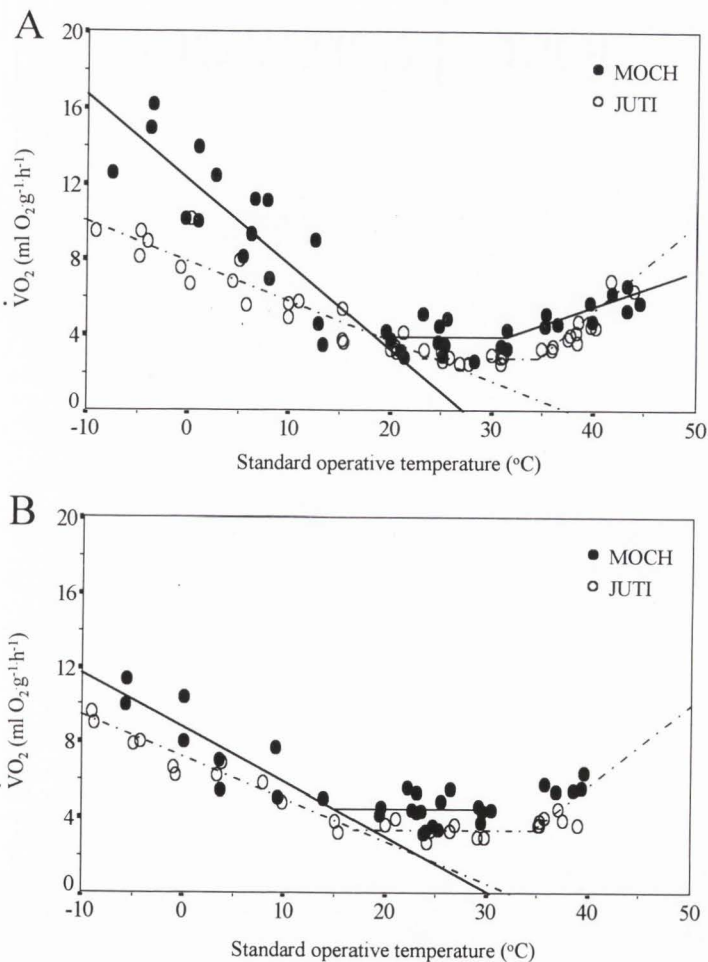


FIG. 3.2. Relationship between metabolism ($\dot{V}O_2$) and standard operative temperature (T_{es}) for (A) summer-acclimatized and (B) winter-acclimatized Mountain Chickadees (MOCH) and Juniper Titmice (JUTI). Horizontal lines represent mean BMR.

TABLE 3.2. Relationship of mass-specific $\dot{V}O_2$ ($\text{ml O}_2 \text{g}^{-1} \text{h}^{-1}$) to standard operative temperature ($^{\circ}\text{C}$) below thermoneutrality for seasonally acclimatized Mountain Chickadees (MOCH) and Juniper Titmice (JUTI).

Species	<i>n</i>	Regression equation	$s_{y,x}$	s_b	r^2	<i>P</i>
sMOCH	15	$\dot{V}O_2 = 12.15 - 0.45 T_{cs}$	0.68	0.09	0.65	< 0.001
sJUTI	17	$\dot{V}O_2 = 7.87 - 0.21 T_{cs}$	0.27	0.03	0.80	< 0.001
wMOCH	9	$\dot{V}O_2 = 8.75 - 0.30 T_{cs}$	0.51	0.07	0.71	0.004
wJUTI	10	$\dot{V}O_2 = 7.08 - 0.21 T_{cs}$	0.18	0.03	0.88	< 0.001

*species and prefixes: s = summer, w = winter; $s_{y,x}$ = standard error of regression coefficient *a*; s_b = standard error of regression coefficient *b*.

the line relating $\dot{V}O_2$ to standard operative temperature only if the curve extrapolates to T_b at zero metabolism. Since the metabolic data from chickadees and titmice did not conform to the Newton-Scholander cooling model (Scholander et al. 1950), I calculated overall thermal conductance (K_{cs}) for individuals using the equation of Bakken (1976)

$$K_{cs} = (M - E)/(T_b - T_{cs}) \quad (3.1)$$

where *M* is metabolic rate and *E* is evaporative heat loss (assuming 2.429 J of heat for each mg of water evaporated). Thermal conductance below thermoneutrality was $1.57 \pm 0.13 \text{ mW g}^{-1} \text{ } ^{\circ}\text{C}^{-1}$ for summer chickadees ($n = 15$), which was significantly higher than $1.02 \pm 0.07 \text{ mW g}^{-1} \text{ } ^{\circ}\text{C}^{-1}$ for summer titmice ($n = 17$, $t = 3.880$, $P = 0.001$). K_{cs} for winter chickadees was $1.21 \pm 0.09 \text{ mW g}^{-1} \text{ } ^{\circ}\text{C}^{-1}$ ($n = 9$), which was not significantly different from winter titmice ($1.10 \pm 0.03 \text{ mW g}^{-1} \text{ } ^{\circ}\text{C}^{-1}$, $n = 10$, $t = 1.600$, $P = 0.139$). K_{cs} was not significantly different between summer and winter titmice ($t = 1.120$, $P = 0.275$) but was significantly lower in winter chickadees compared to summer ($t = -2.240$, $P = 0.035$).

Above thermoneutrality the relationship between mass-specific $\dot{V}O_2$ ($\text{ml O}_2 \text{g}^{-1} \text{h}^{-1}$) and standard operative temperature for summer birds (Fig. 3.2A) and winter birds

(Fig. 3.2B) was best described by least squares regression equations in Table 3.3. For interspecific comparisons of summer birds, the slopes of the two regression lines were significantly different ($t = 4.540, P < 0.001$) but the intercepts were not significantly different ($F_{(1,17)} = 2.760, P = 0.115$). Interspecific comparisons of regression equations for winter birds were significantly different in slopes ($t = 2.530, P = 0.039$) but intercepts were not significantly different ($F_{(1,7)} = 4.310, P = 0.076$). For chickadees, slopes were significantly different between seasons ($t = 3.714, P = 0.003$) and intercepts were also significantly different between seasons ($F_{(1,13)} = 6.960, P = 0.020$). For titmice, slopes were significantly different between seasons ($t = 5.913, P = 0.082$) and intercepts ($F_{(1,11)} = 7.300, P = 0.021$) were significantly different between seasons. Upper critical temperature (UCT) was calculated as the intersection of the regression line above thermoneutrality with a horizontal line through mean BMR for each species and season, respectively. UCT was 31.5°C in summer chickadees, 35.7°C in summer titmice, and 35.0°C in winter titmice. UCT for winter chickadees could not be calculated since metabolism above thermoneutrality was not a linear function of T_{ca} . Mean body

TABLE 3.3. Relationship of mass-specific $\dot{V}O_2$ (ml $O_2 g^{-1} h^{-1}$) to standard operative temperature (°C) above thermoneutrality for seasonally acclimatized Mountain Chickadees (MOCH) and Juniper Titmice (JUTI).

Species	<i>n</i>	Regression equation	s_{y_x}	s_b	r^2	<i>P</i>
sMOCH	11	$\dot{V}O_2 = -2.09 + 0.19 T_{\text{ca}}$	2.14	0.05	0.56	0.007
sJUTI	9	$\dot{V}O_2 = -14.12 + 0.48 T_{\text{ca}}$	4.08	0.10	0.75	0.002
wMOCH	5	$\dot{V}O_2 = 2.60 + 0.08 T_{\text{ca}}$	4.89	0.13	0.12	0.565
wJUTI	5	$\dot{V}O_2 = -16.10 + 0.56 T_{\text{ca}}$	6.21	0.17	0.79	0.044

*species and prefixes: s = summer, w = winter; s_{y_x} = standard error of regression coefficient *a*; s_b = standard error of regression coefficient *b*.

temperature above UCT in summer chickadees was $42.6 \pm 0.7^\circ\text{C}$ ($n = 11$), which was significantly higher than summer titmice (41.4 ± 0.4 , $n = 9$, $t = -1.630$, $P = 0.007$).

Evaporative water loss.-- In summer, above 30°C the rate of EWL of both species increased exponentially (Fig. 3.3A), as is typical of endotherms. In winter, above 20°C the rate of EWL of both species increased exponentially (Fig. 3.3B). In order to compare the EWL response to varying temperature, the natural logarithm of EWL was plotted against T_{es} for both species in summer (Fig. 3.4A) and winter (Fig. 3.4B). The relationship between \ln EWL and T_{es} was best described by the regression equations in Table 3.4. For interspecific comparisons of summer birds, the slopes of the two regression lines were not significantly different ($t = 1.250$, $P = 0.121$) and the intercepts were not significantly different ($F_{(1,65)} = 1.340$, $P = 0.252$). Interspecific comparisons of regression equations for winter birds were not significantly different in slopes ($t = 1.010$, $P = 0.267$) but intercepts were significantly different ($F_{(1,44)} = 6.390$, $P = 0.015$). For chickadees, slopes were significantly different between seasons ($t = 12.936$, $P < 0.001$) and intercepts were also significantly different between seasons ($F_{(1,60)} = 5.050$, $P = 0.028$). For titmice, slopes were significantly different between seasons ($t = 15.036$, $P < 0.001$) and intercepts ($F_{(1,49)} = 13.37$, $P = 0.001$) were significantly different between seasons.

DISCUSSION

Body mass and composition.--Juniper Titmice in this study did not show seasonal variation in body mass, visible fat, or fat content. The decreased morning body mass of winter-acclimatized Mountain Chickadees was probably due to increased length of

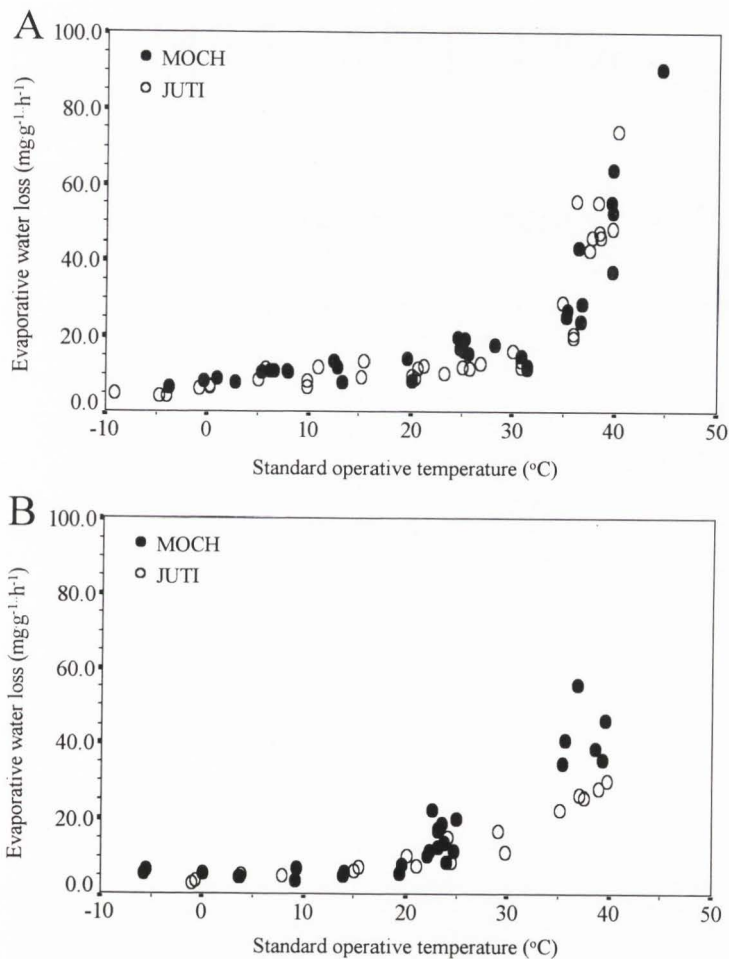


Fig. 3.3. Relationship between evaporative water loss and standard operative temperature for (A) summer and (B) winter acclimatized Mountain Chickadees (MOCH) and Juniper Titmice (JUTI).

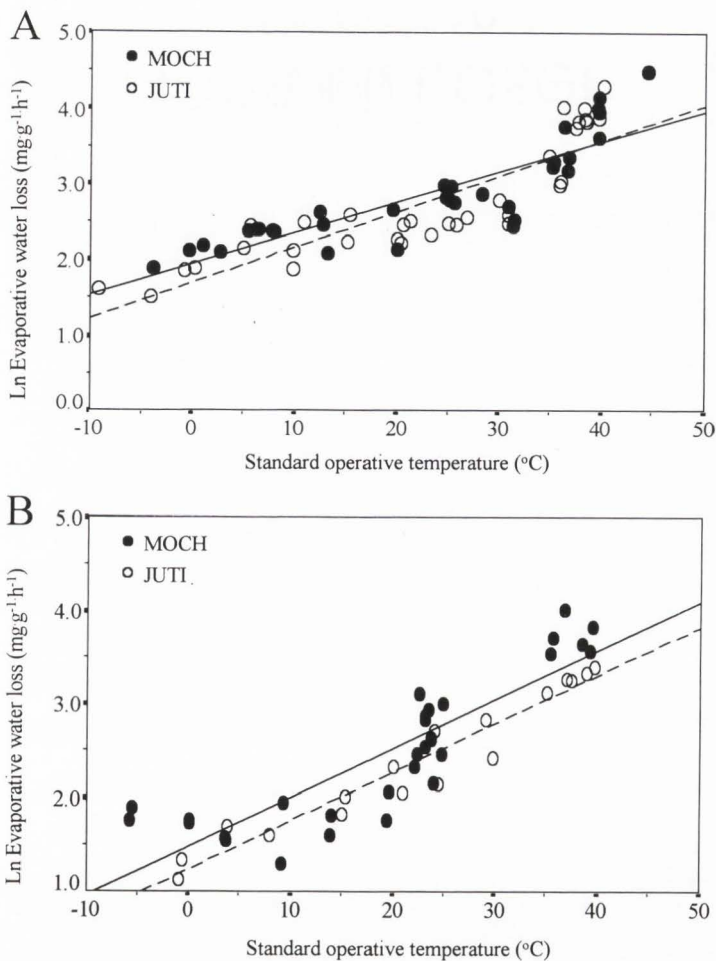


Fig. 3.4. Relationship between natural log of evaporative water loss and standard operative temperature in (A) summer and (B) winter acclimatized Mountain Chickadees (MOCH) and Juniper Titmice (JUTI).

TABLE 3.4. Relationship of evaporative water loss ($\text{mg g}^{-1}\text{h}^{-1}$) to standard operative temperature ($^{\circ}\text{C}$) for seasonally acclimatized Mountain Chickadees (MOCH) and Juniper Titmice (JUTI).

Species	<i>n</i>	Regression equation	$s_{y,x}$	s_b	r^2	<i>P</i>
sMOCH	33	$\ln\text{EWL} = 1.95 + 0.04 T_{cs}$	0.12	0.004	0.73	< 0.001
sJUTI	35	$\ln\text{EWL} = 1.71 + 0.05 T_{cs}$	0.11	0.004	0.78	< 0.001
wMOCH	30	$\ln\text{EWL} = 1.49 + 0.05 T_{cs}$	0.13	0.006	0.76	< 0.001
wJUTI	17	$\ln\text{EWL} = 1.24 + 0.05 T_{cs}$	0.09	0.003	0.94	< 0.001

*species and prefixes: s = summer, w = winter; $s_{y,x}$ = standard error of regression coefficient *a*; s_b = standard error of regression coefficient *b*.

overnight fasting compared to summer. Although visible fat in the furcular region was increased in winter compared to summer for chickadees, overall fat content did not vary seasonally. This contrasts to a pattern of winter increases in body mass and fat content of many small birds that overwinter in seasonal climates (King 1972, Blem 1976, Dawson et al. 1983b, Swanson 1991a, Waite 1992, O'Connor 1995). Summer chickadees in this study did increase body mass over the course of the day, which may reflect increased fat storage as found in Black-capped Chickadees from New York (Chaplin 1974). Consequently, seasonal variation in fat content may have been underestimated. However, in several cold-temperate wintering passerines, significant winter increases in fat also occur in morning-captured birds (Dawson and Carey 1976, Swanson 1991a, Waite 1992, O'Connor 1995). This suggests that chickadees and titmice do not store fat in winter to the same degree as some other cold-temperate wintering passerines and that seasonal increases in fat stores are not a principal component of winter acclimatization in these birds. This finding agrees with body mass and fat stores data from Black-capped Chickadees of Cooper and Swanson (1994) and data of Rogers (1987) and Rogers and

Smith (1993) who found that tree-foraging birds maintain lower fat stores than ground-foraging birds.

In addition to seasonal changes in fat content, winter increments in non-fat body components usually accompany increased fat stores (Helms et al. 1967, Barnett 1970, Carey et al. 1978, Dawson et al. 1983a, O'Connor 1995). The seasonal stability of lean dry mass in this study may be due to small sample size. Seasonal changes in pectoralis mass may play a role in metabolic seasonal acclimatization in passerine birds. The flight muscles (pectoralis and supracoracoideus) are thought to play an important role in shivering thermogenesis (Marsh and Dawson 1989). In this study, pectoralis mass increased significantly in winter compared to summer for both chickadees and titmice. The 33% increase in pectoralis mass in chickadees and 24% increase in titmice parallel a 27% increase in maximal thermogenic capacity (PMR) in chickadees and 11% increase in PMR in titmice (Cooper unpubl. data). In addition, this suggests that the winter increase in BMR of 16% for both species is at least partly due to the increased metabolic machinery of the pectoralis mass, which is needed for increased thermogenic capacity (Swanson 1991b). Similar increases in winter pectoralis muscle mass have been found in Dark-eyed Juncos (Swanson 1991b) and House Finches (O'Connor 1995) and appear to be associated with increased PMR in these species. However, in House Finches, BMR was seasonally stable in spite of increased pectoralis muscle mass in winter (O'Connor 1995). The metabolic significance of seasonally changing BMR is not certain.

Metabolic response to temperature below thermoneutrality.--LCT in both species varied with acclimatization state and was lowest in winter. The Mountain Chickadee's

LCT is 4.2°C lower in summer and 2.4°C lower in winter than the Juniper Titmouse's. In addition, the LCT for Mountain Chickadees is 2.2° and 6.4°C lower than predicted values based on body mass (Weathers and van Riper 1982) for summer and winter, respectively. The LCT for Juniper Titmice is 3.4°C higher in summer and only 1.3°C lower than predicted values based on body mass (Weathers and van Riper 1982). The slope and intercept of the regression line relating metabolic rate to standard operative temperature below thermoneutrality varied seasonally in chickadees but not in titmice. This suggests that chickadees have better insulation in winter, probably as a result of their increased plumage mass, but that increased plumage mass in titmice does not increase insulation. Minimal dry thermal conductance below thermoneutrality also decreases significantly in winter chickadees but not in titmice. Overall insulative capacity in summer is greater in titmice than in chickadees but in winter is not significantly different between the two species based on values of overall minimal thermal conductance. This suggests that seasonal changes in insulation are involved with winter acclimatization of the Mountain Chickadee but not of the Juniper Titmouse. However, winter values of thermal conductance exceed allometrically predicted for passerines (Aschoff 1981) by 26% for titmice and 13% for chickadees, indicating that insulative changes are probably not prominently involved with winter acclimatization in these two species.

