

ACTA

UNIVERSITATIS OULUENSIS

Juli Broggi

PATTERNS OF VARIATION
IN ENERGY MANAGEMENT IN
WINTERING TITS (*PARIDAE*)

FACULTY OF SCIENCE,
DEPARTMENT OF BIOLOGY,
UNIVERSITY OF OULU

A

SCIENTIAE RERUM
NATURALIUM



ACTA UNIVERSITATIS OULUENSIS
A Scientiae Rerum Naturalium 467

JULI BROGGI

**PATTERNS OF VARIATION
IN ENERGY MANAGEMENT IN
WINTERING TITS (*PARIDAE*)**

Academic Dissertation to be presented with the assent of
the Faculty of Science, University of Oulu, for public
discussion in Kuusamonsali (Auditorium YB210),
Linnanmaa, on September 1st, 2006, at 12 noon

OULUN YLIOPISTO, OULU 2006

Copyright © 2006
Acta Univ. Oul. A 467, 2006

Supervised by
Professor Esa Hohtola
Professor Jan-Åke Nilsson
Professor Markku Orell

Reviewed by
Professor Francisco Bozinovic
Professor David Swanson

ISBN 951-42-8172-1 (Paperback)
ISBN 951-42-8173-X (PDF) <http://herkules.oulu.fi/isbn951428173X/>
ISSN 0355-3191 (Printed)
ISSN 1796-220X (Online) <http://herkules.oulu.fi/issn03553191/>

Cover design
Raimo Ahonen

OULU UNIVERSITY PRESS
OULU 2006

Broggi, Juli, Patterns of variation in energy management in wintering tits (*Paridae*)

Faculty of Science, Department of Biology, University of Oulu, P.O.Box 3000, FI-90014 University of Oulu, Finland

Acta Univ. Oul. A 467, 2006

Oulu, Finland

Abstract

Winter energy management in small passerines living year-round in boreal or alpine areas presumably results in strong selective pressure since they need to find food, at a time when natural resources diminish and become less available, and energy requirements increase dramatically.

In this thesis energy management during the non-breeding season was studied in three species of tits (*Parus* spp.) from three different populations: Coll de Pal (Spanish Pyrenees), Lund (Southern Sweden) and Oulu (Northern Finland).

Energy management strategies vary significantly between species and among populations and individuals of the same species. Such differences may depend on several environmental factors, food predictability and individual characteristics. Birds from the studied populations appear to react to energetic challenges on a short-term basis and in a highly flexible way.

The coal tit (*Parus ater*) in Coll de Pal and the willow tit (*Parus montanus*) in Oulu, both hoarding species, relied mostly on short-term management of energy for winter survival. Social and residence status appeared to be the most important factors in determining the level of energy reserves, underlining the importance of food predictability for energy management in wintering tits.

Further studies were carried out on two distinct populations of great tit (*Parus major*) exposed to different winter hardiness. Birds from both populations increased their resting metabolic rate (MR) with experimentally decreasing ambient temperatures. Birds from Oulu maintained higher expenditures than birds from Lund in all cases, but also experienced higher energetic cost of thermoregulation at the lowest temperatures. The differences probably did not arise from a differential insulation capacity between populations, despite the differences in plumage structure found, but from a differential metabolic acclimatization. Birds from Lund probably became hypothermic at the lowest temperatures, which may have exceeded the levels they were acclimatized for.

The observed differences in basal MR in laboratory conditions were consistent in wild birds throughout the non-breeding season. Birds from both populations experienced similar patterns of variation in basal MR, with expenditures increasing with mass but decreasing with day length, size and age.

Great tits modulate their energy expenditure in a flexible way as a means for surviving the non-breeding season. Further, despite such flexibility, populations appear to be locally adapted for such metabolic acclimatization. These results may have important implications on their life-history and distribution.

Winter acclimatization appears to be a complex set of entangled strategies that are based on a metabolic adjustment to cope with changing energy requirements. Other mechanisms that apparently play a secondary role, for example the long term management of reserves through fattening or hoarding, or conserving heat through hypothermia and by developing a better insulative plumage, are certainly important emergency strategies that in natural conditions may explain how some populations can endure winter conditions.

Keywords: avian energetics, ecological physiology, energy reserves, metabolic rate, winter acclimatization

While I'm standing here freezin'...

Jimi Hendrix

To my family

Acknowledgements

First of all I need to acknowledge the collaboration of several hundred bird individuals from different species and populations. They deserve all my admiration and gratitude. I tried to do my best and disturb them the least. One thing that filled me with joy was recapturing old individuals that had already spent the long cold nights inside the warm chambers in the lab, and managed to do so year after year (sometimes more than 10 times during four years). I want to think they were like happy costumers in a hotel. In any case they have taught me a great deal about how to withstand conditions. May the heat be with you.

Then, from going to my first lesson in evolution to finishing my thesis there have been many steps and many people involved two whom I am indebted. First, my school biology teacher Pere Cairó who introduced me to the concept of evolution and in some way everything started there. If there would be more teachers like him, I have the feeling that evolutionary ecology would be a much more popular field of study.