Metabolic response to temperature above thermoneutrality.--Mountain

Chickadees appear to be markedly heat intolerant. The UCT for chickadees is only 31.5°C, which is one of the lowest among birds (Weathers 1981, Weathers and van Riper 1982, Hayworth and Weathers 1984). For Juniper Titmice, a UCT of 35.7°C in summer

and 35.0°C in winter is similar to other passerines (see Weathers 1981). Mountain Chickadees evaporative water loss rates were significantly higher than Juniper Titmice in both summer and winter, also indicating lower heat tolerance. Above the UCT, Mountain Chickadees became more hyperthermic than Juniper Titmice. This permits chickadees to lose more heat by nonevaporative pathways than titmice. However, in spite of hyperthermia, chickadees exhibit a larger increase in $\dot{V}O_2$ as a function of T_{es} , which indicates marked heat stress in chickadees above UCT compared to titmice. Similar heat intolerance has been found in two Hawaiian honeycreepers, the Palila (Weathers and van Riper 1982) and the Amakihi (MacMillen 1974), both of which are restricted to cool, high forests or montane habitats.

I calculated the winter northern boundary metabolic rate (NBMR) for chickadees and titmice using the Eq. 1 of Root (1988a) rearranged to use positive values of conductance:

$$\text{NBMR} = [(\text{TCRIT} - \text{TDIST})\text{COND}] + \text{BMR} \quad (3.2)$$

TCRIT is equal to lower critical temperature, TDIST is equal to the average minimum January temperature at the northern boundaries of each species, COND is overall thermal conductance, and BMR is basal metabolic rate. I used -12°C as TDIST for both species since chickadees and titmice were caught near the northern range limit for titmice. Also, since BMR increases with increasing latitude for many passerines (Weathers 1979), NBMR for Mountain Chickadees at their northern limit would probably exceed NBMR for chickadees in this study. However, the multiple of BMR as a function of NBMR would likely be similar. Calculated NBMR was 56.1 kJ/d for chickadees and 78.2 kJ/d for

titmice. NBMR is equal to $2.47 \times \text{BMR}$ in chickadees and $2.80 \times \text{BMR}$ in titmice. These values are similar to the NBMR of $2.45 \times \text{BMR}$ as predicted by Root (1988a). Energy and water balance data from this study strongly suggest that climate acts directly on the physiology of the Mountain Chickadee and Juniper Titmice to shape the distributional range of these species. Additionally, the calculated NBMR value of $2.80 \times \text{BMR}$ for winter titmice strongly suggests that the northern range limit for titmice is influenced by physiological demands of thermoregulation.

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.
- BAKKEN, G. S. 1976. A heat transfer analysis of animals: Unifying concepts and the application of metabolism chamber data to field ecology. *J. Theor. Biol.* 60:337-384.
- BARNETT, L. B. 1970. Seasonal changes in temperature acclimatization of the House Sparrow, *Passer domesticus*. *Comp. Biochem. Physiol.* 33:559-578.
- BARTHOLOMEW, G. A. 1958. The role of physiology in the distribution of terrestrial vertebrates. Pages 81-95 in *Zoogeography*, Publication no. 51 (C. L. Hubbs, Ed.). American Association for the Advancement of Science, Washington, D.C.
- BLEM, C. R. 1976. Patterns of lipid storage and utilization in birds. *Amer. Zool.* 16:671-684.

CAREY, C., W. R. DAWSON, L. C. MAXWELL, and J. A. FAULKNER. 1978.

Seasonal acclimatization to temperature in Cardueline finches. II. Changes in body composition and mass in relation to season and acute cold stress. *J. Comp. Physiol.* 125:101-113.

CHAPLIN, S. B. 1974. Daily energetics of the Black-capped Chickadee, *Parus atricapillus*, in winter. *J. Comp. Physiol.* 89:321-330.

CICERO, C. 1996. Sibling species of titmice in the *Parus inornatus* complex (Aves: Paridae). University of California Publication in Zoology 128:1-217.

COOPER, S. J., and D. L. SWANSON. 1994. Seasonal acclimatization of thermoregulation in the Black-capped Chickadee. *Condor* 96:638-646.

DAWSON, W. R. 1954. Temperature regulation and water requirements of the brown and Abert Towhees, *Pipilo fuscus* and *Pipilo aberti*. University of California Publications in Zoology 59:81-124.

DAWSON, W. R., and G. A. BARTHOLOMEW. 1968. Temperature regulation and water economy of desert birds. Pages 357-394 in *Desert Biology* (G. W. Brown, Jr., Ed.). Academic Press, New York.

DAWSON, W. R., and C. CAREY. 1976. Seasonal acclimatization to temperature in cardueline finches. I. Insulative and metabolic adjustments. *J. Comp. Physiol.* 112:317-333.

DAWSON, W. R., R. L. MARSH, W. A. BUTTEMER, AND C. CAREY. 1983a. Seasonal and geographic variation of cold resistance in House Finches *Carpodacus mexicanus*. *Physiol. Zool.* 56:353-369.

- DAWSON, W. R., R. L. MARSH, and M. E. YACOE. 1983b. Metabolic adjustments of small passerine birds for migration and cold. *Am. J. Physiol.* 245:R755-R767.
- DOBUSH, G. R., C. D. ANKNEY, and D. G. KREMENTZ. 1985. The effect of apparatus, extraction time, and solvent type on lipid extractions of snow geese. *Can. J. Zool.* 63:1917-1920.
- GODFREY, W. E. 1986. The birds of Canada. National Museums of Canada, Ottawa, Province, Canada.
- HAYWORTH, A. M., and W. W. WEATHERS. 1984. Temperature regulation and climatic adaptation in Black-billed and Yellow-billed Magpies. *Condor* 86:19-26.
- HELMS, C. W., W. H. AUSSIKER, E. B. BOWER, and S. D. FRETWELL. 1967. A biometric study of major body components of the Slate-colored Junco, *Junco hyemalis*. *Condor* 69:560-578.
- HELMS, C. W., and W. H. DRURY, Jr. 1960. Winter and migratory weight and fat field studies on some North American buntings. *Bird-Banding* 31:1-40.
- HINDS, D. S., and W. A. CALDER. 1973. Temperature regulation of the Pyrrhuloxia and the Arizona Cardinal. *Physiological Zoology* 46:55-71.
- HINSLEY, S. A., P. N. FERNS, D. H. THOMAS, and B. PINSHOW. 1993. Black-bellied Sandgrouse (*Pterocles orientalis*) and Pin-tailed Sandgrouse (*Pterocles alchata*): closely related species with differing bioenergetic adaptations to arid zones. *Physiological Zoology* 66:20-42.
- KING, J. R. 1972. Adaptive periodic fat storage by birds. Pages 200-217 in *Proceedings of the XV Ornithological Congress*. Leiden, The Netherlands.

- LASIEWSKI, R. C., A. L. ACOSTA, and M. H. BERNSTEIN. 1966. Evaporative water loss in birds—I. Characteristics of the open flow method of determination, and their relation to estimates of thermoregulatory ability. *Comparative Biochemistry and Physiology* 19:445-457.
- MACMILLEN, R. E. 1974. Bioenergetics of Hawaiian honeycreepers: The Amakihi (*Loxops virens*) and the Anianiau (*L. parva*). *Condor* 76:62-69.
- MARSH, R. L., and W. R. DAWSON. 1989. Avian adjustments to cold. Pages 205-253 in *Advances in comparative and environmental physiology* (L. C. H. Wang, Ed.). Springer, Berlin.
- O'CONNOR, T. P. 1995. Metabolic characteristics and body composition in house finches: effects of seasonal acclimatization. *J. Comp. Physiol. B* 165:298-305.
- RISING, J. D. 1969. A comparison of metabolism and evaporative water loss of Baltimore and Bullock orioles. *Comparative Biochemistry and Physiology* 31:915-925.
- ROGERS, C. M. 1987. Predation risk and fasting capacity: Do wintering birds maintain optimal body mass? *Ecology* 68:1051-1061.
- ROGERS, C. M., and J. N. M. SMITH. 1993. Life-history theory in the nonbreeding period: Trade-offs in avian fat reserves. *Ecology* 74:419-426.
- ROOT, T. 1988a. Energy constraints on avian distributions and abundance. *Ecology* 69:330-339.
- ROOT, T. 1988b. Environmental factors associated with avian distributional boundaries. *Journal of Biogeography* 15:489-505.

- ROOT, T. 1988c. Atlas of wintering North American birds. University of Chicago Press, Chicago, Illinois.
- SCHOLANDER, P. R., R. HOCK, V. WALTERS, F. JOHNSON, and L. IRVING. 1950. Heat regulation in some arctic and tropical mammals and birds. *Biol. Bull.* 99:237-258.
- SWANSON, D. L. 1991a. Seasonal adjustments in metabolism and insulation in the Dark-eyed Junco. *Condor* 93:538-545.
- SWANSON, D. L. 1991b. Substrate metabolism under cold stress in seasonally acclimatized Dark-eyed Juncos. *Physiol. Zool.* 64:1578-1592.
- WAITE, T. A. 1992. Winter fattening in Gray Jays: Seasonal, diurnal, and climatic correlates. *Ornis Scandinavica* 23:499-503.
- WEATHERS, W. W. 1979. Climatic adaptation in avian standard metabolic rate. *Oecologia* 42:81-89.
- WEATHERS, W. W. 1981. Physiological thermoregulation in heat-stressed birds: Consequences of body size. *Physiol. Zool.* 54:345-361.
- WEATHERS, W. W., and C. VAN RIPER. 1982. Temperature regulation in two endangered Hawaiian honeycreepers: The Palila (*Psittirostra bailleui*) and the Laysan Finch (*Psittirostra cantans*). *Auk* 99:667-674.
- WITHERS, P. C. 1977. Measurement of VO_2 , VCO_2 , and evaporative water loss with a flow-through mask. *Journal of Applied Physiology* 42:120-123.
- ZAR, J. H. 1984. Biostatistical analysis, 2nd ed. Prentice-Hall, Englewood Cliffs, New Jersey.

CHAPTER 4
THE ROLE OF DAILY ENERGY EXPENDITURE ON THE
BIOGEOGRAPHY OF THE MOUNTAIN CHICKADEE
AND JUNIPER TITMOUSE

ABSTRACT

I examined seasonal variation in daily energy expenditure (DEE) and its possible role on the biogeography of the Mountain Chickadee (*Parus gambeli*) and the Juniper Titmouse (*Parus ridgwayi*). I used behavioral, meteorological, and laboratory metabolism data to calculate DEE in seasonally acclimatized chickadees and titmice. The laboratory metabolism data analysis revealed that foraging energy requirements were not significantly higher than alert perching energy requirements. DEE in summer was 48.8 kJ/d for chickadees and 48.3 kJ/d for titmice. DEE in winter was 66.3 kJ/d for chickadees and 98.7 kJ/d for titmice. DEE as a multiple of basal metabolic rate (BMR) was 2.31 in summer chickadees and 1.91 in summer titmice. DEE was 2.70 times BMR in winter chickadees and 3.43 times BMR in winter titmice. These values are close to the suggested northern boundary metabolic rate of 2.45 times BMR and indicate that DEE helps shape the northern range limits of these two species. The marked increase in calculated DEE in winter birds compared to summer contrasts a pattern of increased DEE in the breeding season for several avian species. These data suggest that winter may be a period of even greater stringency for small birds than previously believed.

Introduction

Small passerine birds that overwinter in cold temperate regions require prolonged energy expenditure for regulatory thermogenesis. In addition, the onset of winter decreases foraging time due to shorter days and may reduce the availability of foraging substrates due to heavy snow or ice cover. Concurrently with these seasonal changes in photoperiod and climate, cold temperate-wintering passerines undergo seasonal acclimatization that enables thermoregulatory homeostasis. Previous studies of seasonal acclimatization in passerine birds have focused primarily on seasonal variation in basal metabolism, cold tolerance, maximal thermogenic capacity, and substrate metabolism (reviews: Marsh and Dawson 1989a, 1989b; Dawson and Marsh 1989; Dawson and O'Connor 1996). These studies have generally collected metabolic data for individuals over a very short time period (up to a few hours).

Seasonal variation in daily energy expenditure (DEE) in passerines has received some attention (Walsberg 1977; Mugaas and King 1981; Bryant and Tatner 1988; Weathers and Sullivan 1993). The main focus of these studies was the comparison of DEE during the breeding season with DEE during winter. For these studies, DEE during the breeding season typically equaled or exceeded that during winter. Although energetic demands may not be higher in winter than during other periods of the year, the conditions in which they must be met are much harsher. In addition, the winter northern range boundaries of greater than half of North American birds analyzed by Root (1988a) coincide with some isotherm of minimum January temperature. Root (1988b) calculated the resting metabolic rate of 14 species whose metabolism as a function of ambient

temperature was available from the literature at the minimum January temperature at each species' northern range boundary. That northern boundary metabolic rate (NBMR), which includes basal metabolism (BMR) and thermoregulatory metabolism, is equal to 2.45 times the BMR for each of the 14 species. The total DEE of those birds must be somewhat greater than 2.45 times basal, since the birds must also expend energy for foraging, digestion, and other activities. Thus, birds may be limited to overwintering in regions where they do not have to raise their DEE beyond slightly greater than 2.45 times basal levels. In order to determine the role of DEE on biogeographic patterns in birds, closely related species with different northern range distributions need to be examined.

The Mountain Chickadee (*Parus gambeli*) and the Juniper Titmouse (*Parus ridgwayi*) are small, largely nonmigratory passerine birds that occupy regions of western North America. Recently, the Plain Titmouse (*Parus inornatus*) has been split into the Juniper Titmouse and the Oak Titmouse (*Parus inornatus*) (Cicero 1996). The Mountain Chickadee's distributional range extends to northern British Columbia (60° north latitude), whereas the Juniper Titmouse's range extends to portions of southern Idaho (44° north latitude) (Godfrey 1986, Cicero 1996) (see Fig. 2.1). The Mountain Chickadee's northern range limit does not extend beyond a -23°C average minimum January temperature isotherm, whereas the Juniper Titmouse's northern range limit does not extend beyond a -12°C isotherm of minimum January temperature (Root 1988c). Thus, the DEE of these two species may be important in determining their northern range distribution. In this study I compare the DEE of seasonally acclimatized Mountain Chickadees and Plain Titmice.

Materials and Methods

Study Site and Species

The field portions of this study took place between February 5 and 8, 1996 for winter measurements, and between July 31 and August 3, 1996 for summer measurements. Field data for Mountain Chickadees were recorded in the Bear River Mountains, Cache County, Utah (41° 54'N, 111°32'W) near the Beaver Mountain Ski Area at an elevation of 2225 m. The study site consisted of mixed conifers and quaking aspen (*Populus tremuloides*). Field data for Juniper Titmice were recorded in the Raft River Mountains, Box Elder County, Utah (41°50'N, 113°25'W) near Rosette, Utah at an elevation of 1850 m. The study site consisted of primarily Utah juniper (*Juniperus osteosperma*) with sparsely scattered singleleaf pinyon pine (*Pinus monophylla*).

Time-Activity Budgets

I collected 16 time-budget samples totalling 67 min of observation for summer chickadees and 16 time-budget samples totalling 87 min of observation for winter chickadees. I collected 9 time-budget samples totalling 60 min of observation for summer titmice and 8 time-budget samples totalling 80 min of observation for winter titmice. Samples were distributed throughout the day in order to achieve uniform coverage of the birds' active day. I observed focal individuals for 2-30 min (mean \pm SD = 5.3 \pm 2.6) and recorded the time spent in three activities (perching, foraging, or flying). Perching included singing and grooming. I cannot be certain that each of my time-budget samples for Mountain Chickadees within one season was of a different individual because not all

birds observed were banded. However, I made a conscious effort to avoid sampling the same individual twice within a season and to sample as many individuals within a 3.2 km² area per study site. In addition, Plain Titmice adults remain in pairs year-round and also maintain year-round territories (Dixon 1949). Thus, I was able to observe both banded and unbanded pairs within their own territories for relatively long periods of time.

Meteorology

Concurrent with my time-budget measurements, I monitored the birds' thermal environment with a meteorological station placed within typical foraging/perching sites. Microclimate sensors were mounted on metal poles and were placed 2 m above ground level (snow level in winter) within 25 cm of a tree trunk. For Mountain Chickadees I placed the meteorological station near subalpine fir (*Abies lasiocarpa*), and for Plain Titmice I placed the meteorological station near Utah Juniper. These tree species were the most frequently used for foraging by the respective bird species (pers. obs.). Meteorological variables measured were (1) air temperature (T_a) (with a shaded 36-gauge copper-constantan thermocouple), (2) operative temperature (T_e) (with a 3.5-cm diameter copper sphere thermometer painted flat gray; Bakken et al. 1985; Walsberg and Weathers 1986), and (3) wind speed (u) (with a Thornwaite model 901 cup anemometer). Sensor outputs were monitored at 60-s intervals, averaged every 60 min, and recorded with a Campbell Scientific CR10 electronic datalogger. Thermocouples were calibrated with a thermometer traceable to the U.S. Bureau of Standards. The cup anemometer was factory calibrated.

Laboratory Metabolism Measurements

I measured the metabolic heat production of chickadees and titmice by measuring their oxygen consumption ($\dot{V}O_2$) at stable air temperatures between -10° and 30°C . The birds used in these measurements were captured during summer and winter of 1995 and 1996. Birds were transported from the field to Logan, Utah, where they were housed in individual cages ($0.3 \times 0.3 \times 0.3$ m) and held in a temperature-controlled environmental chamber ($3 \times 3 \times 2.5$ m). The chamber temperature and photoperiod were programmed to follow a cycle that approximated the season and study site to which the birds had been accustomed. While in captivity, birds were provided with food (*Tenebrio* larvae and wild bird seed) and water as needed. Birds tested from 1 June to 25 August were designated "summer birds," and those tested from 20 November to 10 February were designated "winter birds."

I measured $\dot{V}O_2$ during the active phase of the daily cycle on fed birds at rest in darkened metabolism chambers to estimate energetic costs of daytime maintenance plus the cost of alert perching and on fed birds in metabolism chambers (equipped with a dish of wild bird seed) exposed to normal fluorescent room lighting to estimate energetic costs of daytime maintenance plus the cost of foraging. Nighttime maintenance-energy requirements were estimated from previous $\dot{V}O_2$ measurements during the rest phase on fasted birds resting in the dark (minimum of 4 h since last meal) (Cooper unpublished data). Measurements were made on individual birds using a 3.8-L metabolic chamber fashioned from a paint can. The inside of the metabolic chamber was painted flat black to provide an emissivity near 1.0. Metabolic chamber temperature was regulated within

$\pm 0.5^{\circ}\text{C}$ by placing it in a temperature-controlled environmental chamber. Metabolic chamber temperature was monitored continuously throughout each test with an Omega thermocouple thermometer (Model Omni IIB, previously calibrated to a thermometer traceable to the U.S. Bureau of Standards) attached to a 30-gauge copper-constantan thermocouple inserted into the inlet port of the metabolic chamber. Individuals were weighed and then placed inside the metabolic chamber where they perched on 1 cm wire mesh placed 3 cm above a 1-cm layer of paraffin oil used for the collection of fecal material. Oxygen consumption ($\dot{V}\text{O}_2$) was then measured using open-circuit respirometry with an Ametek Model S-3A oxygen analyzer. Dry, CO_2 -free air was drawn through the metabolic chamber with a diaphragm pump. Outlet flow rates of dry, CO_2 -free air were maintained at 442-450 mL/min by a Matheson precision rotameter (Model 604), which was calibrated to $\pm 1.0\%$ (Brooks vol-u-meter), and located downstream from the metabolic chamber. These flow rates yielded changes in oxygen content between influx and efflux gas of 0.3 and 0.7% and maintained oxygen content of efflux gas above 20.2%. Fractional concentration of oxygen in efflux gas was determined from a 100 mL/min subsample passed through the oxygen analyzer. Measurements of the efflux gas were recorded every 15 s on a computer using Datacan 5.0 data collection and analysis software (Sable Systems International). EWL was determined over a 60-min timed interval by measuring the increase in mass of a downstream absorbant train containing Drierite. All weighings were made on an analytical balance (Mettler H51AR). At the end of each metabolism trial, birds were removed from the chamber and body temperature (T_b) ($\pm 0.1^{\circ}\text{C}$) was recorded by inserting a 30-gauge copper-constantan thermocouple into the

cloaca to a depth (approx. 10-12 mm) where further insertion did not alter temperature reading.