I learned how to ring with several skillful friends from the Institut Català d'Ornitologia. With them i did not only have a great time in the field but also started to get a glimpse of what it meant to work with birds.

Further, there have been a few “very important people” from whom I have learned a lot (and hope to keep on doing so) and I am much indebted to them.

From the initial steps in Barcelona: my friend Dr. Lluís Brotons, as he taught me the very first steps in the “science business”. I cannot think of any better mentor and colleague. And besides, by following his steps i ended up in Oulu! So, the extent to which he is responsible for this situation is hard to tell... but he has certainly played a significant role. Prof. Jacint Nadal provided all the support that was needed in these initial steps and since then he has always been encouraging and helpful. I could say he has been the person that arranged things and made things happen, always having confidence in me, or at least he made me feel that way. And last but not least Dr. Joan Carles Senar. Besides all that I have learned from him, he has always given me the right dose of confidence and also pressure. Now it is my turn to prove that the confidence was worth it.

Now my collection of supervisors: Markku Orell, thanks in first place for choosing me and giving me the chance to do this thesis and for the support during all the years in Oulu. Jan-Åke Nilsson, although being my long-distance supervisor has been in a way

the most involved from the generation of ideas to the production of manuscripts. It is hard to describe in few words how thankful am I, not only from the science side but in all aspects. Just hope I can visit Lund soon so we can finish some of the many pending projects or we can produce some new ones..... thanks Jocke!. To Esa Hohtola, again it is hard to express my gratitude. Esa has always impressed me ... he not only seems to know about any subject (from bird identification to electronics, red wine to immunology etc. etc.), but most important, his door was always open to me. Whenever I had any type of problem I could be sure that Esa would be there and help me. He is truly a dream-supervisor. Again, I hope we can keep on working together... there are many unfinished projects... and more to come!!. And last but not least, and I'd say the most important has been Kari Koivula. After my ERASMUS experience I thought I'd never see Oulu again. Thanks to Kari I came back. And I stayed.... He has been crucial, not only because of his teaching on how to do science, how to read and to be critical of everything, but he has also been my best guide to Finnish culture. He and his family made me feel at home. Besides, I also learned from him to "understand" certain things such as ice-fishing and hockey... Thank you for allowing me to invade your office every second minute. And remember!! I still think we should organize a golden-retirement in Las Canarias: Drinking Doradas in the shade and watching evolution play around.

These people have always managed to cool me down when i had problems... desperation eventually occurs... and then you need comments such as: If you need more papers in the C.V.? - Try the salami science... or, If you need to put together, for example a thesis, ...try tårta-på-tårta...Or if something is too long... remove the "basic brown sauce".

Thanks for everything. It has been a privilege to learn from all of you.

After all these years I've been collecting many office mates: Jukka Forsman, Folmer Bokma and now Katja Kangas. Although our time schedules haven't overlapped much, I think we managed pretty well. No? They also taught me a great deal about real fitness, and in a way they have kept me "grounded". It has been a pleasure.

Further, there have been several other important people for me department-, work-, coffee- and beer-wise: First of all the old school: Kimmo, Mikko, Seppo and later on Alex, David, Petri, Rob, Sa, Satu, Stefano, Tahe, Vitali ... What can i say... get ready to chachacha.....

During the last stages in the north, I was lucky enough to have met Prof. Claus Bech, and I want to thank him for his help, advice and company during my stage in Trondheim and Svalbard. Finally, I want to thank Juhani Itämies, Petri Kärkkäinen and the people from the Zoo. Their help has been of great value. Special mention for both "magic hands" Kenttis and Matti Rauman that produced the crazy inventions I happened to need during my studies. I also want to thank Esa Läärä for statistical advice. Espero no te sientas muy avergonzado de los resultados. Pero te lo agradezco de todos modos.

The Finish Academy and the Thule Institute of the University of Oulu provided me with financial support, and I'm thankful to them for that. Aaron Bergdahl kindly checked the language of the thesis.

Besides the scientific side of a thesis, someone has to survive the freezing conditions of the Finnish winter. Thomas Ulich has not only been a friend but also an example to follow on how to survive in Finland and at the lowest temperatures (although I never managed to withstand a full Northern light photographic session...maybe next time).

Acclimatization to Oulu's social and environmental conditions took some time (and I still have a ways to go). Heikki Jokela and the Never grow old crew have played a great role there. Another one who should feel in great part responsible of me surviving in there is Mario Iannazzo who (almost always) agreed to join me for the classic one-or-ten beers after work. In my opinion (and I'm aware not everybody may share it) most interesting things happen at night, at least during the Finnish winter!

Many people have been important to me during all this time. Most of them should be aware of their importance, and for the ones who aren't, I guess I'll have to try harder to let them know. Special mention to the Voodoo people that provided me with the proper place and spirit to finish this never ending process called a thesis.

Some of us choose to keep a distance and observe while others choose to fix what is not working. I want to dedicate this work to those brave who fight against natural selection and provide us with the chance to study it. Gràcies Marc, i a tots aquells qui m'han assistit aquests darrers mesos. Finally without my parents and family this would never been possible ... Gràcies per donar-me l'oportunitat. Us estimo.

Oulu, July 2006

Juli Broggi

List of original papers

This thesis is based on the following papers, which are referred to in the text by their Roman numerals:

- I Broggi J & Brotons L (2001) Coal Tit fat-storing patterns during the non-breeding season: the role of residence status. *J Avian Biol* 32: 333-337.
- II Broggi J, Koivula K, Lahti K & Orell M (2003) Seasonality in daily body mass variation in a hoarding boreal passerine. *Oecologia* 137: 627-633.
- III Broggi J, Orell M, Hohtola E & Nilsson J-Å. (2004) Metabolic response to temperature variation in Great tit: An interpopulation comparison. *J Anim Ecol* 73: 967-972.
- IV Broggi J, Gamero A, Hohtola E, Orell M. & Nilsson J-Å (2005) Interpopulation differences in feather structure. (manuscript)
- V Broggi J, Hohtola E, Koivula K, Orell M, Thomson RL & Nilsson, J-Å (2005) Sources of variation in winter basal metabolic rate in the great tit *Parus major*. (manuscript)
- VI Broggi J, Hohtola E, Orell M & Nilsson J-Å (2005) Local adaptation to winter conditions in a passerine spreading north: a common garden approach. *Evolution* 59: 1600-1603.

Contents

Abstract	
Dedication	
Acknowledgements	
List of original papers	
Contents	
1 Introduction	15
1.1 Energy acquisition and storage	15
1.1.1 Environmental factors	16
1.1.2 Food predictability	16
1.1.3 Starvation vs. predation trade-off	17
1.1.4 Food hoarding	18
1.2 Energy expenditure	19
1.2.1 Metabolic rate	19
1.2.2 Sources of variation in metabolic rate and physiological costs	20
1.3 Energy conservation	21
1.3.1 Facultative nocturnal hypothermia	21
1.3.2 Plumage	22
1.4 The aim of the study	22
2 Materials and methods	24
2.1 Study species	24
2.2 Study areas	25
2.3 Capturing and processing of birds	25
2.4 Measuring fat and body mass	26
2.5 Measuring Metabolic Rate	26
2.6 Measuring feather structure	27
2.7 Aviaries and the “common garden” experiment	27
3 Results	29
3.1 Management of internal energy reserves in hoarding species	29
3.2 Interpopulation differences in winter energy management	29
4 Discussion and concluding remarks	31
4.1 Long-term vs. short-term winter energy management	31
4.2 Environmental effects on winter energy management	32

4.3 Effects of food predictability on winter energy management	33
4.4 Effects of individual characteristics on winter energy management.....	35
4.5 Integrated approach to winter energy management	35
4.5.1 Integrated approach on an individual level.....	35
4.5.2 Differences between populations.....	36
4.5.3 Implications on individual life-history	38
5 Final remarks and questions for further studies.....	39
References	
Original papers	

1 Introduction

Homeotherms in winter face the double jeopardy of higher energetic demands (cold and long nights) and reduced food supply (non-renewable resources decrease in quantity and quality). These conditions are especially harsh for year-round resident passerine birds as compared to other homeotherms. First, many of these birds are small and thus lose heat at a relatively higher rate than larger species due to their high surface/volume ratio (Peters 1983). Second, flight requirements prevent them on one hand from storing large amounts of internal reserves, to the extent that internal energy stores can only last for a few days at the most. On the other hand, due to their small size they show a limited ability for seasonal changes in the amount of plumage insulation in order to meet aerodynamic requirements. Third, the activity of birds is restricted to above the snow layer, unlike small mammals which enjoy much milder conditions in the subniveal niche. Finally, due to their diurnal habits, and especially in populations living at high latitudes, the time available for feeding decreases as day length shortens. In this way, small passerines wintering in the north represent a classic study subject known as the “small-bird-in-winter dilemma”.

To survive this stressful period small birds undergo a process of winter acclimatization that facilitates maintenance of thermoregulatory homeostasis, which is mainly achieved through enhanced regulatory thermogenesis and increased accumulation of energy reserves to fuel it. Further, birds develop a complex set of behavioral and physiological strategies to manage energy acquisition and expenditure in order to cope with the situation.

So far, the study of this has been approached from three main perspectives that correspond largely to the type of measurements being used i.e. level of reserves, energy expenditure and energy loss.

1.1 Energy acquisition and storage

The study of body mass regulation in wintering passerines has been a popular research subject during the last decades for behavioral ecologists (King 1972, Brooks 1968, Evans 1969, Pinowski & Myrcha 1970, see Pravosudov & Grubb Jr. 1997, Blem 1990, Biebach 1996 for later reviews).

Day-feeding birds acquire food during the day and store it internally in order to fuel thermoregulatory and other metabolic needs. Fat constitutes the major source of metabolic fuel during winter fasts such as sudden harsh conditions and long cold nights (Blem 1990). From an ecological perspective, energy acquisition and storage has been studied in relation to a trade-off between risks of starvation and predation (Lima 1986, Houston *et al.* 1993). In order to minimize starvation risk birds should carry the maximum amount of fat that prevailing conditions allow. The fact that they rarely do so implies some costs in carrying fat reserves. Instead they seem to actively manage their reserve levels taking into account food predictability *i.e.* variance in supply, food availability *i.e.* average supply, energy requirements due to environmental conditions, predation risk and other factors (see Witter & Cuthill 1993, Pravosudov & Grubb Jr. 1997 for reviews).