$\dot{V}O_2$ and EWL were measured on individual birds exposed to a single randomized temperature in the dark and also in normal room lighting. Individuals were given 24-h rest in between $\dot{V}O_2$ measurements. All individuals were tested within 1 week of capture. Individual birds were placed in the metabolic chamber for a total of 2 hours. The first hour was an equilibration time and $\dot{V}O_2$ was measured over the last 60 min of the trial. Oxygen consumption was calculated as steady state $\dot{V}O_2$ using Eq. 4a of Withers (1977). All values were corrected for STP. Rates of metabolic heat production were calculated assuming that 20.1 kJ of heat was produced per liter of oxygen consumed for both fed and fasted birds.

*Time-Activity-Laboratory Estimate
of DEE*

I calculated the DEE of seasonally acclimatized chickadees and titmice using time-budget, meteorological, and laboratory metabolism data from the following equation:

$$DEE = (t_{\rho} \dot{H}_m) + (t_{ap} \dot{H}_{ap}) + (t_{fo} \dot{H}_{fo}) + (t_{fl} \dot{H}_{fl}), \quad (4.1)$$

where t represents durations (in hours), of the activity phases and of the type of activity, and \dot{H} is the energy requirements for a given activity (in kJ/h). The subscripts represent the time of day (ρ = nighttime) or the type of activity (m = maintenance metabolism, ap = active perch, fo = foraging, and fl = flight). The first bracketed term, nocturnal energy expenditure, consists of basal and thermoregulatory energy requirements of a sleeping bird. The second bracketed term represents maintenance-energy requirements plus active

perching-energy requirements of a daytime bird. The third bracketed term represents maintenance-energy requirements plus foraging-energy requirements of a daytime bird. The second and third bracketed terms subsume thermoneutral and thermoregulatory energy requirements during the bird's active phase and include the heat increment of feeding (HI). The fourth bracketed term represents flight-energy requirements of a daytime bird. In applying my metabolic measurements to equation (1), I related laboratory measurements of \dot{H}_m , \dot{H}_{ap} , and \dot{H}_{fo} directly to the 60-min recordings of microclimate measurements associated with each bird's diurnal and nocturnal phases, respectively.

Equation (1) usually provides mean DEE values within 5% of the mean DEE determined by doubly labeled water (DLW) of free-ranging birds provided certain criteria are met. First, maintenance and activity costs must be determined for the study population(s) at the same season as time budgets are recorded (Weathers and Sullivan 1993). Secondly, maintenance and activity costs under field conditions must be evaluated using heat transfer theory that uses standard operative temperature to calculate thermoregulatory costs (Weathers et al. 1984; Bakken et al. 1985; Buttemer et al. 1986; Weathers and Sullivan 1989; Webster and Weathers 1990; Mock 1991; Weathers and Sullivan 1993). Appendix C presents the details of my evaluation of equation (1) and estimation of standard operative temperature and thermoregulatory costs. I did not use DLW to determine DEE in chickadees and titmice due to the difficulty in recapturing marked individuals.

Results

Weather

During the summer and winter study period, no precipitation fell. T_a , T_e , and u were within normal ranges for each study site (Utah State Climate Center) and are shown for summer chickadees (Fig. 4.1a), summer titmice (Fig. 4.1b), winter chickadees (Fig. 4.2a), and winter titmice (Fig. 4.2b).

Time-Activity Budgets

In summer, chickadees and titmice began foraging around 0500 and went to roost around 1900, making their active day about 14 h long. In winter, chickadees and titmice began foraging around 0730 and went to roost around 1630, making their active day about 9 h long. These time intervals were used to calculate TAL estimates of DEE. Chickadees and titmice spend over 50% of their active day foraging in both summer and winter (Table 4.1). The time budgets of the two species were comparable and did not change seasonally (Table 4.1). Time spent perching for chickadees was not significantly different than titmice in summer ($t = -0.440$, $P = 0.664$) or winter ($t = 0.320$, $P = 0.765$). Time spent perching did not vary seasonally in chickadees or titmice (chickadees, $t = 1.570$, $P = 0.130$; titmice, $t = 0.360$, $P = 0.723$). Time spent foraging for chickadees was not significantly different than titmice in summer ($t = 0.390$, $P = 0.702$) or winter ($t = -0.350$, $P = 0.727$). Time spent foraging did not vary seasonally in chickadees or titmice (chickadees, $t = -1.650$, $P = 0.111$; titmice, $t = -0.420$, $P = 0.684$). Time spent flying for chickadees was not significantly different than titmice in summer ($t = 0.730$,

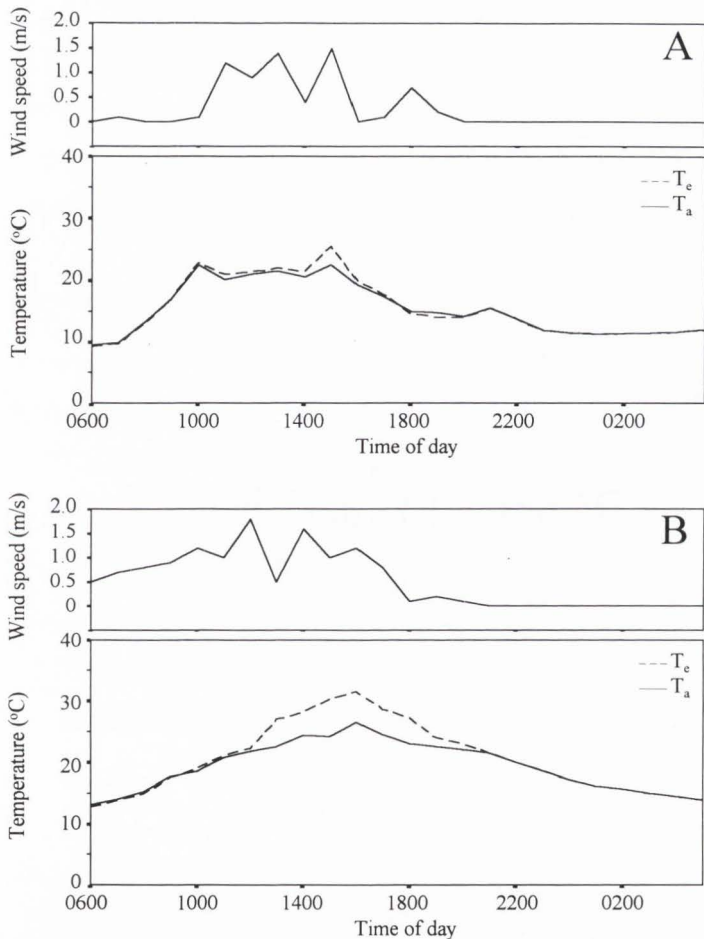


Figure 4.1. Temperature and wind speed for Mountain Chickadees (A) and Juniper Titmice (B) during the summer study period, August 1996.

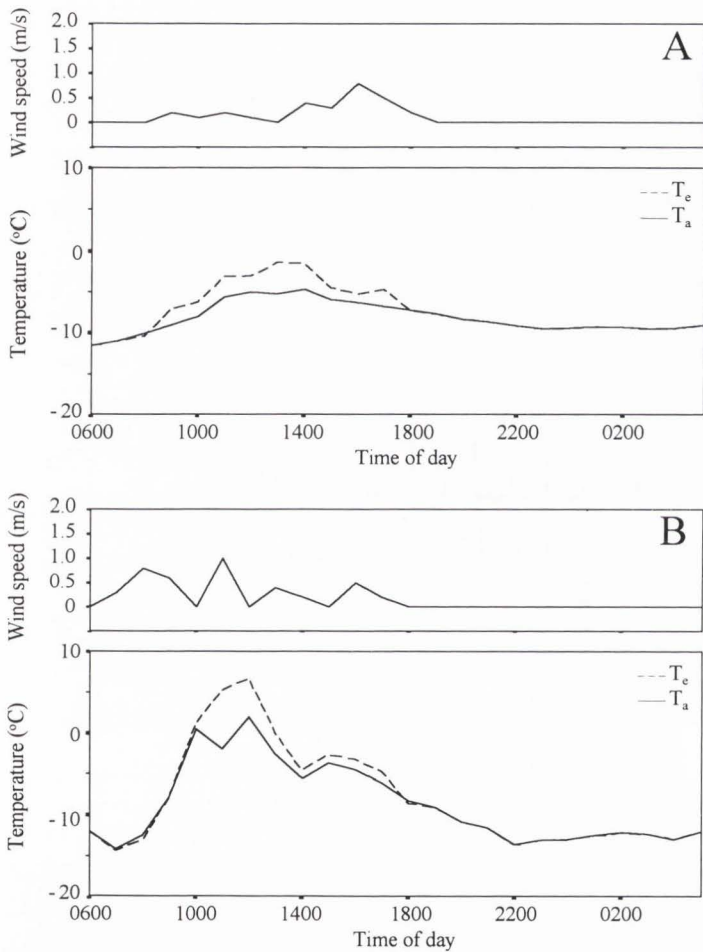


Figure 4.2. Temperature and wind speed for Mountain Chickadees (A) and Juniper Titmice (B) during the winter study period, February 1996.

Table 4.1: Percentage of the active day that seasonally acclimatized Mountain Chickadees (MOCH) and Juniper Titmice (JUTI) spent in various activities

Percentage of Active Day Spent	Summer		Winter	
	MOCH (<i>n</i> = 16)	JUTI (<i>n</i> = 9)	MOCH (<i>n</i> = 16)	JUTI (<i>n</i> = 8)
Perching	27.5 ± 5.2	34.5 ± 7.3	39.4 ± 6.7	40.5 ± 4.1
Foraging	68.7 ± 4.7	61.5 ± 6.8	53.0 ± 5.4	54.9 ± 5.2
Flying	3.8 ± 0.4	4.0 ± 0.3	7.6 ± 1.2	4.6 ± 0.2

Note. Sample sizes are the number of 1-30 min observation periods for the indicated focal individuals. *t*-tests were performed on arcsine transformed percentages.

$P = 0.472$) or winter ($t = 0.530$, $P = 0.604$). Time spent flying did not vary seasonally in chickadees or titmice (chickadees, $t = 0.910$, $P = 0.368$; titmice, $t = 1.270$, $P = 0.238$).

Laboratory Metabolic Rates

Under the conditions of my laboratory metabolism measurements (isothermal metabolism chamber with no significant shortwave radiation or forced convection), T_a is the same as standard operative temperature (T_{so}). Although normal fluorescent room lighting illuminated the metabolic chamber to determine foraging costs, this would amount to a negligible amount of irradiance received by the bird due to construction of the chamber. For example, Verdins exposed to normal fluorescent room lighting in glass metabolic chambers were subject to an irradiance of $<3 \text{ W/m}^2$ (Wolf and Walsberg 1996). Heat production of fed summer chickadees in lighted conditions (Fig 4.3a) was best described by:

$$\dot{V}O_2 = 11.97 - 0.18T_{so}, \quad (4.2)$$

($n = 15$, $r^2 = 0.55$, $F = 16.07$, $P < 0.001$)

whereas that of fed summer chickadees in dark conditions (Fig 4.3a) was best described by:

$$\dot{V}O_2 = 12.27 - 0.26T_{so}. \quad (4.3)$$

($n = 16$, $r^2 = 0.72$, $F = 36.20$, $P < 0.001$)

Heat production of fed summer titmice in lighted conditions (Fig 4.3b) was best described by:

$$\dot{V}O_2 = 9.73 - 0.22T_{so}, \quad (4.4)$$

($n = 11$, $r^2 = 0.79$, $F = 32.86$, $P < 0.001$)

whereas that of fed summer titmice in dark conditions (Fig 4.3b) was best described by:

$$\dot{V}O_2 = 9.63 - 0.21T_{es} \quad (4.5)$$

($n = 15$, $r^2 = 0.83$, $F = 61.52$, $P < 0.001$)

Heat production of fed winter chickadees in lighted conditions (Fig 4.4a) was best described by:

$$\dot{V}O_2 = 11.91 - 0.36T_{es} \quad (4.6)$$

($n = 13$, $r^2 = 0.79$, $F = 41.07$, $P < 0.001$)

whereas that of fed winter chickadees in dark conditions (Fig 4.4a) was best described by:

$$\dot{V}O_2 = 15.46 - 0.17T_{es} \quad (4.7)$$

($n = 14$, $r^2 = 0.64$, $F = 21.43$, $P < 0.001$)

Heat production of fed winter titmice in lighted conditions (Fig 4.4b) was best described by:

$$\dot{V}O_2 = 11.46 - 0.30T_{es} \quad (4.8)$$

($n = 10$, $r^2 = 0.87$, $F = 52.48$, $P < 0.001$)

whereas that of fed winter titmice in dark conditions (Fig 4.4b) was best described by:

$$\dot{V}O_2 = 11.39 - 0.30T_{es} \quad (4.9)$$

($n = 10$, $r^2 = 0.78$, $F = 29.20$, $P < 0.001$)

The comparison of slopes and intercepts of these regression equations allows comparison of perching and foraging energy costs. For summer chickadees, slopes ($t = 34.44$, $P < 0.001$) were significantly different between perching and foraging-energy requirements but intercepts ($F_{(1,28)} = 1.71$, $P = 0.20$) were not significantly different. For

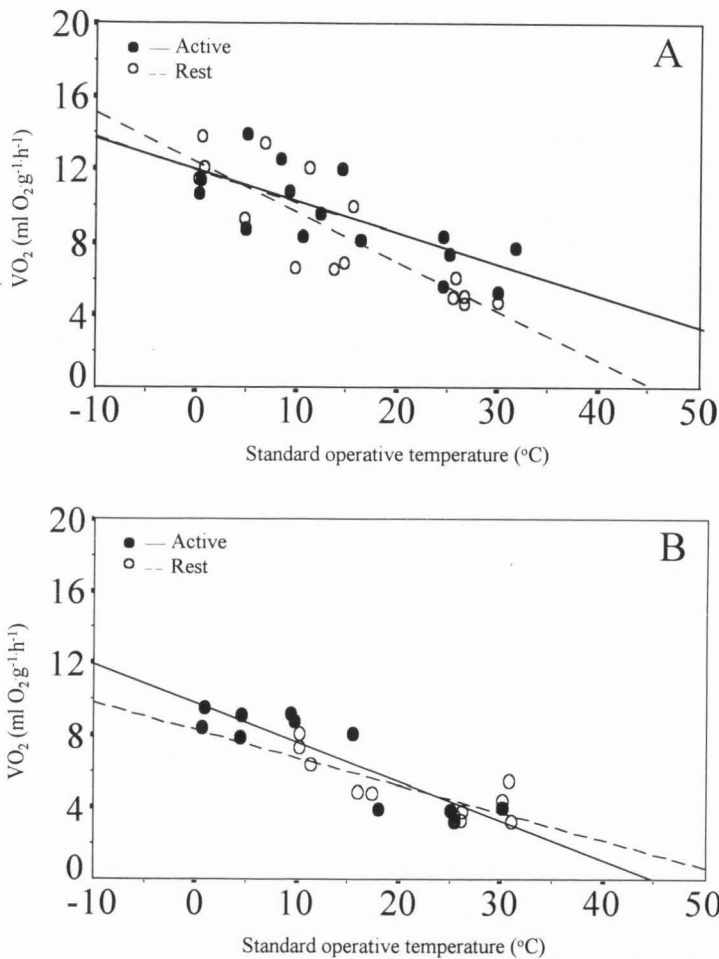


Figure 4.3. Relationship between oxygen consumption and standard operative temperature for summer-acclimatized Mountain Chickadees (A) and Juniper Titmice (B) during the active phase of their daily cycle. Dots represent active birds under lit conditions and open circles represent resting birds under dark conditions.

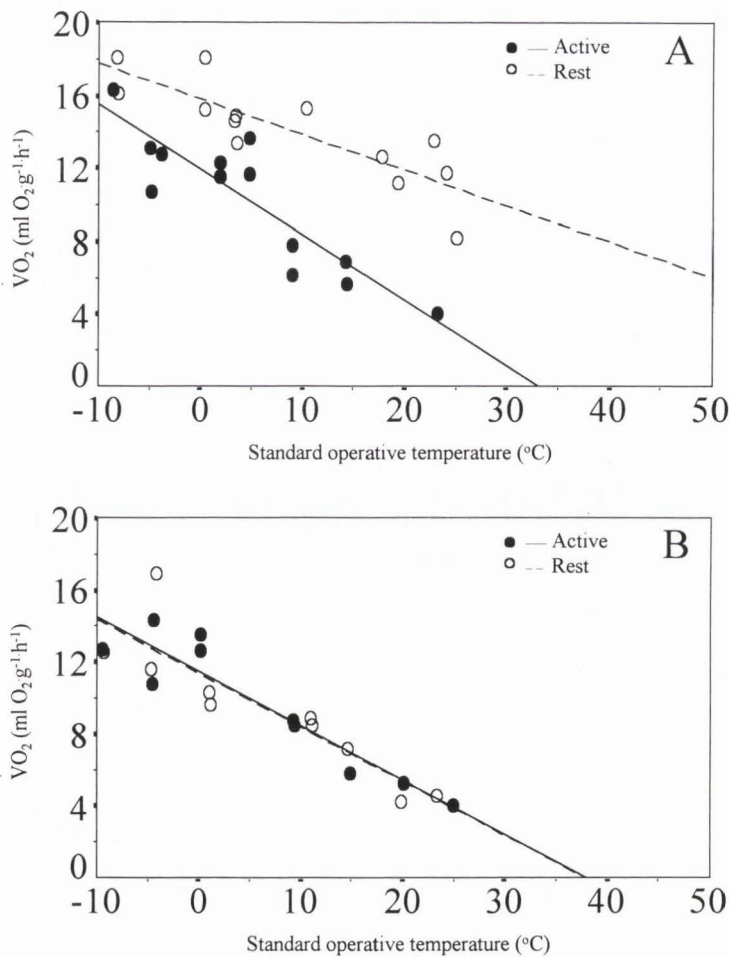


Figure 4.4. Relationship between oxygen consumption and standard operative temperature for winter-acclimatized Mountain Chickadees (A) and Juniper Titmice (B) during the active phase of their daily cycle. Dots represent active birds under lit conditions and open circles represent resting birds under dark conditions.

summer titmice, neither slopes ($t = -0.877$, $P = 0.40$) nor intercepts ($F_{(1,23)} = 0.01$, $P = 0.93$) were significantly different between perching and foraging-energy requirements. For winter chickadees, slopes were significantly different between perching and foraging costs ($t = 9.980$, $P < 0.001$) and intercepts were also significantly different between perching and foraging costs ($F_{(1,24)} = 36.81$, $P < 0.001$). For winter titmice, neither slopes ($t = 0.121$, $P = 0.81$) nor intercepts ($F_{(1,17)} = 0.01$, $P = 0.94$) were significantly different between perching and foraging-energy requirements.

Time-Activity Laboratory Estimate of DEE

Daily energy expenditure estimated by the TAL method averaged 48.8 and 48.3 kJ/d for summer Mountain Chickadees and Juniper Titmice, respectively (Table 4.2). These values are 86.8% and 63.8%, respectively, of predicted DEE based on body mass (Nagy 1987). Daily energy expenditure averaged 66.3 and 98.7 kJ/d for winter chickadees and titmice, respectively (Table 4.2). These values are 118.0% and 130.4%, respectively of allometrically predicted DEE (Nagy 1987). For both chickadees and titmice, DEE was significantly higher in winter compared to summer (chickadees, $t = 10.980$, $P < 0.001$; titmice, $t = 34.510$, $P < 0.001$). Juniper Titmice weighed significantly more than Mountain Chickadees in both summer and winter (Cooper, unpublished data), and the mass difference confounds direct comparison of DEE. However, the difference in body mass can be removed by converting DEE to units of $\text{kJ g}^{-0.63} \cdot \text{d}^{-1}$, where $M^{0.63}$ is the interspecific scaling of DEE (Weathers and Sullivan 1989). Using 11.7 g as the mean daily mass of chickadees and 17.4 g as the mean daily mass of titmice (Cooper,

Table 4.2: Daily energy budget of seasonally acclimatized Mountain Chickadees (MOCH) and Juniper Titmice (JUTI) as calculated by the TAL method.