1.1.1 Environmental factors

A number of environmental factors are involved in the regulation of winter acclimatization and thus in the management of reserves. Birds are able to respond to local conditions and adjust their reserves accordingly (Nolan & Jr. Ketterson 1983, Rogers *et al.* 1993). Photoperiod is a direct measure of the time available for feeding and consequently the night length, which is a forced fasting period for birds. Some studies have shown that changes in photoperiod are used as a proximate cue to manage energy reserves (King 1972, Hitchcock & Houston 1994, Meijer *et al.* 1994, Rogers *et al.* 1994, Pilastro *et al.* 1995, Rogers & Reed, 2003) but see (King & Mewaldt 1981, Gosler 1996). Further, ambient temperature, which is highly correlated to changes in day length, is a well-known proximate factor regulating body mass in small birds, and is apparently more important than photoperiod (King 1972, Dawson & Marsh 1986, Jenni & Jenni-Eiermann 1987, Rogers *et al.* 1994, Rogers 1995, Gosler 1996, Lilliendahl *et al.* 1996, Pravosudov & Grubb Jr. 1998a, Gosler 2002, Rogers & Reed 2003). Overall, birds tend to accumulate more reserves as day length shortens and temperatures drop, but despite the number of studies on this subject, it has proven difficult to partition the independent effects of seasonal changes in temperature, and other environmental variables *i.e.* snow fall, from photoperiod that are commonly associated with winter (see Biebach 1996, Pravosudov & Grubb Jr. 1997, Carey & Dawson 1999 for reviews).

1.1.2 Food predictability

Since food availability changes almost continuously in time and space, individuals have to track these changes in order to predict future resource availability and adjust their reserves accordingly (Carey & Dawson 1999). Food predictability can vary due to several factors which may interact with each other. First, food supply may be limited or changing with time. Second, food accessibility may also be restricted due to other factors than the supply itself such as environmental stochasticity. During winter at high altitudes or latitudes, sudden weather changes, snowfall and frost disturb and even prevent birds from

reaching their usual feeding substrates (Brotons 1997). In these situations, when food abundance and/or availability decreases, birds tend to accumulate larger internal reserves, if they have the opportunity (Rogers 1987, Brittingham & Temple 1988, Rogers & Smith 1993, Bednekoff & Krebs 1995, Hake 1995, Witter *et al.* 1995, Gosler 1996, Cuthill *et al.* 2000, Karpouzou *et al.* 2005, but see Koivula *et al.* 2002, Rogers & Heath-Coss 2003).

Further, in species that spend the non-breeding season in social groups as most tits (*Paridae*) do (Ekman 1989), food predictability may also be dependent on the relations of dominance within their group and with other groups (Lahti 1997, Krams 1998, Barluenga *et al.* 2001). In this case, by definition, dominant birds have priority of access to resources. The argument is that priority of access to food should increase food predictability and thus allow dominants to decrease their internal reserves (Verhulst & Hogstad 1996). However, the relationship between the social hierarchy and the management of reserves remains controversial; in some studies dominant birds carry smaller reserves than subdominants (Rogers 1987, Piper & Wiley 1990, Ekman & Lilliendahl 1993, Witter & Swaddle 1995, Gosler 1996, Hake 1996, Krams 1998, Pravosudov *et al.* 1999, Haftorn 2000, Pravosudov & Lucas 2000b), while in some others it is not so clear or even opposite (Koivula *et al.* 1995, Gosler & Carruthers 1999, Pravosudov & Lucas, 2000b, Koivula *et al.* 2002, Polo & Bautista 2002), see (Clark & Ekman 1995, Verhulst & Hogstad 1996, Lundborg & Brodin 2003) for discussion.

1.1.3 Starvation vs. predation trade-off

Predation risk, either through increased time exposed to predators or through impaired ability to escape them, is believed to influence the strategic regulation of body mass. The patterns of acquisition and maintenance of body reserves have been modeled according to a trade-off between the risk of starvation and predation (Lima 1986, McNamara & Houston 1987, McNamara & Houston 1990, Houston *et al.* 1993, Houston & McNamara 1993). The general assumption is that remaining lean entails lower predation risk, and some empirical data gives support to this view (Gosler *et al.* 1995, Lilliendahl 1997, Van der Veen & Sivars 2000, Rands & Cuthill 2001, Gentle & Gosler 2001), but see (Pravosudov & Grubb Jr. 1998c, Lilliendahl 1998, Carrascal & Polo 1999, Lilliendahl 2000). The reason behind such controversial results appears to be related to different experimental approaches, and the intrinsic difficulty in splitting the effects of feeding interruption from predator encounter on body mass (see Rands & Cuthill, 2001 for discussion).