Variable (kJ/d)	Summer		Winter	
	MOCH	JUTI	MOCH	JUTI
DEE	48.8 ± 0.6	48.3 ± 1.0	66.3 ± 1.5	98.7 ± 0.1
Basal metabolism ^a	23.3 ± 1.0	27.9 ± 1.5	25.4 ± 0.9	27.8 ± 0.4
Nocturnal thermoregulation	6.5 ± 0.1	4.5 ± 0.1	14.5 ± 0.0	32.9 ± 0.0
Alert Perching ^b	4.2 ± 1.1	3.8 ± 1.3	10.3 ± 1.0	15.6 ± 0.7
Foraging ^b	9.2 ± 1.0	6.4 ± 0.9	11.3 ± 1.1	17.1 ± 0.6
Flying	5.6 ± 0.7	5.7 ± 1.2	4.8 ± 0.5	5.3 ± 0.1

Note. Values are means ± SE. ^aData are calculated for field conditions incorporating the circadian rhythm in basal metabolism. ^bData include thermoregulation and heat increment of feeding.

unpublished data), I computed the mass-adjusted DEE for summer and winter-acclimatized individuals. Summer chickadees' mass-adjusted DEE (10.4 ± 0.13 $\text{kJ g}^{-0.63} \text{d}^{-1}$, $n = 16$) was significantly higher than mass-adjusted DEE of summer titmice (8.0 ± 0.16 $\text{kJ g}^{-0.63} \text{d}^{-1}$, $n = 9$) ($t = 11.06$, $P < 0.001$). In winter, mass-adjusted DEE was significantly lower for chickadees (14.1 ± 0.3 , $\text{kJ g}^{-0.63} \text{d}^{-1}$, $n = 16$) than titmice (16.3 ± 0.1 $\text{kJ g}^{-0.63} \text{d}^{-1}$, $n = 4$).

Discussion

Activity Heat and Thermoregulation

By comparing the regression equations relating metabolism to T_{a} for fed daytime birds resting in the dark with equations for fed daytime birds exposed to light, the energetic cost of physical activity associated with foraging can be calculated. In summer chickadees, slopes of the regression lines were significantly different but the intercepts

were not. For both summer and winter titmice, regression equations did not differ significantly. These data indicate that heat produced as a by-product of activity may substitute for thermoregulatory requirements. For winter chickadees, the slopes and intercepts were significantly different. Winter chickadees in illuminated chambers had lower metabolism than those resting in the dark. How actively foraging birds can possibly have lower metabolism than inactive perching birds is certainly unclear. The apparent substitution of heat produced as a by-product of activity indicates that chickadee and titmouse behavior has no net energy cost at cold temperatures. A similar circumstance applies to Yellow-eyed Juncos (Weathers and Sullivan 1993), to the foraging behavior of winter Verdins (Webster and Weathers 1990) and terrestrial locomotion in cold-exposed White-crowned Sparrows (Paladino and King 1984).

Seasonal Variation in DEE

The seasonal patterns observed thus far in avian FMR support two alternative hypotheses (see Weathers and Sullivan 1993). The reallocation hypothesis predicts little seasonal variation in DEE. The increased demand hypothesis holds that breeding results in a substantial increase in adult energy demand and subsequently, DEE is highest during breeding. Data from the present study indicate that winter, due to its increased thermoregulatory costs, represents a substantial energy increase compared to summer. DEE in winter represents a 36% increase for chickadees and a 104% increase in titmice compared to their respective summer counterparts. One possible confounding variable with my study is that I did not collect my time-budgets during the peak of the breeding

season and therefore do not know if my TAL DEE calculations would change. However, during the summer period when I collected time-budgets, individuals were storing food items, possibly resulting in increased foraging times relative to non-breeding birds and probably resembling foraging times of adults feeding nestlings. The amount of time spent foraging by summer birds is very close to that recorded for Yellow-eyed Juncos feeding nestlings and fledglings (Weathers and Sullivan 1989).

The markedly increased DEE in winter relative to summer contrasts with data from most passerines tested to date. Only male dippers (*Cinclus cinclus*) have increased DEE in winter compared to breeding (a 13% increase) (Bryant and Tatner 1988). All other passerines in which DEE has been measured seasonally have relatively stable DEE or markedly increased DEE during the breeding season (see Weathers and Sullivan 1993). Two possible factors may explain the seasonal changes in DEE found in chickadees and titmice in this study. First, the birds in this study were exposed to much colder environmental temperatures, therefore increasing thermoregulatory costs, compared to other birds so far tested (with the exception of dippers) (Bryant and Tatner 1988). Secondly, winter-acclimatized Mountain Chickadees have 13% higher thermal conductance than allometrically predicted and winter-acclimatized Juniper Titmice have 26% higher thermal conductance than allometrically predicted (Cooper, unpublished data). Thus, the relatively poor insulation of these birds, especially of titmice, increases their thermoregulatory costs.

Role of DEE on Northern Range Limits

DEE as a multiple of basal metabolic rate (BMR) was 2.31 in summer chickadees and 1.91 in summer titmice. DEE was 2.70 times BMR in winter chickadees and 3.43 times BMR in winter titmice. These values are close to the suggested northern boundary metabolic rate of 2.45 times BMR. The total DEE of these birds must be somewhat greater than 2.45 times basal, since the birds must also expend energy for digestion, and flight. For winter-acclimatized Siberian Tits (*Parus cinctus*) and Willow Tits (*Parus montanus*) tested from their northern January isotherm, DEE was 2.55 times BMR and 2.50 times BMR, respectively (Carlson et al. 1993). Thus, it appears that the northern range limit of small passerines, especially chickadees and titmice, is shaped by a DEE that does not exceed beyond 3.5 times BMR.

Literature Cited

- Bakken, G.S., W.R. Santee, and D.J. Erskine. 1985. Operative and standard operative temperature: tools for thermal energetics studies. *Am. Zool.* 25:933-943.
- Bryant, D.M. and P. Tatner. 1988. Energetics of the annual cycle of Dippers *Cinclus cinclus*. *Ibis* 130:17-38.
- Buttemer, W.A., A.M. Hayworth, W.W. Weathers, and K.A. Nagy. 1986. Time-budget estimates of avian energy expenditure: physiological and meteorological considerations. *Physiol. Zool.* 59:131-149.

- Carlson, A., J. Moreno, and R. V. Alatalo. 1993. Winter metabolism of coniferous forest tits (*Paridae*) under arctic conditions: a study with doubly labeled water. *Ornis Scand.* 24:161-164.
- Cicero, C. 1996. Sibling species of titmice in the *Parus inornatus* complex (Aves: *Paridae*). *Univ. Calif. Publ. Zool.* 128:1-217.
- Dawson, W.R. and R.L. Marsh. 1989. Seasonal acclimatization to cold and seasons in birds. Pp. 83-94 in C. Bech and R.E. Reinertsen, eds. *Physiology of Cold Adaptation in Birds*. Plenum Press, New York.
- Dawson, W.R. and T.P. O'Connor. 1996. Energetic features of avian thermoregulatory Responses. Pp. 85-124 in C. Carey, ed. *Avian Energetics and Nutritional Ecology*. Chapman and Hall, New York.
- Dixon, K.L. 1949. Behavior of the Plain Titmouse. *Condor* 51:110-136.
- Godfrey, W.E. 1986. *The Birds of Canada*. National Museums of Canada, Ottawa.
- Marsh, R.L. and W.R. Dawson. 1989a. Avian adjustments to cold. Pp. 205-253 in L.C.H. Wang, ed. *Advances in Comparative and Environmental Physiology*. Springer, Berlin.
- Marsh, R.L. and W.R. Dawson. 1989b. Energy substrates and metabolic acclimatization in small birds. Pp. 105-114 in C. Bech and R.E. Reinertsen, eds. *Physiology of Cold Adaptation in Birds*. Plenum Press, New York.
- Mock, P.J. 1991. Daily allocation of time and energy of Western Bluebirds feeding nestlings. *Condor* 93:598-611.

- Mugaas, J.N. and J.R. King. 1981. Annual variation of daily energy expenditure by the Black-billed Magpie. *Stud. Avian Biol.* 5:1-78.
- Nagy, K. A. 1987. Field metabolic rate and food requirement scaling in mammals and birds. *Ecol. Monographs.* 57:111-128.
- Paladino, F. and J.R. King. 1984. Thermoregulation and oxygen consumption during terrestrial locomotion by white-crowned sparrows *Zonotrichia leucophrys gambelii*. *Physiol. Zool.* 57:226-236.
- Root, T. 1988a. Energy constraints on avian distributions and abundance. *Ecology* 69:330-339.
- . 1988b. Environmental factors associated with avian distributional boundaries. *J. Biogeography* 15:489-505.
- . 1988c. Atlas of wintering North American birds. Univ. of Chicago Press, Chicago, Illinois.
- Walsberg, G.E. 1977. Ecology and energetics of contrasting social systems in *Phainopepla nitens* (Aves: Ptilonotidae). *Univ. Calif. Publ. Zool.* 108:1-63.
- Walsberg, G.E. and W.W. Weathers. 1986. A simple technique for estimating operative environmental temperature. *J. Therm. Biol.* 11:67-72.
- Weathers, W.W., W.A. Buttemer, A.M. Hayworth, and K.A. Nagy. 1984. An evaluation of time-budget estimates of daily energy expenditure in birds. *Auk* 101:459-472.
- Weathers, W.W. and K.A. Sullivan. 1989. Juvenile foraging proficiency, parental effort, and reproductive success. *Ecol. Monogr.* 59:223-246.

- Weathers, W.W. and K.A. Sullivan. 1993. Seasonal patterns of time and energy allocation by birds. *Physiol. Zool.* 66:511-536.
- Webster, M.D. and W.W. Weathers. 1990. Heat produced as a by-product of foraging activity contributes to avian thermoregulation. *Physiol. Zool.* 63:777-794.
- Withers, P.C. 1977. Measurement of $\dot{V}O_2$, $\dot{V}CO_2$, and evaporative water loss with a flow-through mask. *J. Appl. Physiol.* 42:120-123.
- Wolf, B.O. and G.E. Walsberg. 1996. Thermal effects of radiation and wind on a small bird and implications for microsite selection. *Ecology* 77:2228-2236.

CHAPTER 5

NOCTURNAL HYPOTHERMIA IN SEASONALLY ACCLIMATIZED
MOUNTAIN CHICKADEES AND JUNIPER TITMICE

Abstract Mountain chickadees (*Parus gambeli*) and juniper titmice (*Parus ridgwayi*) are small passerine inhabitants of western North America that have different northern range limits. The seasonal regulation of body temperature and metabolism, especially the utilization of nocturnal hypothermia, was examined in order to evaluate possible ecological consequences of body temperature in these two species. Both species utilized nocturnal hypothermia year-round. Depth of hypothermia did not vary seasonally in these two species. Nocturnal body temperature was regulated 3-11° lower than daytime values for both species. Nocturnal body temperature was a linear function of standard operative temperature for all birds except summer-acclimatized mountain chickadees. In addition to standard operative temperature effects on body temperature, metabolic downregulation may be involved with decreased nocturnal body temperature in these two species. Depth of hypothermia was inversely correlated to body mass in seasonally acclimatized juniper titmice but not in mountain chickadees. Nocturnal energy savings range from 7.1-49.8% in chickadees and from 9.7-27.8% in titmice. These nocturnal energy savings result in lower daily energy expenditures of 8.6-17.1% for mountain chickadees and 5.8-9.8% for juniper titmice. These energy savings are critically important for survival throughout the annual cycle for these birds and may limit the northern range in these two species.

Introduction

Hypothermia is defined as any core body temperature (T_b) below the set-point specified for the active state of the species. For birds, hypothermia generally occurs nocturnally and is characterized by a shallow depression of body temperature to 30-38°C (Reinertsen 1996). Nocturnal hypothermia has been documented for several passerine species in the family Paridae, such as black-capped chickadees (*Parus atricapillus*), carolina chickadees (*Parus carolinensis*), Siberian tits (*Parus cinctus*), and willow tits (*Parus montanus*) (Steen 1958; Haftorn 1972; Chaplin 1976; Mayer et al. 1982; Reinertsen and Haftorn 1983). For these species, body temperature reduction resulted in savings in overnight energy expenditure ranging from 10-33%. However, generalizations concerning use of nocturnal hypothermia in parids are lacking. Black-capped chickadees, living near the species' northern range boundary in Alaska, had nocturnal body temperature of only 3°C below daytime body temperature (Grossman and West 1977). In addition, Reinertsen and Haftorn (1986) found that great tits (*Parus major*) did not utilize nocturnal hypothermia unless energy reserves entering the roost were below normal.

Although low T_b s and low metabolic rates (MRs) have been observed in many passerine species, the physiological mechanisms causing the reduction of MR and the relationship between the drop of MR and T_b during hypothermia has been largely ignored. Bartholomew et al. (1983) present two models to explain the pattern of hypothermia in two species of manikins. The first model suggests that manikins increase their thermal conductance at night resulting in decreased T_b . Thus, MR is reduced by the lowered T_b due to Q_{10} -effects. The second model proposes that thermal conductance is maintained at

near minimal levels at night and MR during hypothermia is proportional to the difference between T_b and T_a (ΔT).

The aims of this current study were twofold. First, the ecological consequences of body temperature regulation, especially the occurrence and utilization of nocturnal hypothermia in two small-sized species of parids that have different northern range distributions, were examined. The mountain chickadee (*Parus gambeli*) and the juniper titmouse (*Parus ridgwayi*) are nonmigratory inhabitants of western North America. The mountain chickadee's northern range extends to 60° north latitude, whereas the juniper titmouse's northern range extends to only 44° north latitude. Use of nocturnal hypothermia and subsequent overnight energy savings may play a role in the ability of the mountain chickadee to survive in colder regions than that occupied by juniper titmice. Secondly, physiological mechanisms involved with nocturnal hypothermia in these two species were examined by measuring daily variation in body temperature and metabolism in seasonally acclimatized mountain chickadees and juniper titmice.

Materials and Methods

Animals and collection sites

Mountain chickadees and juniper titmice were captured in Box Elder and Cache County, Utah, by mist net in summer and winter 1994, 1995, and 1996. Body mass was measured upon capture to the nearest 0.1 g with a portable electronic balance (Ohaus CT-1200). Following capture, birds were transported to the laboratory where they were housed individually in cages (30 x 25 x 30 cm) placed inside a temperature-controlled

environmental chamber (3 x 3 x 2.5 m). The environmental chamber and photoperiod followed a daily cycle that approximated the season and study site to which the bird had been accustomed. While in captivity, birds were provided free access to water, grit, and food (*Tenebrio* larvae and sunflower seeds). All birds maintained mass while in captivity. Individuals were tested within 1 week of capture. Birds tested from 11 May to 30 August were designated "summer birds," and those tested from 25 November to 1 March were designated "winter birds."

Body temperature measurements

All body temperature measurements were taken using a 30-gauge copper-constantan thermocouple attached to an Omega Model HH25-TC thermometer. The thermocouples were calibrated to a mercury thermometer traceable to the U.S. Bureau of Standards. The thermocouple was inserted into the cloaca to a depth (approximately 10-12 mm) where further insertion did not alter temperature reading. Body temperature was recorded immediately upon capture and after daytime and nighttime metabolic measurements. Although continuous records of T_b using implanted telemetry transmitters would have been desirable in this study, this was not possible given the small size of the species studied.

Measurements of metabolism

Measurements of metabolism at operative temperatures ranging from -10 to 30°C were recorded previously (Cooper unpubl. data). Briefly, birds were placed into a metabolic chamber constructed from a 3.8-L paint can. The inside of the can was painted

flat black to provide an emissivity near 1.0. Birds rested on hardware cloth above paraffin oil to collect excreta. Rates of oxygen consumption ($\dot{V}O_2$) were measured continuously using open-circuit respirometry with an Ametek S-3A oxygen analyzer. Dry, CO₂-free air was drawn through the metabolic chamber using a diaphragm pump. Outlet flow rates of dry, CO₂-free air were maintained at 452-460 ml min⁻¹, which yielded oxygen extraction rates between 0.3 and 0.6%. Measurements of outlet gas concentrations were recorded every 15 s on a computer using Datacan 5.0 data collection and analysis software (Sable Systems International). $\dot{V}O_2$ was measured on individual birds exposed to a single temperature within the series for 2 h. The first hour was an equilibration period and $\dot{V}O_2$ was measured over the last hour of the trial. Oxygen consumption was calculated as steady state $\dot{V}O_2$ using Eq. 4a of Withers (1977). All values were corrected to STP. Body mass was measured at the beginning and end of each metabolism trial. Constant mass loss throughout the tests were assumed and average mass during the last hour of the trial was used to correct $\dot{V}O_2$ to mass-specific values.

Statistics

All means are presented with their corresponding standard deviations. Intraspecific and interspecific means were compared using Student's *t*-tests as variances were not significantly different. Least squares linear regression was used to evaluate the relationship between operative and body temperature and also the relationship between ΔT and metabolism. Statistical significance is reported at $P < 0.05$. All statistics were computed using SPSS 6.1.

Results

Body temperature

For summer birds, daytime T_b ranged from 38.0- 43.0°C in chickadees and from 38.5-45.0°C in titmice. Nocturnal T_b decreased to a low of 28.3°C in titmice and 31.5°C in chickadees (Fig. 5.1A). In winter birds, daytime T_b ranged from 38.0-42.6°C in chickadees and from 38.0-41.6°C in titmice. Nocturnal T_b decreased as low as 31.1°C in chickadees and 31.2°C in titmice (Fig. 5.1B). Both species utilized nocturnal hypothermia for approximately 9 h in summer and 14 h in winter (Fig. 5.1). Since continuous T_b recordings for individuals were not recorded, the time taken for individual chickadees and titmice to enter and arouse from hypothermia is uncertain.