Further, the supposed mass-dependent costs of predation risk through impaired take-off or flight maneuverability also remains a controversial issue (Metcalfe & Ure 1995, Kullberg 1998, Veasey *et al.* 1998, Lind *et al.* 1999, Van der Veen 1999b, Lind 2001, Veasey *et al.* 2001, Krams 2002, Burns & Ydenberg 2002, Kullberg *et al.* 2002a, Kullberg *et al.* 2002b, Kullberg *et al.* 2005). Furthermore, assuming that exposure to predators entails a higher risk of predation than the flight costs per se, yields different predictions than the “lean-is-safe” assumption (Brodin 2001). On the other hand, behavioral modulation of such strategic response depends on the rates of food acquisition and on the length of the daily activity period. Birds are able to increase their feeding rates

at the expense of vigilance tasks (Morrison *et al.* 1988), and expand their working days by starting their feeding bouts earlier or finishing them later, with the consequent increase in the risk of predation due to dim-light conditions (Lahti *et al.* 1997, Haftorn 1999, Krams, 2000).

So far, studies dealing with the effects of predation on energy management have focused on daytime and airborne predation. Only a few studies have considered other types of predation, e.g. night-time or mammalian predation risk, despite these being common risks during winter at high latitudes (Carrascal & Polo 1999, Bautista & Lane, 2000).

1.1.4 Food hoarding

Some species, including most tits except the blue *Parus caeruleus* and great tit *Parus major*, may hoard food as an external energy storage that ensures or at least enhances local food availability during future energy-demanding periods (Vander Wall 1990, Brodin & Ekman 1994). Among tits, food is normally stored as small scattered caches within the winter territory (Sherry 1989). Although hoarding is performed most actively while food supply is plentiful, i.e. during autumn, hoarding birds devote considerable time and energy to this activity (Sherry 1989). Food hoarding is supposed to increase local food predictability for the hoarder, and in that sense several studies have focused on the relationship between hoarding behavior and the management of internal energy reserves. Since time available for feeding or hoarding is limited, especially during the non-breeding season, it has been proposed that there should be a trade-off between feeding and hoarding in order to optimize reserves throughout the day (McNamara *et al.* 1990, Pravosudov & Lucas, 2001a, Pravosudov & Lucas 2001b) and winter (Grubb Jr. & Pravosudov 1994, Brodin & Clark 1997, Brodin 2000). But so far, empirical support remains, at best, weak (Hurly 1992, Lucas 1994, Lucas & Zielinski 1998, Pravosudov & Grubb Jr. 1998b, Karpouzou *et al.* 2005). Further, the effects of factors affecting food predictability, such as social dominance, predation risk or environmental conditions on hoarding and internal energy management have also been intensively studied (Lahti *et al.* 1998a, Pravosudov & Lucas 2000b, Brotons 2000a, Brodin *et al.* 2001, Pravosudov & Lucas 2001b, Brodin & Lundborg 2003). Nevertheless, despite the obvious fact that hoarding plays an important role in energy management, the precise nature of its relationship with internal reserve management remains obscure.

As a result of this combination of factors, birds not only show differences in instant level of reserves, but also different patterns of seasonal and daily accumulation of reserves. Such patterns have been intensively studied both theoretically (McNamara *et al.* 1994, Bednekoff & Houston 1994a, Bednekoff & Houston 1994b, Grubb Jr. & Pravosudov 1994, Houston *et al.* 1997) and empirically (Lehikoinen 1987, Rogers & Rogers 1990, Haftorn 1992, Polo & Carrascal 1997), focusing on the effects of dominance (Haftorn 1989, Pravosudov & Lucas 2000b, Polo & Bautista 2002), hoarding behavior (Brotons 2000a, Brodin 2000, Pravosudov & Lucas 2000b, Lilliendahl 2002), food availability (Rands & Cuthill 2001, Koivula *et al.* 2002, Polo & Bautista 2002), environmental conditions (Blem & Shelor 1986, Waite 1992, Meijer *et al.* 1994,

Lilliendahl *et al.* 1996) and predation risk (Lilliendahl 1998, Van der Veen 1999a, Van der Veen & Sivars 2000, Lilliendahl 2000, Rands & Cuthill 2001, Pravosudov & Lucas 2001b).

1.2 Energy expenditure

As winter progresses and the temperatures drop, birds need to compensate for their heat loss into the environment to maintain a constant body temperature. Most heat in birds is produced by shivering, primarily in the flight muscles (Hohtola & Stevens 1986). Besides voluntary thermogenesis, birds may generate heat as a by-product of other daily activities such as normal movement (McNamara *et al.* 2004), or digestion (Rashotte *et al.* 1999, Laurila *et al.* 2003), which may reduce daytime thermogenic requirements as compared to night-time.

1.2.1 Metabolic rate

Seasonal metabolic adjustments generally include increases in cold tolerance, thermogenic endurance and maximum thermogenic capacity or summit metabolism in winter-acclimatized birds relative to summer birds. In situations where an increased sustained work rate is needed, increased energy expenditure is, in most cases, accompanied by a concomitant increment in the basal metabolic rate (MR), *e.g.* cold endurance by shivering thermogenesis (Liknes *et al.* 2002, Swanson, in press), but see (Dawson *et al.* 1983), migratory disposition (Lindström 1997) and breeding (Nilsson 2002). To be able to process large amounts of food and produce more heat, birds need to enlarge their “physiological machinery” *i.e.* digestive and cardiovascular systems, which in turn raises their basal cost of maintenance (*i.e.* basal metabolic rate) (Alexander 1999, Dutenhoffer & Swanson 1996). Whether the increases in basal rates of metabolism are a contributing factor to these improvements, a byproduct of them or a separate response is still unclear. Some studies have, however, found a negative relationship between high rates of energy expenditure and basal MR. Such a reduction in basal MR has probably come at the expense of other functions that may reduce the overall metabolic cost of living (Bautista *et al.* 1998, Deerenberg *et al.* 1998, Nudds & Bryant 2001).