The mean daytime T_b of summer-acclimatized chickadees was $39.5 \pm 1.6^\circ\text{C}$ ($n = 63$), which was significantly lower than mean daytime T_b of summer titmice ($40.2 \pm 1.8^\circ\text{C}$, $n = 23$, $t = -2.570$, $P = 0.012$). The mean daytime T_b of winter chickadees was $38.9 \pm 1.2^\circ\text{C}$ ($n = 42$), which was not significantly different from mean daytime T_b of winter titmice ($39.5 \pm 1.1^\circ\text{C}$, $n = 17$, $t = -1.680$, $P = 0.099$). There was no seasonal difference in mean daytime T_b for either species (chickadee, $t = 0.770$, $P = 0.442$; titmice, $t = 1.49$, $P = 0.145$). The mean nocturnal T_b of summer chickadees was $35.5 \pm 1.8^\circ\text{C}$ ($n = 18$), which was not significantly different from mean nocturnal T_b of summer titmice ($35.9 \pm 2.6^\circ\text{C}$, $n = 24$, $t = -0.53$, $P = 0.600$). In summer birds, mean nocturnal T_b was significantly lower than mean daytime T_b (chickadees, $t = -8.140$, $P < 0.001$; titmice, $t = -6.600$, $P < 0.001$). The mean nocturnal T_b of winter chickadees was $36.0 \pm 2.2^\circ\text{C}$ ($n = 23$), which was not significantly different than mean nocturnal T_b of winter titmice

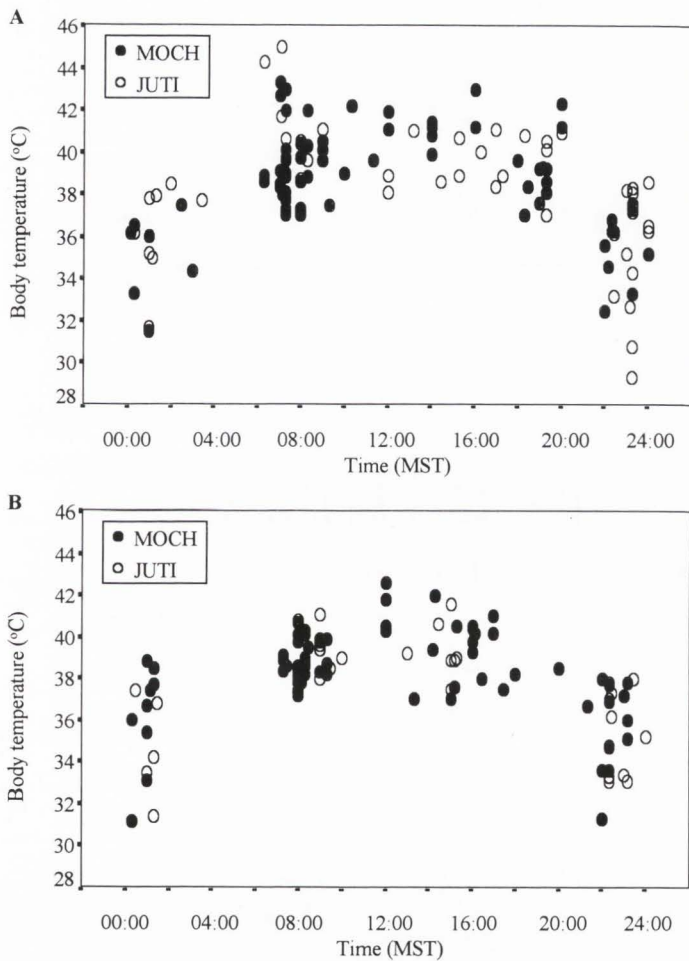


Fig. 5.1 Daily body temperature rhythm of summer (A) and winter (B) acclimatized mountain chickadees (MOCH) and juniper titmice (JUTI) from northern Utah

($35.3 \pm 2.0^\circ\text{C}$, $n = 18$, $t = 1.08$, $P = 0.288$). There was no seasonal difference in mean nocturnal T_b for either species (chickadees, $t = -0.870$, $P = 0.389$; titmice, $t = 0.730$, $P = 0.471$).

Depth of hypothermia in seasonally acclimatized birds varied with changing T_{es} for summer titmice, but not for summer chickadees. The relationship between T_b and T_{es} for summer birds (Fig. 5.2A) was best described by:

$$\text{chickadees: } T_b = 35.3 + 0.23T_{es} \quad (5.1)$$

$$(n = 18, r^2 = 0.01, P = 0.66)$$

$$\text{titmice: } T_b = 33.7 + 0.21T_{es} \quad (5.2)$$

$$(n = 24, r^2 = 0.74, P < 0.001)$$

In winter, T_b decreased with decreasing T_{es} for both chickadees and titmice. The relationship between T_b and T_{es} for winter birds (Fig. 5.2B) was best described by:

$$\text{chickadees: } T_b = 34.3 + 0.14T_{es} \quad (5.3)$$

$$(n = 23, r^2 = 0.61, P < 0.001)$$

$$\text{titmice: } T_b = 33.9 + 0.15T_{es} \quad (5.4)$$

$$(n = 18, r^2 = 0.91, P < 0.001)$$

The effect of body reserves on depth of hypothermia in seasonally acclimatized individuals was determined by multiple regression using body mass (BM) and T_{es} as independent variables and T_b as the dependent variable. For chickadees, BM did not contribute to depth of hypothermia (summer, $n = 15$, $P = 0.230$; winter, $n = 10$, $P = 0.080$). For titmice, BM and T_{es} were significantly correlated with T_b (summer, $n = 16$, $r^2 = 0.81$, $P < 0.001$; winter, $n = 10$, $r^2 = 0.67$, $P = 0.020$).

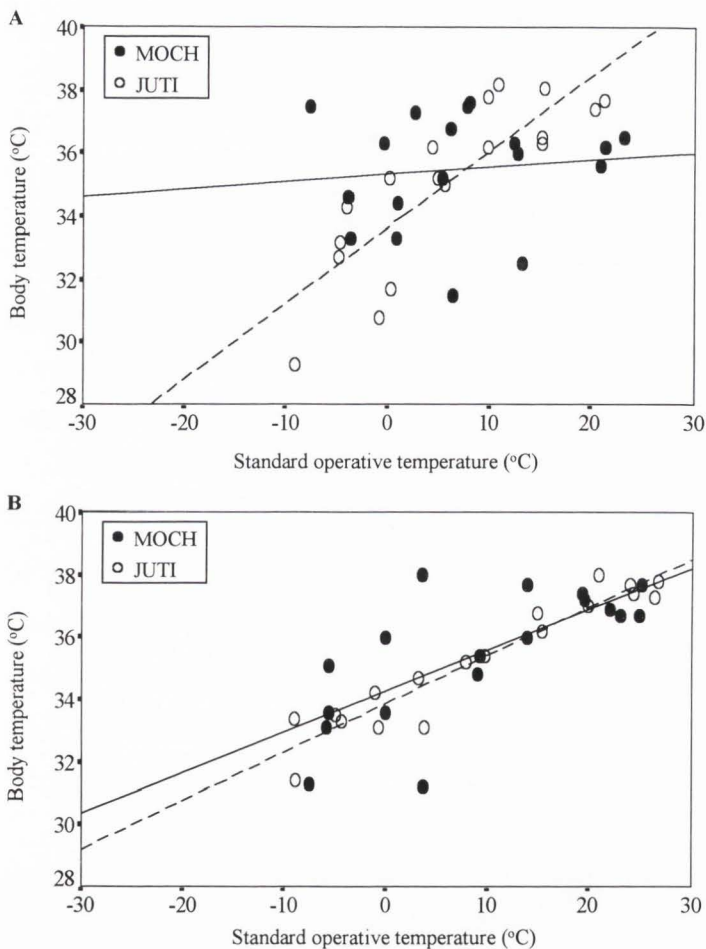


Fig. 5.2 The relationship between nocturnal body temperature and standard operative temperature for summer (A) and winter (B) acclimatized mountain chickadees (MOCH) and juniper titmice (JUTI) from northern Utah

Metabolic rates and thermal conductance

The lack of association between T_b and T_{es} suggests that reduction in body temperature is not merely a Q_{10} effect. In order to evaluate this possibility, the relationship between ΔT ($T_b - T_{es}$) and $\dot{V}O_2$ below thermoneutrality for seasonally acclimatized individuals was determined. The regression equations for ΔT and $\dot{V}O_2$ ($ml O_2 g^{-1} h^{-1}$) for summer birds (Fig. 5.3A) are:

$$\text{chickadees: } \dot{V}O_2 = -2.08 + 0.40 \Delta T \quad (5.5)$$

$$(n = 15, r^2 = 0.53, P = 0.001)$$

$$\text{titmice: } \dot{V}O_2 = -0.07 + 0.23 \Delta T \quad (5.6)$$

$$(n = 16, r^2 = 0.54, P = 0.001)$$

The regression equations for ΔT and VO_2 ($ml O_2 g^{-1} h^{-1}$) for winter birds (Fig. 5.3B) are:

$$\text{chickadees: } \dot{V}O_2 = -5.03 + 0.42 \Delta T \quad (5.7)$$

$$(n = 10, r^2 = 0.71, P = 0.002)$$

$$\text{titmice: } \dot{V}O_2 = -1.15 + 0.24 \Delta T \quad (5.8)$$

$$(n = 10, r^2 = 0.86, P < 0.001)$$

In order to determine if thermal conductance, $C = MR/T_b - T_{es}$, is near minimum throughout nocturnal hypothermia, the relationship between C and T_{es} was examined. Locally weighted scatterplot smoothing (LOWESS) regression and linear regression were used to determine nocturnal patterns of C . The LOWESS technique is useful because it makes no assumptions about the form of the underlying distribution (Cleveland 1985). For summer birds, C increased rapidly at a T_{es} of $15^\circ C$ and then became relatively stable at

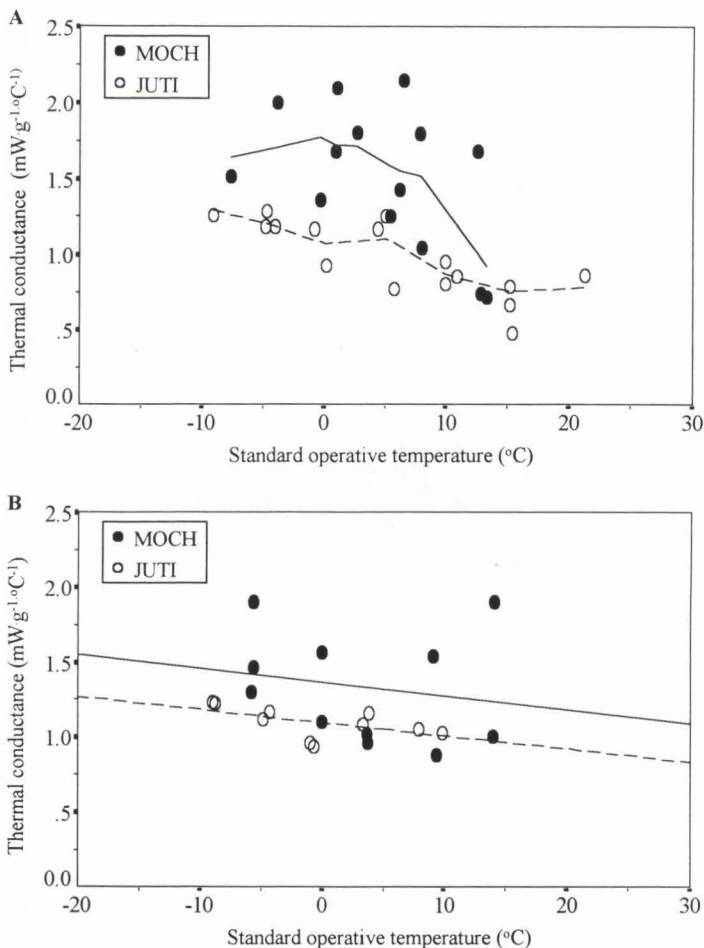


Fig. 5.3 Relationship of thermal conductance to standard operative temperature in summer (A) and winter (B) acclimatized mountain chickadees (MOCH) and juniper titmice (JUTI). LOWESS regression lines are shown for summer (A) birds and linear regression lines are plotted for winter (B) birds as slopes in winter are near zero

approximately 5°C (Fig. 5.4A). Winter C was very different from summer C. In winter, C remained relatively stable at all temperatures below thermoneutrality (Fig 5.4B).

Nocturnal energy savings due to hypothermia for chickadees and titmice were determined as the difference between the MR of normothermic individuals and the MR of hypothermic individuals. MR was calculated at 10°C intervals over the T_{cs} range of -10 to 20°C. Predicted normothermic MRs were calculated using the equation $MR = C(T_b - T_{cs})$. Equations 5.2, 5.3, and 5.4 were used to compute T_b for each T_{cs} . For summer chickadees, the mean hypothermic T_b of 35.5°C was used for each T_{cs} . Minimal C values of 0.33, 0.23, 0.24, and 0.21 ml O₂·g⁻¹·h⁻¹·°C⁻¹ were used for summer chickadees, summer titmice, winter chickadees, and winter titmice, respectively (Cooper unpubl data). Hypothermic MRs were determined for each temperature interval by inserting T_{cs} into linear regression equations relating MR to T_{cs} (Cooper unpubl data). Nocturnal energy savings were determined as percent reduction in metabolism for hypothermic birds compared to predicted metabolism for normothermic individuals. Nocturnal energy savings ranged from 7.1-49.8% in chickadees and from 9.7-27.8% in titmice (Fig. 5.5).

Discussion

Hypothermia

Seasonally acclimatized mountain chickadees and juniper titmice utilize nocturnal hypothermia. In summer birds, nocturnal T_b was typically 4-11°C below mean daytime T_b for each species. In winter, nocturnal T_b was typically 3-9°C below mean daytime T_b for each species. In addition, there were no seasonal differences in mean daytime or mean

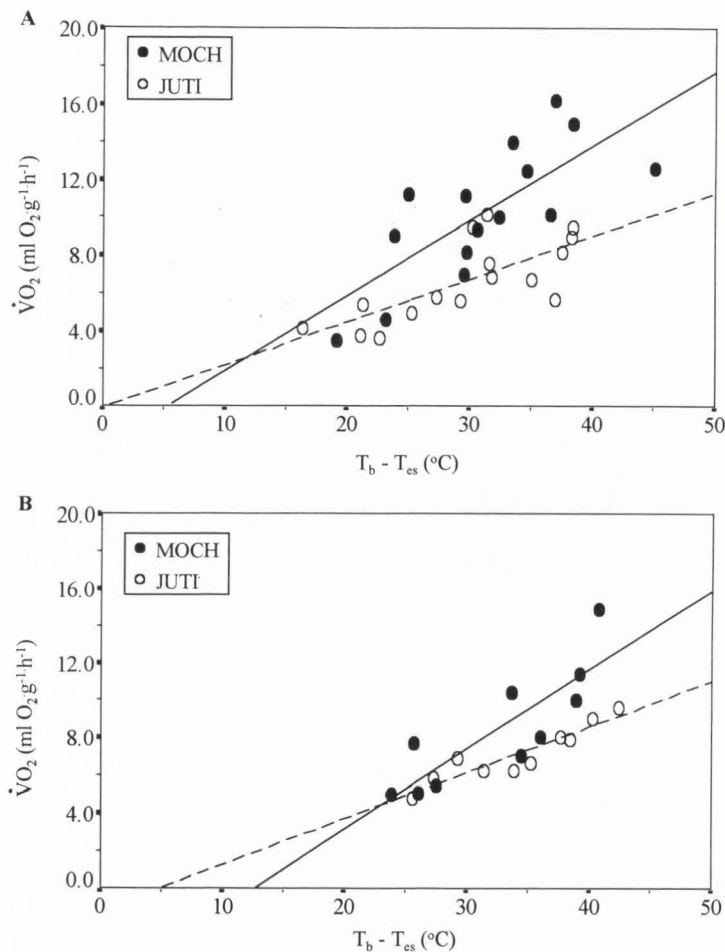


Fig. 5.4 Relationship of oxygen consumption to the difference between T_b and T_{es} for summer (A) and winter (B) acclimatized mountain chickadees (MOCH) and juniper titmice (JUTI) from northern Utah.

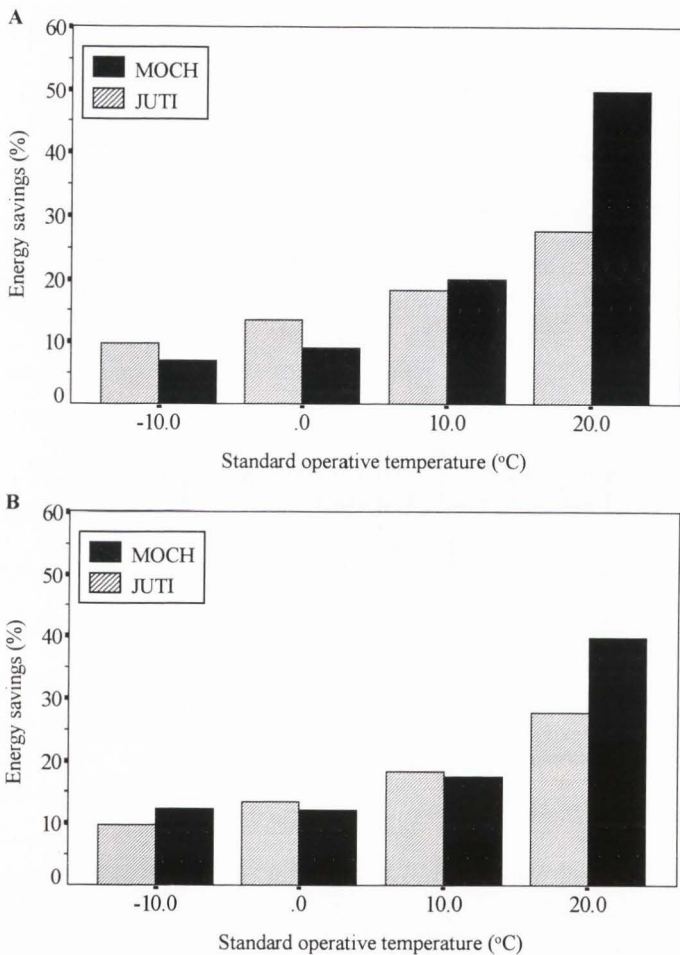


Fig. 5.5 Energy savings associated with nocturnal hypothermia in summer (A) and winter (B) acclimatized mountain chickadees (MOCH) and juniper titmice (JUTI). Energy savings are % reduction in metabolism compared to predicted euthermic rates

nocturnal T_b for either chickadees or titmice. Therefore, the depth of hypothermia in chickadees and titmice in this study did not vary seasonally. This contrasts to a pattern of increased depth of hypothermia in winter-acclimatized black-capped chickadees (Chaplin 1974) and willow tits (Reinertsen and Haftorn 1983).

Although season did not affect depth of hypothermia, several other factors did affect the degree of hypothermia in these species. For titmice, and winter chickadees, degree of hypothermia was dependent on T_{es} . A similar relationship has been found for several birds, including the Siberian tit (Haftorn 1972), the black-capped chickadee (Chaplin 1976), and willow tits (Reinertsen and Haftorn 1983). For summer-acclimatized mountain chickadees, this lack of association between T_b and T_{es} was characterized by a greater reduction in T_b between 10° and 25°C compared to titmice (Fig. 5.2A). This ability to maintain decreased T_b at relatively high environmental temperatures may be a very important energy savings for chickadees during the breeding season.

In addition to T_{es} , body reserves appear to be important in the regulation of depth of hypothermia in titmice. For titmice, T_b was dependent on the combined effects of T_{es} and BM. Thus, birds with lower energy reserves entering the roost at night will subsequently decrease T_b more than a bird with greater reserves. The dependence of the degree of hypothermia on body reserves has also been recorded for great tits, common redpolls (Reinertsen and Haftorn 1986), and willow tits (Reinertsen and Haftorn 1983). For chickadees, BM does not contribute to depth of hypothermia in summer or winter. Food was not experimentally restricted in this study and therefore, chickadees may show the same pattern when energy reserves are sufficiently depleted. However, overnight

resting metabolic rates and T_b s were not dependent on energy stores in winter-acclimatized black-capped chickadees (Hester 1996). The lack of association between T_b and BM may provide significant energetic savings for mountain chickadees even when foraging is not restricted.

Energy metabolism and thermal conductance

For seasonally acclimatized chickadees and titmice, MR is a linear function of ΔT (Fig. 5.3). Bartholomew et al. (1983) stated that for MR to be a linear function of ΔT , C would be at a minimal level and that while reducing MR, T_b will decline to a level determined by MR. This active downregulation of metabolism has also been proposed for mammals that use torpor (Heldmaier and Ruf 1992). In summer birds, C was not minimal throughout the range of T_{es} s used. However, summer birds appear to modify C, possibly through plumage and/or postural adjustments to increase C at T_{es} s above 5°C. Increased C would allow T_b to drop passively by Q_{10} effects and result in lower MRs. This would be advantageous for birds at ecologically relevant temperatures. The mean daily minimum July temperature is 5.3°C for chickadees and 12.8°C for titmice (Utah Climate Center). In winter birds, C is fairly constant below thermoneutrality, which supports the possibility of active downregulation of MR. Bartholomew et al. (1983) suggested that birds might use both Q_{10} effects and active downregulation in combination in order to conserve energy. Entrance into hypothermia might be accomplished by increasing thermal conductance, and once hypothermic, maintaining minimal C would allow active downregulation of MR to occur. In this study, T_b was not recorded continuously, and therefore it is unknown if this

pattern occurs. However, for winter chickadees and titmice in this study, plumage mass is significantly greater compared to summer (Cooper unpubl data). Thus, the ability to modify C by plumage and postural adjustments would be hindered. However, peripheral vasodilation and vasoconstriction could possibly allow modification of C in birds year-round. Clearly, several factors are involved with T_b and MR reduction during nocturnal hypothermia and more detailed physiological studies are needed to understand this complex phenomenon.

Energetic significance

Utilization of nocturnal hypothermia provides substantial overnight energy savings in chickadees and titmice. Perhaps ecologically more important, is how overnight energy savings translate into reduction in overall daily energy expenditure (DEE) in these species. Using the allometric equation of Nagy (1987) to compute predicted DEE in these two species, nocturnal energy savings can be calculated as DEE savings. In summer, at 10°C and based upon a 9-h evening, chickadees would conserve 4.75 kJ overnight and titmice would conserve 4.34 kJ overnight. These totals represent a 8.6% reduction in DEE for chickadees and 5.8% reduction for titmice. In winter, during a 14-h evening at -10°C , chickadees would conserve 9.08 kJ, while titmice would conserve 7.27 kJ and chickadees would reduce DEE by 17.1% while titmice would reduce DEE by 9.8%.

The results of this study demonstrate the energetic importance of nocturnal hypothermia for both mountain chickadees and juniper titmice. By utilizing nocturnal hypothermia, chickadees and titmice save substantial amounts of energy on both an

overnight and daily basis. These energy savings translate into increased fasting endurance upon leaving the roost, which may be critical to the energy balance of individuals, especially during inclement winter weather. The greater reduction in predicted DEE due to nocturnal hypothermia in winter chickadees compared to titmice indicates that hypothermia may be important in allowing chickadees to survive at higher latitudes than titmice.

References

- Bartholomew GA, Vleck CM, Bucher TL (1983) Energy metabolism and nocturnal hypothermia in two tropical passerine frugivores, *Manacus vitellinus* and *Pipra mentalis*. *Physiol Zool* 56:370-379
- Chaplin SB (1974) Daily energetics of the black-capped chickadee, *Parus atricapillus*, in winter. *J Comp Physiol* 89B:321-330
- Chaplin SB (1976) The physiology of hypothermia in the black-capped chickadee, *Parus atricapillus*. *J Comp Physiol* 112B:335-344
- Cleveland WS (1985) The elements of graphing data. Wadsworth, Monterey.
- Grossman AF, West GC (1977) Metabolic rate and temperature regulation of winter acclimatized black-capped chickadees *Parus atricapillus* in interior Alaska. *Ornis Scand* 88:127-138
- Haftorn S (1972) Hypothermia in tits in the arctic winter. *Ornis Scand* 3:153-166
- Heldmaier G, Ruf T (1992) Body temperature and metabolic rate during natural hypothermia in endotherms. *J Comp Physiol B* 162:696-706

- Hester, LL (1996) What determines overnight metabolic rate in wintering chickadees?
Am. Zool. 36:67A
- Mayer L, Lustick S, Battersby B (1982) The importance of cavity roosting and
hypothermia to the energy balance of the winter acclimatized carolina chickadee.
Int. Biometeor. 26:231-238
- Nagy, KA (1987) Field metabolic rate and food requirement scaling in mammals and birds.
Ecol. Monog. 57:111-128
- Reinertsen RE (1996) Physiological and ecological aspects of hypothermia. In: Carey C
(ed) Avian energetics and nutritional ecology. Chapman and Hall, New York.
pp 125-157
- Reinertsen RE, Haftorn S (1983) Nocturnal hypothermia and metabolism in the willow
tit, *Parus montanus*, at 63°N. J Comp Physiol 151B:109-118
- Reinertsen RE, Haftorn S (1986) Different metabolic strategies of northern birds for
nocturnal survival. J Comp Physiol 156B:655-663
- Steen, JB (1958) Climatic adaptation in some small northern birds. Ecology 39:625-629
- Withers PC (1977) Measurement of $\dot{V}O_2$, $\dot{V}CO_2$, and evaporative water loss with a flow-
through mask. J Appl Physiol 42:120-123

CHAPTER 6
THE THERMAL AND ENERGETIC SIGNIFICANCE OF CAVITY
ROOSTING IN SEASONALLY ACCLIMATIZED MOUNTAIN
CHICKADEES AND JUNIPER TITMICE

Abstract. I examined the thermal and energetic benefits of cavity roosting in summer- and winter-acclimatized Mountain Chickadees (*Parus gambeli*) and Juniper Titmice (*Parus ridgwayi*). Microclimatological variables measured at open sites and cavity roosts were combined with laboratory measurements of nocturnal metabolism to determine thermal and energetic savings due to cavity roosting. For summer birds, reduction of wind speed inside the cavity increased standard operative temperature 2.5 to 5.9°C compared to the open sites. Nocturnal energy savings ranged from 23.8 to 27.9% for summer birds roosting in cavities. Wind speed was significantly lower inside cavities compared to open sites for winter birds. Lower wind speed in cavities, combined with metabolic heating by the bird of air within a cavity, increased standard operative temperature 12.1 to 14.7°C compared to open sites. Nocturnal energy savings ranged from 25.1 to 37.6% for winter birds roosting in cavities. These energy savings result in increased fasting endurance of 2.2 to 3 hours in summer and 5.7 to 7.3 hours in winter, which may be critically important for survival throughout the annual cycle for these two species.

INTRODUCTION

Most birds are diurnal and forage only during daylight hours. Therefore, birds must rely on energy reserves to survive overnight fasting. This fasting period occurs when

energy demands for thermoregulatory homeostasis may be greatest due to cold nighttime temperatures. Roost-site selection by small birds can minimize thermoregulatory stress during the overnight fast. Factors that might be important in roost-site selection include local air temperature, shelter from wind and precipitation, and radiation balance (Walsberg 1986). Studies of roost-site selection by small birds in winter have received considerable attention since harsh climatic conditions and short daylength potentially threaten energy balance in winter-acclimatized individuals. These studies have shown that small birds reduce their energy exchange to the environment by selecting roosts that provide warmer air temperatures (Kendeigh 1961, Korhonen 1981, du Plessis et al. 1994), reduced convective heat loss (Kely and Lustick 1977, Mayer et al. 1982, Buttemer 1985, Walsberg 1986, Webb and Rogers 1988), and reduced radiative heat loss (Mayer et al. 1982, Buttemer 1985, Walsberg 1986). However, since basal and thermoregulatory costs typically account for 40-60% of total daily energy expenditure in birds, variation in thermoregulatory demands can determine the proportion of a bird's energy budget that is available for allocation to elective activities such as social activities, resource defense, and reproduction (Walsberg 1983). Therefore, roost-site selection and the resulting microclimate may be important in the ecological energetics of small birds throughout the annual cycle.

In order to determine the possible year-round importance of nocturnal roost-site selection on the energy balance of small birds, I examined micrometeorological variables at the roost in both summer and winter for two small passerine species, the Mountain Chickadee (*Parus gambeli*) and the Juniper Titmouse (*Parus ridgwayi*), which are year-

round residents of coniferous forests in western North America. Both species use natural and artificial cavities as nocturnal roost sites (Bent 1946). These two species are good models for a seasonal study of roost-site selection since they inhabit relatively high altitude habitats characterized by harsh climatic conditions nearly year-round. For example, unexpected spring snowstorms may occur during the breeding season of Mountain Chickadees in northern Utah (pers. obs.)

METHODS

STUDY AREA

Mountain Chickadee roost sites were studied within Cache National Forest, Cache County, in northeastern Utah (41°52'N 111°34'W) at an elevation of 2200 m. Juniper Titmice roost sites were studied in the Raft River Mountains, near Rosette, Box Elder County, in northwestern Utah (41°50'N 113°25'W) at an elevation of 1700 m. Mean minimum air temperatures in February for each study site are -11.6°C for Mountain Chickadees and -7.1°C for Juniper Titmice. For July, the mean minimum air temperatures are 5.1°C and 12.8°C at the chickadee and titmouse sites, respectively (Utah Climate Center).

CAVITY ROOSTS

In April of 1994 I placed nest boxes (15 x 15 x 25 cm, 32-mm entrance hole) in both study areas. During December 1995, I removed four boxes that had been used by either chickadees or titmice. For microclimate sampling I attached each of these four nest boxes separately on an adjustable 19-mm diameter metal pole. The nest boxes were

placed at a height of 1.5 m with the back of the box touching the trunk of a known roost site. Known roost sites were locations from which a nest box had been removed. The four nest boxes were oriented so that each one faced a different compass direction.

MICROCLIMATE SAMPLING

Microclimate data were collected at 15-minute intervals and averaged over 2-hour periods by an electronic datalogger (Model CR10, Campbell Scientific, Inc., Logan, Utah). Microclimate data were recorded from the four nest boxes (cavities) and from duplicate instruments placed 3 m away from the nearest nest box in the open. Microclimate sensors in the open were at the same height as the nest boxes. Microclimate variables measured in the open were: (1) air temperature (T_a) (shaded 36-gauge copper-constantan thermocouple), (2) operative temperature (T_o) (3.5-cm diameter copper sphere thermometer painted flat gray; Bakken et al. 1985, Walsberg and Weathers 1986), and wind speed (u) (Thornwaite model 901 cup anemometer). In order to evaluate possible metabolic heating of the air inside the cavity, I placed a single Mountain Chickadee or Juniper Titmice inside each of the nest boxes. I then placed a 15-mm wire mesh cover over the nest box opening so that the birds would not escape. I placed the birds inside the nest box shortly before sunset and allowed them to calm down before recording any microclimate data. I measured T_a in the nest boxes using 36-gauge copper constantan thermocouple placed approximately 5 cm above each bird's head. Wind speed inside the cavities was measured on separate nights in the absence of a bird and was always below the anemometer's lowest detectable wind speed (< 0.05 m/s). Thus, I used 0 m/s wind

speed as the value inside the roost cavities. Operative temperature thermometers could not be placed inside the cavity occupied by a bird. Instead, T_c in the cavity was assumed to equal T_a in the cavity since it is an isothermal enclosure with no shortwave radiation or forced convection (Bakken 1980). T_c helps define the sensible heat flow between a bird and its environment but it cannot establish equivalence between two environments that differ in factors that affect overall thermal conductance, notably wind (see Bakken 1992). Therefore, I calculated standard operative temperature (T_{es}) using Bakken's (1990) generalized passerine T_{es} scale:

$$T_{es} = T_b - (1 + 0.26u^{0.5})(T_b - T_c) \quad (6.1)$$

T_{es} was computed for both the open and in the cavity environment and then used to extrapolate laboratory metabolism data to the field. Nocturnal metabolism and body temperature were measured from -10 to 30°C in chickadees and titmice in an earlier investigation (Cooper unpubl. data). Microclimate data were collected from 21:00 to 0:500 hr (MST) in summer and from 20:00 to 0:700 hr (MST in winter)

STATISTICS

Data are presented as means \pm SE. Data for T_a , T_c , u , T_{es} , and predicted metabolism were averaged for the two open sites and for the four cavities. The microclimate values for each 15-minute interval for a given 2-hour period with the lowest temperature or highest wind speed for the entire nocturnal period were compared using Student's t-tests since variances were equal (F-test for equality of variance).

RESULTS

The extent to which the sites occupied by birds reduce their energy exchange with the environment is revealed by comparing measurements taken at open sites versus cavity roosts (Figs. 6.1-6.4). For summer chickadees, the greatest difference in wind speed between the open sites and the cavity roosts occurred from 22:00 to 00:00 hr (Fig. 6.1). During this period wind speed averaged 0.5 m/s. This wind speed resulted in a T_{es} of 5.1°C in the open sites compared to 11.6°C in the cavity roosts. Owing to these different convective regimes, energy expenditure over the 2-hour period for birds roosting in cavities would be reduced 34% relative to the open sites. For summer titmice, wind speed averaged 2.6 m/s from 22:00 to 00:00 hr (Fig. 6.2), resulting in a 38% reduction in energy expenditure for birds roosting in cavities. In summer birds, neither T_a nor T_c varied significantly between open sites and cavities (T_a : chickadees, $t = -1.23$, $P = 0.252$; titmice, $t = -0.150$, $P = 0.887$; T_c : chickadees, $t = -1.410$, $P = 0.188$; titmice, $t = -0.470$, $P = 0.652$; Table 1). Wind speed, T_{es} , and predicted energy expenditure were significantly lower in cavities than in open sites for summer titmice (u , $t = 4.74$, $P = 0.001$; T_{es} , $t = -2.450$, $P = 0.040$; energy expenditure, $t = 2.45$, $P = 0.040$) but not for summer chickadees (u , $t = 1.000$, $P = 0.347$; T_{es} , $t = -1.61$, $P = 0.146$; energy expenditure, $t = 1.61$, $P = 1.46$; Table 6.1).

In winter, T_a within the cavity ranged from 4.3-5.6°C higher than open sites for chickadees and from 1.7-6.3°C higher for titmice. Wind speed at the open sites was higher throughout the evening for winter chickadees and titmice. The combined effect of lower T_c and greater wind speeds in the open resulted in an increased T_{es} in the cavities,

FIGURE 6.1. Micrometeorological measurements at open sites (°) and at cavity roosts (•) for Mountain Chickadees on 31 July-1 August. Variables measured were averaged over 2-h periods.

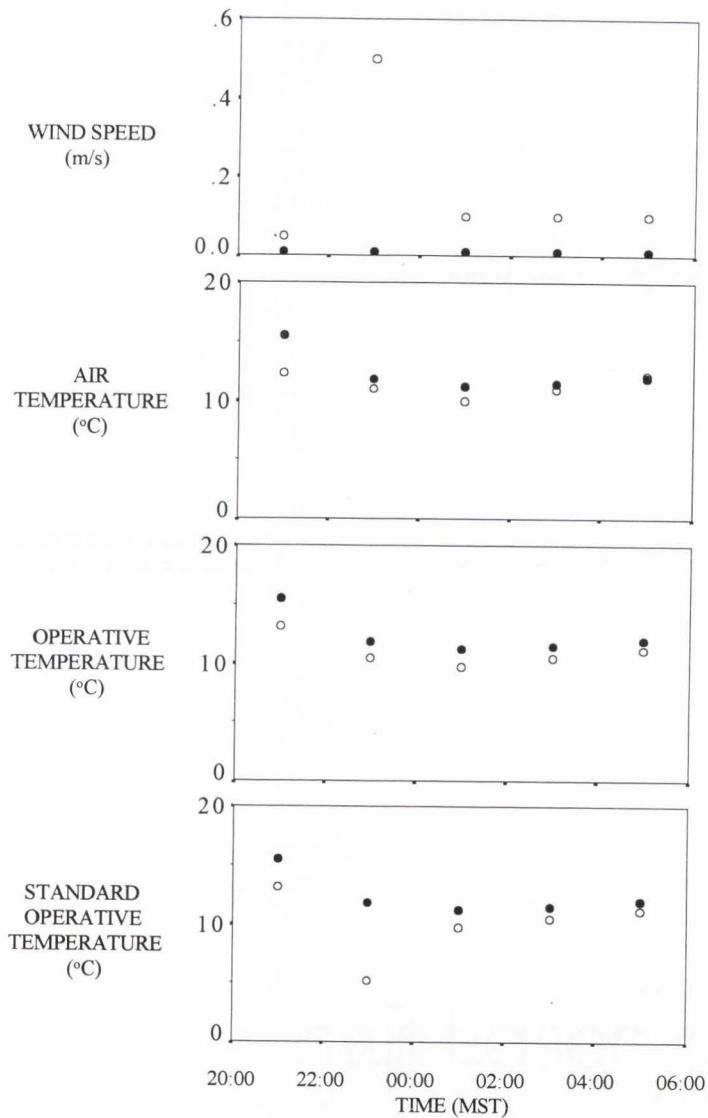


FIGURE 6.2. Micrometeorological measurements at open sites (◦) and at cavity roosts (•) for Juniper Titmice 2 August-3 August. Variables measured were averaged over 2-h periods.

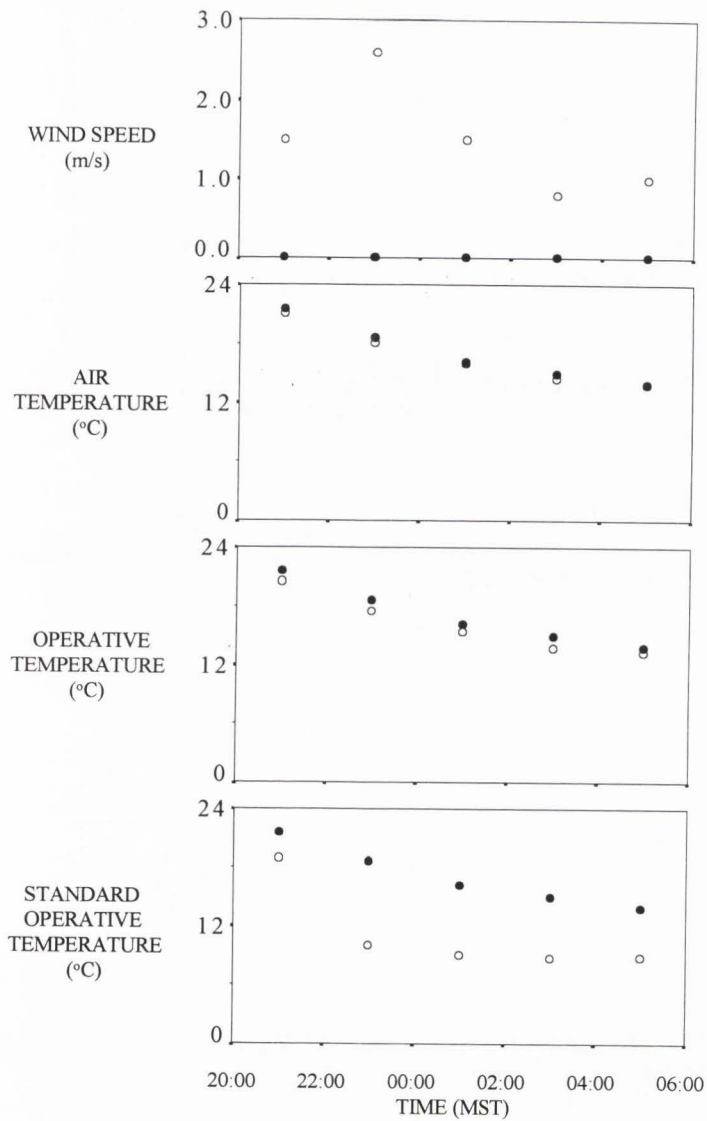


FIGURE 6.3. Micrometeorological measurements at open sites (○) and at cavity roosts (●) for Mountain Chickadees on 6 February-7 February. Variables measured were averaged over 2-h periods.