Basal MR has been widely used as a standard measurement of the cost of living and has acted as a baseline for multiple comparisons (Ricklefs *et al.* 1996, McNab 1997, Frappell & Butler 2004, White & Seymour 2004). Considerable information is available on basal rates of metabolism among species, that has led to a profusion of allometric equations linking basal MR to body mass and aspects of the species biology (see McNab 1988, Read 1988, Gavrilov 1999, Lovegrove 2000, Gillooly *et al.* 2001, Johnson *et al.* 2001, Mueller & Diamond 2001, Rezende *et al.* 2004, for examples).

Recent evidence suggests that intraspecific variation in basal MR has a strong genetic component (Wikelski *et al.* 2003, Ksiazek *et al.* 2004). Nevertheless, resting metabolic rate is also an extremely plastic character that not only varies among populations, but also at an individual level (Bech *et al.* 1999, Horak *et al.* 2002, Tieleman *et al.* 2003, Labocha

et al. 2004, Speakman *et al.* 2004, Vézina & Williams 2005, Rønning *et al.* 2005). On the other hand, other measurements of metabolism, such as maximum cold induced MR or daily energy expenditure, suffer from even higher rates of variation (Frappell & Butler 2004, White & Seymour 2004).

1.2.2 Sources of variation in metabolic rate and physiological costs

Despite the long tradition of the study of avian energetics, most studies from an evolutionary perspective have dealt with the allocation of energy between competing activities or life history episodes, but little effort has been dedicated to study the sources of variation in patterns of energy expenditure (see Ricklefs 1996, for review).

So far, most studies have focused on the seasonal changes in MR and especially in the role of winter temperature in regulating metabolism (Swanson & Olmstead 1999). In free-living, as well as in laboratory-acclimated small birds, mass-specific basal MR is normally higher in winter than in summer (see Swanson, in press for a review). Further, widespread bird populations wintering in temperate climates show a negative relation between basal MR and temperature (Dawson & O'Connor 1996, Swanson, in press). Other environmental or ecological aspects potentially explaining the variation in MR (e.g. predictability, diet quality, or predation) have rarely been studied, especially not in populations of wild animals (but see McNab 1988, Geluso & Hayes 1999, Mueller & Diamond 2001, Cruz-Neto & Bozinovic 2004, Laurila & Hohtola 2005).

Many species live, at least part of their lives, in social groups that are normally organized in dominance hierarchies (Matthysen 1990). A large amount of studies have explored the underlying mechanisms determining such dominance hierarchies (Koivula 1994). Behavioral dominance is understood as priority of access to resources, and in order for the system to be stable, hierarchies should be based on condition-dependent characters that would prevent potential cheaters from achieving high status. Basal MR has been claimed to be one of these characters underlying dominance status, dominant birds having higher rates of expenditure than subdominants (Røskaft *et al.* 1986, Hogstad 1987, Bryant & Newton 1994, Metcalfe *et al.* 1995). On the other hand some other studies have found no relationship between dominance and basal MR or even negative relationships (Hammond *et al.* 2000, Senar *et al.* 2000, Vézina & Thomas, 2000). Overall, it is still not clear whether dominance determines the individuals' expenditure or if the individuals' expenditure determines their dominance status.

On a short-term basis, birds may reduce certain energetically expensive activities (Piersma *et al.* 2004) as a way to manage reserves instead of investing time and energy in searching for food, and incurring higher predation risk (Bednekoff & Krebs 1995, Dall & Witter 1998). Facultative nocturnal hypothermia is another way to lower the energetic costs of maintenance by reducing expenditure on thermogenesis by decreasing the thermal gradient between the body-core and the environment (see 1.3.1).

Finally, there may be costs involved with increasing the rates of energy expenditure. Besides the potential physical damage, because of accidents or predation due to increased activity, there may also be physiological costs of high MR's. Metabolic processes that continuously consume oxygen generate reactive oxidative substances which damage

DNA, proteins and lipids (Von Schantz *et al.* 1999). Accumulating such oxidative stress is thought to be one of the key mechanisms in causing cellular senescence and death (Beckman & Ames 1998). Thus, it may be possible that increased rates of energy expenditure increase oxidative stress resulting in an accelerated senescence, but see (Speakman *et al.* 2002, Speakman 2005).