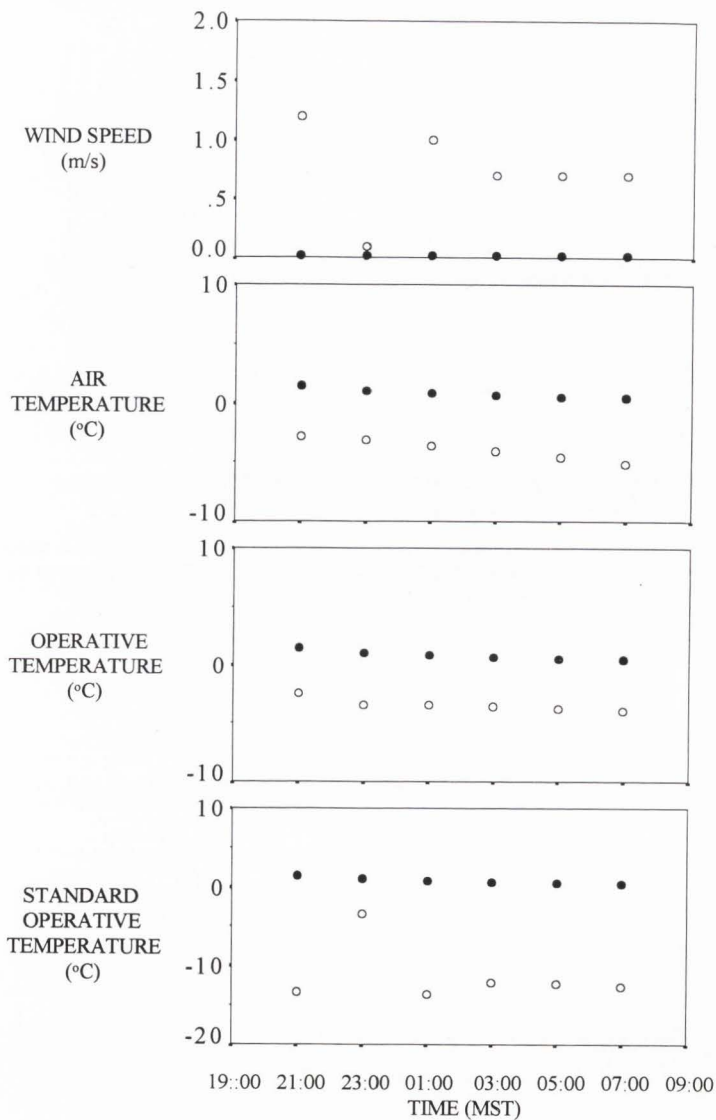


FIGURE 6.4. Micrometeorological measurements at open sites (◦) and at cavity roosts (●) for Juniper Titmice 27 February-28 February. Variables measured were averaged over 2-h periods.

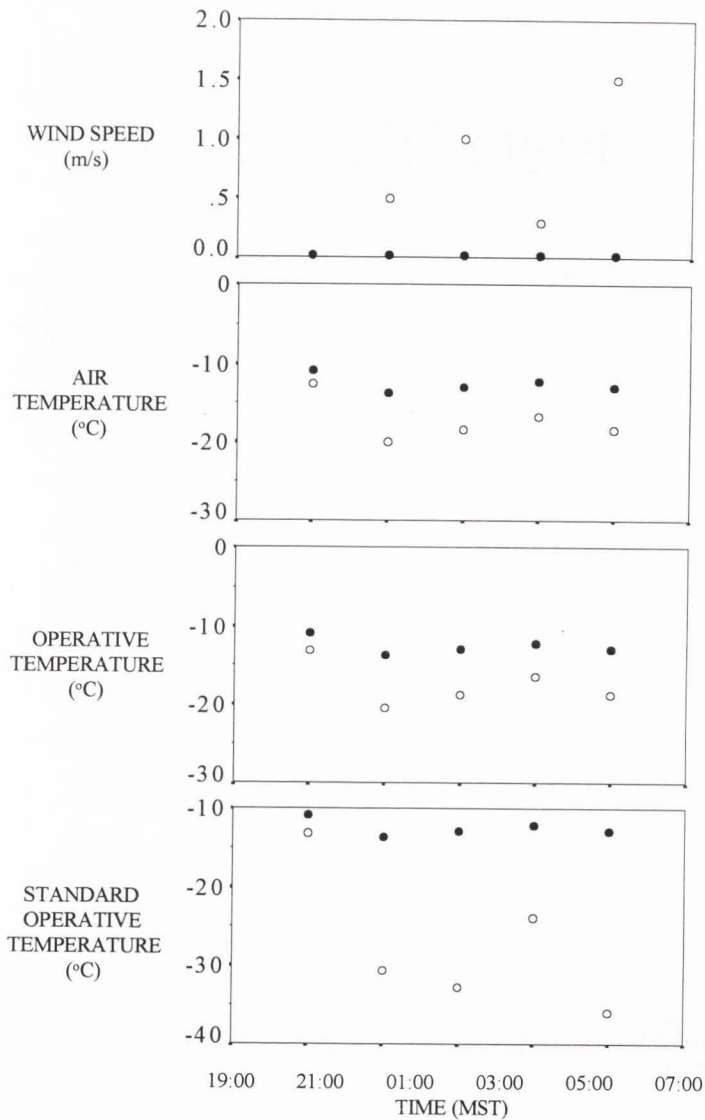


TABLE 6.1. Average overnight micrometeorological variables and predicted energy expenditure (means \pm SE) at open sites compared to cavity roosts for Mountain Chickadees (MOCH) and Juniper Titmice (JUTI) for summer roost periods.

Variable	31 Jul. - 1 Aug.		2 Aug. - 3 Aug.	
	MOCH		JUTI	
	Open sites	Cavity roosts	Open sites	Cavity roosts
Air temperature ($^{\circ}$ C)	11.3 \pm 0.4	12.5 \pm 0.8	16.8 \pm 1.3	17.1 \pm 1.4
Operative temperature ($^{\circ}$ C)	11.0 \pm 0.6	12.5 \pm 0.8	16.2 \pm 1.3	17.1 \pm 1.4
Wind speed ^a (m/s)	0.1 \pm 0.1	0	1.5 \pm 0.3	0*
Standard operative temperature ^b ($^{\circ}$ C)	10.0 \pm 1.3	12.5 \pm 0.8	11.2 \pm 2.0	17.1 \pm 1.4*
Estimated live-bird energy expenditure ^c (kJ)	10.1 \pm 1.3	7.7 \pm 0.8	12.2 \pm 1.1	8.8 \pm 0.8*

^aWind speed in cavity assumed to be 0 m/s. ^bComputed using equation (6.1). ^cEstimate represents a 9-hour roost period. *Indicates significant differences in intraspecific comparisons between the two sites ($P < 0.05$).

ranging from 4.5-14.8 $^{\circ}$ C for chickadees and from 3.2-23.0 $^{\circ}$ C for titmice (Figs. 6.3 and 6.4). Cavities had significantly higher T_a , T_e , and T_{es} compared to open sites for chickadees and titmice (T_a : chickadees, $t = -12.33$, $P < 0.001$; titmice, $t = -3.44$, $P = 0.009$; T_e : chickadees, $t = -16.38$, $P < 0.001$; titmice, $t = -3.71$, $P = 0.006$; T_{es} : chickadees, $t = -7.62$, $P < 0.001$; titmice, $t = -3.62$, $P = 0.007$). Wind speed was significantly higher at open sites compared to inside cavities for chickadees ($t = 4.31$, $P = 0.002$) and for titmice ($t = 2.48$, $P = 0.038$). Predicted energy expenditure in cavities was 25.1% lower for titmice and 37.6% lower for chickadees compared to open sites (Table 6.2).

DISCUSSION

In summer, T_a and T_e were slightly, but not significantly higher in cavities than in open sites. Since net radiation was not measured in this study, it is difficult to separate radiative heat gain in the cavity compared to the open, versus metabolic heating of the air

TABLE 6.2. Average overnight micrometeorological variables and predicted energy expenditure (means \pm SE) at open sites compared to cavity roosts for Mountain Chickadees (MOCH) and Juniper Titmice (JUTI) for winter roost periods.

Variable	6 Feb. - 7 Feb.		27 Feb. - 28 Feb.	
	MOCH		JUTI	
	Open sites	Cavity roosts	Open sites	Cavity roosts
Air temperature ($^{\circ}$ C)	-3.9 ± 0.4	$0.9 \pm 0.1^*$	-17.1 ± 1.3	$-12.5 \pm 0.5^*$
Operative temperature ($^{\circ}$ C)	-3.4 ± 0.2	$0.9 \pm 0.1^*$	-17.5 ± 1.2	$-12.5 \pm 0.5^*$
Wind speed ^a (m/s)	0.7 ± 0.2	0*	0.7 ± 0.3	0*
Standard operative temperature ^b ($^{\circ}$ C)	-11.2 ± 1.6	$0.9 \pm 0.1^*$	-27.2 ± 4.0	$-12.5 \pm 0.5^*$
Estimated live-bird energy expenditure ^c (kJ)	37.2 ± 1.8	$23.2 \pm 0.2^*$	52.9 ± 3.6	$39.6 \pm 0.4^*$

^aWind speed in cavity assumed to be 0 m/s. ^bComputed using equation (6.1). ^cEstimate represents a 14-hour roost period. *Indicates significant differences in intraspecific comparisons between the two sites ($P < 0.05$).

within the cavity. However, Walsberg (1983) calculated that changing the radiative environment such that a bird is completely shielded by vegetation, rather than being exposed to the night sky, increases heat gain due to radiative effects by an equivalent of only 1-2 $^{\circ}$ C. In addition, since $T_e = T_a + \Delta T_R$ (where T_R is radiation conductance per $^{\circ}$ C) (Eq. 1, Bakken 1992), by examining the difference between T_a and T_e in the open sites, one can determine the summary effect of radiative heat loss experienced by the bird. In summer, T_e in the open was 0.3-0.6 $^{\circ}$ C lower than T_a in the open. This demonstrates the minor thermal importance of radiative heat loss for birds, even if they roost in the open. In summer, T_a within the cavity was 0.3-1.2 $^{\circ}$ C higher than the open sites, which indicates that metabolic heating by the bird of the air inside the cavity was also unimportant. Decreased wind speed inside the cavity accounted for the most significant thermal and energetic benefit for summer birds. Reduction in wind speed resulted in T_{ca} being

2.5-4.9°C higher inside cavities compared to the open, which resulted in a 23.8% reduction in nocturnal energy expenditure for chickadees and a 27.9% reduction for titmice.

Air temperatures inside winter cavities were 4.6-4.8°C higher than open sites. This increase in T_a indicates that metabolic heating by the birds of air inside the cavity provides significant thermal benefits for winter-acclimatized individuals. The increased T_a inside cavities may also be due to thermal inertia of the cavities. For Acorn Woodpecker cavities, with one bird inside, thermal inertia accounted for 4.3 of a total of 5.5°C increase in T_a compared to open sites (du Plessis et al. 1994). However, in this study, the artificial cavities were held at outside T_a and kept shaded until microclimate measurements began. Thus, it is unlikely that the cavities would have been warmer than the surrounding T_a and that thermal inertia is responsible for the increased T_a inside the cavities. However, for natural cavities, it is possible that thermal inertia of cavities would cause an even greater increase in T_a compared to roosting in the open. Reduction of wind speed inside the cavities in winter resulted in an increased T_{es} of 12.1°C for chickadees and 14.7°C for titmice compared to open sites. This significant increase in T_{es} results in a nocturnal energy savings of 25.1% for winter titmice and 37.6% for winter chickadees.

Reduction of nocturnal energy metabolism due to cavity roosting is important for chickadees and titmice because nocturnal energy savings translate to increased fasting endurance. I determined the increase in fasting endurance due to cavity roosting by subtracting predicted nocturnal energy expenditure for birds roosting in cavities from the predicted nocturnal energy expenditure for birds roosting in the open for the four nights

microclimate data was measured. I took these energy metabolism values and divided them by the resting metabolic rate of chickadees and titmice at the mean daily temperature for each season. This results in the amount of time that a bird can fast while maintaining resting metabolism. For summer birds, fasting endurance increased 2.2 hours for chickadees and 3.0 hours for titmice roosting in cavities compared to open sites. For winter birds, fasting endurance increased 7.3 hours for chickadees and 5.7 hours for titmice. Average fat content of birds that were captured in the morning soon after leaving nightly roosts in summer was 0.36 g for chickadees and 0.77 g for titmice. Average fat content in winter was 0.36 g for chickadees and 0.72 g for titmice (Cooper unpubl.). Assuming a thermal equivalent of 39.3 kJ/g (Schmidt-Nielsen 1990) and that 0.1 g of this fat is unavailable for thermogenic needs (Newton 1969), the effect of temperature on the ability of seasonally acclimatized birds to endure fasting can be further evaluated. For chickadees, 0.26 g of available fat would yield 10.2 kJ, which would support resting metabolism at 16.2 and -5°C (the mean daily temperature for July and January, respectively, for Tony Grove, UT; Utah State Climate Center) for 9.3 hours in summer and 5.3 hours in winter upon leaving the roost. For titmice, available fat would yield 26.3 kJ in summer and 24.4 kJ in winter. These energy equivalents would support resting metabolism at 21.3 and 1°C (the mean daily temperature for July and January, respectively, for Rosette, UT; Utah State Climate Center) and allow summer titmice to fast for 22.8 hours and winter titmice to fast 10.4 hours upon leaving the roost. For summer birds, additional fasting endurance may be important in allowing adults to feed nestlings, especially upon leaving the roost. For winter birds, increased fasting endurance

may be especially important during inclement weather, which might reduce foraging ability.

My analysis demonstrates the importance of cavity roosts on reduction in convective heat loss in Mountain Chickadees and Juniper Titmice. In addition, in winter, it appears that metabolic heating of the air within the cavity is an important thermal benefit for these two species. However, studies of natural cavities need to be undertaken in order to separate the effect of metabolic heating from thermal inertia. Clearly, use of cavity roosts by chickadees and titmice offers significant nocturnal energy savings, which translates into increased fasting endurance that is important throughout the annual cycle of these birds.

LITERATURE CITED

- BAKKEN, G. S. 1980. The use of standard operative temperature in the study of thermal energetics of birds. *Physiol. Zool.* 53:108-119.
- BAKKEN, G. S. 1990. Estimating the effect of wind on avian metabolic rate with standard operative temperature. *Auk* 107:587-594.
- BAKKEN, G. S. 1992. Measurement and application of operative and standard operative temperature in ecology. *Am. Zool.* 32:194-216.
- BAKKEN, G. S., W. R. SANTEE, and D. J. ERSKINE. 1985. Operative and standard operative temperature: tools for thermal energetic studies. *Am. Zool.* 25:933-943.
- BENT, A. C. 1946. Life histories of North American jays, crows, and titmice. *U.S. Natl. Mus. Bull.* 191.

- BUTTEMER, W. A. 1985. Energy relations of winter roost-site utilization by American goldfinches (*Carduelis tristis*). *Oecologia* 68:126-132.
- DU PLESSIS, M. A., W. W. WEATHERS, and W. D. KOENIG. 1994. Energetic benefits of communal roosting by Acorn Woodpeckers during the nonbreeding season. *Condor* 96:631-637.
- KELTY, M., and S. LUSTICK. 1977. Energetics of the starling (*Sturnus vulgaris*) in a pine woods. *Ecology* 58:1181-1185.
- KENDEIGH, S. 1961. Energy of birds conserved by roosting in cavities. *Wilson Bull.* 73:175-182.
- KORHONEN, K. 1981. Temperature in the nocturnal shelters of the Redpoll (*Acanthis flammea*) and the Siberian Tit (*Parus cinctus*) in winter. *Ann. Zool. Fenn.* 18:165-168.
- MAYER, L., S. LUSTICK, and B. BATTERSBY. 1982. The importance of cavity roosting and hypothermia to the energy balance of the winter acclimatized Carolina Chickadee. *Int. Biometeor.* 26:231-238.
- NEWTON, I. 1969. Winter fattening in the Bullfinch. *Physiol. Zool.* 42:96-107.
- SCHMIDT-NIELSEN, K. 1990. *Animal physiology*. Cambridge Press, New York.
- WALSBERG, G. E. 1983. Avian ecological energetics, p. 161-220. *In* D. S. Farner, and K. C. Parkes [eds.], *Avian biology*. Vol. 7. Academic Press, New York.
- WALSBERG, G. E. 1986. Thermal consequences of roost-site selection: the relative importance of three modes of heat conservation. *Auk* 103:1-7.

- WALSBERG, G.E., and W. W. WEATHERS. 1986. A simple technique for estimating operative environmental temperature. *J. Therm. Biol.* 11:67-72.
- WEBB, D. R., and C. M. ROGERS. 1988. Nocturnal energy expenditure of Dark-eyed Juncos roosting in Indiana during winter. *Condor* 90:107-112.

CHAPTER 7

SUMMARY

The objective of this dissertation was to determine the role of cold acclimatization on the biogeography of the Mountain Chickadee (*Parus gambeli*) and the Juniper Titmouse (*Parus ridgwayi*). Specifically, I examined the relative role of physiological, physical, and behavioral adjustments to cold on the northern range limits of these two species. Winter birds tolerated colder helox test temperatures than summer birds for both chickadees and titmice. This improved cold tolerance was associated with a significant increase in maximal thermogenic capacity in winter chickadees (27%) and titmice (11%) compared to summer. Chickadees and titmice had significantly lower thermal conductance in helox in winter than in summer, which also improved cold tolerance. Basal metabolic rate was significantly higher in winter birds (16%) compared to summer birds for both species. Basal metabolism and maximal thermogenic capacity were significantly higher for chickadees compared to titmice in both summer and winter. Winter chickadees were able to withstand colder test temperatures than winter titmice. These data demonstrate the importance of metabolic adjustments in seasonal acclimatization of thermoregulation in small birds. In addition, these data illustrate that Mountain Chickadees have significantly increased metabolic capacities compared with Juniper Titmouse, which may shape the northern range limit of these species.

Pectoralis muscle mass increased 33% in chickadees and 24% in titmice in winter and paralleled increased basal and peak metabolic rates. Dry mass of contour plumage

increased in winter for both species and was associated with decreased thermal conductance in air for winter chickadees compared to summer chickadees. The Mountain Chickadee's lower critical temperature is decreased compared to the Juniper Titmouse's in summer and in winter. The Mountain Chickadee's upper critical temperature is also lower than the Juniper Titmouse's and chickadees also had significantly higher evaporative water loss rates compared to titmice. Seasonal acclimatization in Mountain Chickadees involves insulatory as well as metabolic changes. For Juniper Titmice, winter acclimatization appears to be primarily a metabolic process similar to other passerines.

Calculated northern boundary metabolic rates of winter chickadees is 2.47 times their basal metabolic rate and 2.80 times the basal metabolic rate for titmice. This is in close agreement with a proposed 2.45 times basal metabolic rate as a limit to northern range distributions in passerines. In addition, the data for cold tolerance and heat tolerance suggest that climate acts directly to shape the biogeographic patterns of the Mountain Chickadee and Juniper Titmouse.

I used behavioral, meteorological, and laboratory metabolism data to calculate DEE in seasonally acclimatized chickadees and titmice. The laboratory metabolism data analysis revealed that heat produced as a by-product of physical activity substitutes for thermoregulatory requirements. DEE in summer was 48.8 kJ/d for chickadees and 48.3 kJ/d for titmice. DEE in winter was 66.3 kJ/d for chickadees and 98.7 kJ/d for titmice. DEE as a multiple of basal metabolic rate (BMR) was 2.31 in summer chickadees and 1.91 in summer titmice. DEE was 2.70 times BMR in winter chickadees and 3.43 times BMR in winter titmice. These values are close to the suggested northern boundary metabolic

rate of 2.45 times BMR and indicate that DEE helps shape the northern range limits of these two species. The marked increase in calculated DEE in winter birds compared to summer contrasts a pattern of increased DEE in the breeding season for several avian species. The data suggest that winter may be a period of even greater stringency for small birds than previously believed.