1.3 Energy conservation

Birds operate most effectively at relatively high constant body temperatures (diurnal body temperature = 42 °C) that are normally above the surrounding thermal environment. They lose heat mostly by conduction, convection and also radiation to the surroundings as long as they maintain surface temperatures higher than ambient temperatures (Walsberg 1988, Wolf & Walsberg 2000). Heat loss can be reduced actively by behavioral and physiological adjustments such as the choice of appropriate microhabitats (Carrascal *et al.* 2001, Wolf & Walsberg 1996), special roosting places (Walsberg 1986, Geiser & Ruf 1995, Cooper 1999, Ferguson *et al.* 2002), the optimization of body posture (Lustick *et al.* 1980; Lustick *et al.* 1978), the habit of huddling together with other individuals for roosting (Buttemer *et al.* 1987, Calf *et al.*, 2002), vasoconstriction of the peripheral tissues to decrease the thermal gradient (McNab 2002), or the decrease in whole body temperature, *i.e.* facultative nocturnal hypothermia, to minimize the temperature gradient between the core body and ambient temperatures while resting (Reinertsen 1983, McKechnie & Lovegrove 2002).

1.3.1 *Facultative nocturnal hypothermia*

Facultative nocturnal hypothermia (FNH) is considered to be a strategic decrease in body temperature (down to 30°-38°C) during resting hours (see Reinertsen 1996 for review). Further, it has been suggested to be more usual than previously thought (McKechnie & Lovegrove 2002), but the difficulties involved in the measurement of core body temperature have prevented empiricists to obtain the necessary information to fully understand its importance (Hill *et al.* 1980, Reinertsen 1982). The few empirical studies have shown that FNH is a plastic strategy (Reinertsen 1984) mostly triggered by food shortage and low temperatures (Haftorn 1972, Chaplin 1976, Hohtola *et al.* 1991, Waite 1991, Downs & Brown 2002, Lovegrove & Smith 2003, Dolby *et al.* 2004, Cooper & Gessaman 2005, Laurila *et al.* 2005). Nevertheless, these studies suggest that birds are reluctant to engage in FNH, suggesting that there are some costs involved. Presumably, such costs are related to an increased predation risk, since birds are less responsive while in hypothermia and thus less likely to escape predators (Reinertsen 1996). In fact, birds under increased predation risk are more reluctant to become hypothermic (Bautista & Lane 2000, Laurila & Hohtola 2005). However, physiological costs associated with the deprivation of restorative sleep or increased metabolism while arousing from hypothermia need to be considered (Hohtola *et al.* 1994). For example, in small species such as the goldcrest, *Regulus regulus*, the energy savings from being hypothermic at

very low ambient temperatures may not compensate for the costs of rewarming (Reinertsen *et al.* 1988).

Still, for species over a certain body mass and at certain ranges of ambient temperatures, energy savings would be important (Reinertsen 1983), and thus the effect of such behavior on energy management should be considerable (Grubb Jr. & Pravosudov 1994, Pravosudov & Lucas 2000a, Welton *et al.* 2002). Overall, the ecological and physiological circumstances that influence the use of FNH in small birds remain largely unknown.

1.3.2 Plumage

Plumage is the main insulation layer in birds preventing body heat from escaping to the environment. Although plumage provides limited insulation, presumably reflecting a compromise between thermal and flight requirements, it serves as a critical buffer against low ambient temperatures with a thermal gradient sometimes over 60°C across 3 cm. Plumage structure and quantity are crucial in regulating such heat transfer processes (Wolf & Walsberg 2000). Plumage characteristics are defined and fixed at the time of moulting and after that, modulation of the insulation capacity of the plumage can only be achieved by means of ptiloerection i.e. feather fluffing (Hill *et al.* 1980, Hohtola *et al.* 1980, Saarela *et al.* 1984). Although ptiloerection can greatly decrease heat loss, it is fully utilized only during sleep (Hohtola *et al.* 1980). Populations of the same species, differing in winter conditions, have been found to possess plumages varying in thermal conductance (Swanson 1993). Likewise, the mass of contour feathers has been found to vary between populations from different origins, and also within populations as part of a seasonal acclimatization process (Dawson & Carey 1976, Dawson *et al.* 1983, Middleton 1986, Swanson 1991, Saarela *et al.* 1995, Cooper 2002). Furthermore, it has been suggested that reductions in thermal conductance could not depend only on an increased amount of feathers but probably also on improvements in feather quality (Dawson & Carey 1976, Middleton 1986, Root *et al.* 1991, Novoa *et al.* 1994). However, studies linking the effects of plumage structure and composition on winter energetics of small passerines are still missing.

1.4 The aim of the study

Winter survival is a crucial aspect in the life history of small resident passerines living in high altitudes or at high latitudes (Lahti *et al.* 1998b, Lampila *et al.* 2006). Since winter mortality is high, strategies to endure it are probably under strong selective pressure. However, characters presumably being optimized by selective forces may in some cases change due to other correlated characters under stronger selection. Furthermore, optimal strategies are probably dependent on the state and characteristics of the individual, resulting in between-individual variation in the choice of strategies (Speakman *et al.* 2004).

Studying how organisms use energy provides little insight into why they use energy the way they do. Birds from different populations face different conditions, and in order to survive, need to change their strategies accordingly. So far, most studies have been concerned with within-population variation in these traits, but to study how species spread and adapt to new or changing environmental conditions it is important to make interpopulational comparisons. In that way the study of differences in energy management between populations can yield an extremely valuable insight into trait variation in different natural conditions (King & Mewaldt 1981, Nolan Jr. & Ketterson 1983, Rogers *et al.* 1991, Rogers *et al.* 1993, Wikelski *et al.* 2003).