The seasonal regulation of body temperature and metabolism, especially the utilization of nocturnal hypothermia, was examined in order to evaluate possible ecological consequences of body temperature in these two species. Both species utilized nocturnal hypothermia year-round. Depth of hypothermia did not vary seasonally in these two species. Nocturnal body temperature was regulated 3-11° lower than daytime values for both species. Nocturnal body temperature was a linear function of standard operative temperature for all birds except summer-acclimatized Mountain Chickadees. In addition to standard operative temperature effects on body temperature, metabolic downregulation may be involved with decreased nocturnal body temperature in these two species. Depth of hypothermia was inversely correlated to body mass in seasonally acclimatized Juniper Titmice but not in Mountain Chickadees. Nocturnal energy savings range from 7-50% in chickadees and from 10-28% in titmice. These nocturnal energy savings result in lower daily energy expenditures of 9-17% for Mountain Chickadees and 6-10% for Juniper Titmice. These energy savings may be critically important for survival throughout the annual cycle for these birds.

I examined the thermal and energetic benefits of cavity roosting in summer- and winter-acclimatized Mountain Chickadees (*Parus gambeli*) and Juniper Titmice

(*Parus ridgwayi*). Microclimatological variables measured at open sites and cavity roosts were combined with laboratory measurements of nocturnal metabolism to determine thermal and energetic savings due to cavity roosting. For summer birds, reduction of wind speed inside the cavity increased standard operative temperature 3 to 6°C compared to the open sites. Nocturnal energy savings ranged from 24 to 28% for summer birds roosting in cavities. Wind speed was significantly lower inside cavities compared to open sites for winter birds. Lower wind speed in cavities, combined with metabolic heating by the bird of air within a cavity, increased standard operative temperature 12 to 15°C compared to open sites. Nocturnal energy savings ranged from 25 to 38% for winter birds roosting in cavities. These energy savings result in increased fasting endurance of 2.2 to 3 hours in summer and 5.7 to 7.3 hours in winter, which may be critically important for survival throughout the annual cycle for these two species.

The Mountain Chickadee and Juniper Titmouse undergo winter acclimatization that enables them to maintain thermoregulatory homeostasis. Winter acclimatization in Juniper Titmice appears to be primarily a metabolic process, while insulatory adjustments are also involved in Mountain Chickadees. Chickadees and titmice utilize nocturnal hypothermia and utilize cavity roosts, which enable them to reduce overnight energy expenditure and increase fasting endurance upon leaving the roost in the morning. The data from this study suggest that the northern range limit of small passerines can be limited by physiological demands of energy and water balance.

APPENDICES

APPENDIX A. ANOVA TABLES

Table A1. Analysis of variance of the effect of helox test temperature ($^{\circ}\text{C}$) on the mass-specific $\dot{V}\text{O}_2$ ($\text{mL O}_2\text{g}^{-1}\text{h}^{-1}$) of summer-acclimatized Mountain Chickadees.

Source	<u>DF</u>	<u>SS</u>	<u>MS</u>	<u>F</u>	<u>P</u>
Between temperatures	2	5.6965	2.8483	0.1645	0.8493
Within temperatures	23	398.2217	17.3140		
Total	25	403.9182			

Table A2. Analysis of variance of the effect of helox test temperature ($^{\circ}\text{C}$) on the mass-specific $\dot{V}\text{O}_2$ ($\text{mL O}_2\text{g}^{-1}\text{h}^{-1}$) of summer-acclimatized Juniper Titmice.

Source	<u>DF</u>	<u>SS</u>	<u>MS</u>	<u>F</u>	<u>P</u>
Between temperatures	2	31.3497	15.6748	4.8347	0.0194
Within temperatures	20	64.8436	3.2422		
Total	22	96.1933			

Table A3. Analysis of variance of the effect of helox test temperature ($^{\circ}\text{C}$) on the mass-specific $\dot{V}\text{O}_2$ ($\text{mL O}_2 \text{g}^{-1} \text{h}^{-1}$) of winter-acclimatized Juniper Titmice.

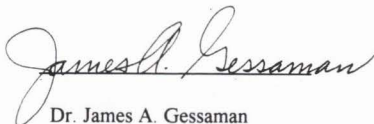
<u>Source</u>	<u>DF</u>	<u>SS</u>	<u>MS</u>	<u>F</u>	<u>P</u>
Between temperatures	2	14.3673	7.1837	1.1133	0.3579
Within temperatures	13	83.8839	6.4526		
Total	15	98.2512			

Table A4. Analysis of variance of the effect of helox test temperature ($^{\circ}\text{C}$) on the mass-specific $\dot{V}\text{O}_2$ ($\text{mL O}_2 \text{g}^{-1} \text{h}^{-1}$) of winter-acclimatized Mountain Chickadees.

<u>Source</u>	<u>DF</u>	<u>SS</u>	<u>MS</u>	<u>F</u>	<u>P</u>
Between temperatures	3	9.2598	3.0866	5.3146	0.0062
Within temperatures	23	13.3578	.5808		
Total	26	22.6175			

APPENDIX B. CONTRIBUTION ACKNOWLEDGMENT FROM COAUTHOR

Although I have coauthored one publication arising from the work in this dissertation, by signing below I acknowledge that each of the chapters herein was written by Sheldon J. Cooper, and the majority of the intellectual contribution was his.

A handwritten signature in cursive script that reads "James A. Gessaman". The signature is written in black ink and is positioned above the printed name.

James A. Gessaman

Dr. James A. Gessaman

APPENDIX C. DEE ENERGETIC COST ESTIMATES

Energy Costs Estimates

I estimated the energy cost of flight (\dot{H}_n) in eq. (1) as 11.7 times nighttime \dot{H}_b as found in Willow Tits (Carlson and Moreno 1992) using doubly labeled water. My estimate for active or alert perching energy cost differs from several other studies in that the energy cost of active perching was measured on fed birds resting in the dark rather than in lighted conditions (Weathers et al. 1984, Buttemer et al. 1986, Weathers and Sullivan 1993). Chickadees and titmice in this study became very active inside the metabolic chamber with any amount of incoming light. Thus, I used energy costs associated with fed, perching in the dark as alert perch costs. Foraging cost estimates were derived using birds inside a "typical" metabolic chamber and not within a specialized foraging metabolic chamber. Thus, the birds may not have moved around as much as if they were actually foraging in the wild and thus, foraging costs may be slightly underestimated. However, both chickadees and titmice remained very active (judging from $\dot{V}O_2$ data and from visual observations) throughout the time period of the metabolic trial and this probably does not constitute appreciable error in energetic estimates. In order to determine total daily energy costs of each activity (perching, flight, foraging, nocturnal maintenance) for chickadees and titmice I subtracted basal metabolism from each activity. Since, basal metabolic rate averages 20-25% higher during the active phase of the daily cycle than during the rest phase (Aschoff and Pohl 1970) I assumed that active phase basal metabolism was 1.2 times \dot{H}_b for chickadees and titmice in order to correct each activity for the daily cycle.

Estimating Energy Costs Under Field Conditions

In equation (1), maintenance metabolism is (\dot{H}_m) is included in all 4 bracketed terms and represents the obligatory energy requirement (the sum of basal metabolism and thermoregulatory costs). The costs of physical activity are added to \dot{H}_m to obtain DEE. However, \dot{H}_m cannot be measured directly in free-ranging animals and methods for estimating it under field conditions are still being worked out. Both empirical and theoretical studies indicate that accounting for the effects of shortwave radiation and wind on heat transfer is critical to accurate time-budget estimates of \dot{H}_m (Bakken 1976; Weathers et al. 1984; Williams and Nagy 1984; Buttemer et al. 1986; Weathers and Sullivan 1993). There are two approaches to accurately determine these effects. One approach uses heated taxidermic mounts that are calibrated against living animals in the laboratory to accommodate radiation and wind effects directly (e.g., Bakken et al. 1981; Masman et al. 1988). The other approach uses unheated taxidermic mounts or sphere thermometers to measure operative temperature (T_e) and then computes the effect of wind using laboratory metabolism data and heat transfer theory (e.g., Weathers et al. 1984; Weathers and Sullivan 1993). I used the second approach and calculated the complex thermal environment encountered by my birds by calculating standard operative temperature (T_{es}) on the basis of the measured field T_e and wind speed (u) using Bakken's (1990) generalized passerine T_{es} scale:

$$T_{es} = T_b - (1 + 0.26u^{-0.5})(T_b - T_e) \quad (C1)$$

The use of this method yielded remarkably similar results compared to the first approach on data for Yellow-eyed Juncos and also provides "significant economy in calculation"

(Weathers and Sullivan 1993). However, Walsberg and Wolf (1996) found that the utility of taxidermic mounts vary greatly by species.

Estimating the Birds Microclimate

Details of nocturnal microclimate measurement can be found in chapter six. In brief, for nocturnal microclimate measurement I used T_a measured inside nest boxes occupied by a single bird for both chickadees and titmice. Wind speed was measured on different nest boxes which did not contain a bird and was always zero.

Literature Cited

- Aschoff, J., and H. Pohl. 1970. Rhythmic variations in energy metabolism. *Fed. Proc.* 29:1541-1552.
- Bakken, G. S. 1976. A heat transfer analysis of animals: unifying concepts and the application of metabolism data to field ecology. *J. Theor. Biol.* 60:337-384.
- Bakken, G. S. 1990. Estimating the effect of wind on avian metabolic rate with standard operative temperature. *Auk* 107:587-594.
- Bakken, G. S., W. A. Buttemer, W. R. Dawson, and D. M. Gates. 1981. Heated taxidermic mounts: a means of measuring standard operative temperatures affecting small animals. *Ecology* 62:311-318.
- Buttemer, W. A., A. M. Hayworth, W. W. Weathers, and K. A. Nagy. 1986. Time-budget estimates of avian energy expenditure: physiological and meteorological considerations. *Physiol. Zool.* 59:131-149.
- Carlson, A., and J. Moreno. 1992. Cost of short flights in the Willow Tit measured with doubly labeled-water. *Auk* 109:389-393.

- Masman, D., S. Daan, and H. J. A. Beldhuis. 1988. Ecological energetics of the kestrel: daily energy expenditure throughout the year based on time-energy budget, food intake and doubly labeled water methods. *Ardea* 76:64-81.
- Walsberg, G. E., and B. O. Wolf. 1996. An appraisal of operative temperature mounts as tools for studies of ecological energetics. *Physiol. Zool.* 69:658-681.
- Weathers, W. W., W. A. Buttemer, A. M. Hayworth, and K. A. Nagy. 1984. An evaluation of time-budget estimates of daily energy expenditure in birds. *Auk* 101:459-472.
- Weathers, W. W., and K. A. Sullivan. 1993. Seasonal patterns of time and energy allocation by birds. *Physiol. Zool.* 66:511-536.
- Williams, J. B., and K. A. Nagy. 1984. Daily energy expenditure of Savannah Sparrows: comparison of time-energy budget and doubly-labeled water estimates. *Auk* 101:221-229.

CURRICULUM VITAE

Sheldon J. Cooper

PERSONAL

- Date of Birth: 5 October 1967
- Place of Birth: Hettinger, North Dakota
- Current Position: Visiting Instructor
 Department of Biology
 St. Lawrence University
 Canton, NY 13617
 (315) 229-5314
 E-mail: scoo@music.stlawu.edu

EDUCATION

- Ph.D. December 1997. Biology. Utah State University, Logan, Utah.
- M.A. August 1992. Biology. University of South Dakota, Vermillion.
- B.S. August 1990. Biology. Northern State University, Aberdeen, South Dakota.

RESEARCH EXPERIENCE

- Dec. 1997 - present Pew faculty-student research program: Seasonality of the daily mass cycle in temperate overwintering passerine birds
 Department of Biology, St. Lawrence University
- Sept. 1992 - Dec. 1996. Dissertation research: The role of cold acclimatization on the biogeography of the Mountain Chickadee (*Parus gambeli*) and the Juniper Titmouse (*Parus ridgwayi*).
 Department of Biology, Utah State University
 Advisor: James A. Gessaman
- September 1995. Research technician. Conducted a bomb calorimetry study of the energy content of winter kokanee salmon which are the primary prey item of overwintering Bald Eagles in Montana. Department of Biology, Montana State University.
 Supervisor: Marco Restani

- July 1993 - Sept. 1994. Research technician. Conducted a study of seasonal variation in metabolism and thermal conductance in the American marten (*Martes americana*). Utah Cooperative Fish and Wildlife Research Unit, Utah State University. Supervisors: John Bissonette and Bill Adair
- January 1991 - May 1992. Thesis research: Seasonal thermoregulation and sex determination of the Black-capped Chickadee (Passeriformes: *Parus atricapillus*). Department of Biology, University of South Dakota. Advisor: David L. Swanson

TEACHING EXPERIENCE

August 1997 - Present Visiting Instructor. Biology Department, St. Lawrence University.

Courses Taught: BIOL 326 Animal Physiology (Fall 1997)
 BIOL 347 Environmental Physiology (Fall 1997)
 (to be Taught): BIOL 218 Ornithology (Spring 1998)
 BIOL 247 Human Anatomy (Spring 1998)

Sept. 1992 - June 1997. Graduate Teaching Assistant. Department of Biology, Utah State University.

Courses Taught: BIOL 101 Biology and the Citizen
 BIOL 125 General Biology I
 BIOL 127 General Biology III
 PHYSL 103 Human Anatomy
 PHYSL 130 Human Physiology
 PHYSL 135 Brain and Behavior
 PHYSL 505 Animal Physiology
 ZOOL 461 Field Ornithology
 ZOOL 561 Avian Biology

January 1991 - May 1992. Graduate Teaching Assistant. Department of Biology, University of South Dakota.

Courses Taught: BIOL 103 General Biology II.
 BIOL 151 Introductory Biology I.
 BIOL 153 Introductory Biology II.

January 1991 - Dec. 1991. Biology Tutor for visually impaired students. South Dakota Services for the Visually Impaired, University of South Dakota.

Courses Taught: BIOL 151 Introductory Biology I.
 BIOL 153 Introductory Biology II.
 ZOOL 381 Animal Anatomy and Development.

SERVICE

Sept. 1997 - present. Undergraduate Honors Thesis Committee, (2 students), Department of Biology, St. Lawrence University.

Sept. 1996 - June 1997. Graduate Programs Committee, Department of Biology Utah State University. Graduate student representative.

AWARDS

November 1996. Student travel award from the Society for Integrative and Comparative Biology for the SICB 1996 Annual Meeting.

April 1996. Department of Biology, Graduate Teaching Assistant of the Year. Utah State University.

August 1995. Marcia Brady Tucker travel award for the 113th Stated Meeting of the American Ornithologists' Union.

April 1995. Datus M. Hammond Memorial Scholarship. Department of Biology, Utah State University.

April 1995. Department of Biology, Graduate Teaching Assistant of the Year. Utah State University.

April 1994. Department of Biology, Graduate Teaching Assistant of the Year. Utah State University.

GRANTS

November 1997. Pew Program in Undergraduate Science Education
 Title: Seasonality of the daily mass cycle in temperate overwintering passerine birds.

- November 1997. St. Lawrence University Faculty Research Grant.
 Title: Seasonality of the daily mass cycle in temperate overwintering passerine birds.
- January 1994. North American Bluebird Society, Student Grant.
 Title: Physiological, physical and behavioral adaptations to cold in the Mountain Chickadee and the Plain Titmouse.
- January 1994. Sigma Xi, Grants-in-Aid of Research.
 Title: Physiological and physical adjustments to cold in the Mountain Chickadee and Plain Titmouse.
- January 1992. Sigma Xi, Grants-in-Aid of Research.
 Title: Seasonal variation in cold-hardiness and maximal thermogenic capacity in the Black-capped Chickadee (*Parus atricapillus*)

HONOR SOCIETIES

- Sigma Xi. Associate Member, the Scientific Research Society, Utah State University Chapter.
- Phi Sigma. Biological Honor Society, Alpha Gamma Chapter, University of South Dakota.

PROFESSIONAL ORGANIZATIONS

American Association for the Advancement of Science
 American Ornithologists' Union
 Association of Field Ornithologists'
 British Ornithologists' Union
 Cooper Ornithological Society
 Society for Integrative and Comparative Biology
 South Dakota Ornithologists' Union
 Western Bird Banding Association
 Wilson Ornithological Society

PUBLICATIONS

- Cooper, S.J. 1996. Problems in using morphometrics to sex monomorphic birds: an example using Black-capped Chickadees. *N. Amer. Bird Bander* 21:45-48.
- Cooper, S.J., and D.L. Swanson. 1994. Seasonal acclimatization of thermoregulation in the Black-capped Chickadee. *Condor* 96:638-646.

MANUSCRIPTS IN REVIEW

- Wilson, G.R., S.J. Cooper, and J.A. Gessaman. The effects of temperature and rain on the metabolism of the American Kestrel (*Falco sparverius*). *Physiol. Zool.*
- Adair, W.A., S.J. Cooper, and J.A. Bissonette. Seasonal variation in metabolism and thermal conductance in American marten (*Martes americana*). *Can. J. Zool.*

ABSTRACTS

- Cooper, S.J. 1996. Hypothermia in seasonally acclimatized Mountain Chickadees and Plain Titmice. *American Zoologist* 36:66A.
- Cooper, S.J. 1992. Sex identification of Black-capped Chickadees: a comparison of methods. *Proc. S.D. Acad. Sci.* 71:179.
- Cooper, S.J., and D.L. Swanson. 1992. Seasonal variation in cold resistance and peak rates of cold-induced thermogenesis in the Black-capped Chickadee. *Proc. S.D. Acad. Sci.* 71:177.
- Cooper, S.J. 1991. Exploration and movement behavior in corn snakes (*Elaphe guttata*). *Proc. S.D. Acad. Sci.* 70:257.

PAPERS PRESENTED

1997. The role of daily energy expenditure on the biogeography of the Mountain Chickadee and the Plain Titmouse. 115th Stated Meeting of the American Ornithologists' Union. 13-16 August. Minneapolis, Minnesota.
1997. Thermal and energetic consequences of roost-site selection in seasonally acclimatized Mountain Chickadees and Plain Titmice. 115th Stated Meeting of the American Ornithologists' Union. 13-16 August. Minneapolis, Minnesota.
1996. Hypothermia in seasonally acclimatized Mountain Chickadees and Plain Titmice. Annual Meeting of the Society for Integrative and Comparative Biology. 26-30 December. Albuquerque, New Mexico.
1996. Seasonal variation in metabolism, evaporative water loss, and fat storage in the Mountain Chickadee and Plain Titmouse. 114th Stated Meeting of the American Ornithologists' Union. 13-17 August. Boise, Idaho.

1996. Seasonal variation in the metabolism and insulation of the American marten (*Martes americana*). 1996 Physiological Ecology Meetings. 7-9 June. Bishop, California.
1995. Cold tolerance and maximal thermogenic capacity in seasonally acclimatized Mountain Chickadees and Plain Titmice. 113th Stated Meeting of the American Ornithologists' Union. 15-19 August. Cincinnati, Ohio.
1993. Sex identification of Black-capped Chickadees from southeastern South Dakota. 63rd Annual Meeting of the Cooper Ornithological Society. 13-18 April. Sacramento, California.
1992. Seasonal variation in cold resistance and maximal thermogenic capacity of the Black-capped Chickadee. 110th Stated Meeting of the American Ornithologists' Union. 24-27 June. Ames, Iowa.
1992. Seasonal thermoregulation and sex determination of the Black-capped Chickadee. The University of South Dakota Graduate Seminar. 8 May. Vermillion, South Dakota.
1992. Seasonal variation in cold resistance and peak rates of cold-induced thermogenesis in the Black-capped Chickadee. 77th Meeting of the South Dakota Academy of Science. 10-11 April.
1992. Sex identification of Black-capped Chickadees: a comparison of methods. 77th Meeting of the South Dakota Academy of Science. 10-11 April.
1991. Exploration and movement behavior in corn snakes (*Elaphe guttata*). 76th Meeting of the South Dakota Academy of Science. 19-20 April.