Different approaches were combined in order to enlarge the empirical knowledge on how some of these traits vary under natural conditions within and between populations. By doing so, winter energy management can be understood on a broader scale, not only from an ecobehavioral perspective but also in relation to the life history and evolution of such strategies.

Specifically, the daily and seasonal patterns of accumulation of reserves in different social classes of two hoarding species were investigated (I, II). Then the differences in energy expenditure in great tits from two populations differing in latitude exposed to different night temperatures (III), and the sources of variation in the cost of living i.e. basal MR, among individuals from these two populations during winter and across years (V) were studied. In addition the feather structure of the individuals from these two populations (IV) was further studied. Finally, the mechanisms underlying the inter-population differences found previously were investigated (III) by performing a “common garden” experiment to test whether these differences were genetically based (VI).

2 Materials and methods

2.1 Study species

All three species studied are small passerine birds belonging to the *Parus* genus. They are all forest dwelling species that differ slightly in morphology, feeding habits and distribution. The populations under study are year-round residents and show different degrees of territoriality. During most of the year they are insectivorous and switch to a seed-based diet during the winter months. Coal and willow tits also store food within their winter territories to buffer future episodes of food scarcity (Ekman 1989, Harrap & Quinn 1996). Because of their sedentary nature, and propensity to use nestboxes to nest and roost as well as human provided feeders, they are an ideal bird genus for experimental studies.

The coal tit (*Parus ater*) is a small forest passerine (9-10g) typically inhabiting coniferous forests. It is widely distributed throughout Europe and in large areas of central and north Asia. Although it is a sedentary species in large areas of its distribution, it also sometimes makes irruptive movements. Winter social organization can be characterized by one of two states: territorial or floater. Territorial individuals constitute a portion of the population that remains sedentary in breeding territories throughout their lives in socially stable groups. Floaters range over wide areas in big flocks of loose composition (Matthysen 1990, Brotons 2000b). Resident individuals are dominant within their territory, where they claim priority of access to resources over any floaters visiting (Brotons, 2000b).

The willow tit (*Parus montanus*) is a small (10-12g) species, widely distributed throughout the Palearctic region, inhabiting mostly boreal and arctic coniferous and taiga forests. The winter social organization can be considered as stable territorial, as adults remain sedentary in their breeding territory throughout their lives, while the proportion of floater individuals is relatively small as compared with other species (Lahti 1998). Such stable flocks, as in the coal tit, comprise the breeding adults and normally a couple of juvenile individuals that are dominant over any intruders (Matthysen 1990).

The great tit is relatively big (18-20g) and the most widely distributed member of the genus, ranging throughout the Palearctic from Portugal to Singapore and from Morocco to northern Norway. It is one of the few non-hoarding species in the genus and during the winter months they show a loose social organization. In western Europe they are closely

associated with man from whom they obtain winter food, that probably allows the species to persist in areas otherwise unsuitable (Jansson *et al.* 1981, Orell 1989). The great tit is one of the most intensively studied species of bird.

2.2 Study areas

Coll de Pal: The study area consists of a 150 ha plot located in the eastern Pyrenees (north-eastern Iberian Peninsula) (42°30'N 1°89'E) at an elevation between 1800 and 2100 m. Mountain pine (*Pinus uncinata*) dominates the study area with scots pine (*Pinus sylvestris*) predominant on southern slopes and at lower elevations. Snow covers the ground from December to April, and during this period average temperatures regularly fall below 0°C.

Oulu: The study area lies in Oulu, northern Finland (65°N 25°30'E). The area is a mosaic of mixed forests of different ages, dominated by scots pine, spruce (*Picea abies*) and birch (*Betula sp.*). During six winter months, ambient mean temperatures are below 0°C and regularly fall below -20°C. On average, permanent snow cover remains for five months. Great tits in northern Finland breed in mixed deciduous-coniferous forest, and winter close to human settlements. During the non-breeding season they feed on human-provided food that they are probably highly dependent upon for their winter survival (Orell 1989).

Lund: The study area lies near Lund, southern Sweden (55° 40'N, 13°25'E). The area consists of mixed deciduous and pine forests fragmented by agricultural landscapes. Average winter temperatures range from -3°C to 7°C and snow cover rarely remains for more than a couple of weeks. Great tits are year round residents in the study area and do not rely on feeders for winter survival.

2.3 Capturing and processing of birds

All birds were trapped during the non-breeding season, except for the ones used in paper VI (see 2.7). Birds in Lund were trapped soon after dusk, while roosting in nestboxes. Birds in Oulu were captured by means of funnel traps that were permanently installed in the study area and worked as feeders except when trapping (Senar *et al.* 1997). To control for possible bias when comparing birds from the two populations due to the trapping method, a sample of birds were trapped at permanent feeders in Lund, which did not differ from the ones captured while roosting (III).

Birds in Coll de Pal were attracted with tape lures and then mist-netted.

The sex and age of the birds was determined using standard methods (Jenni & Winkel 1994) and the corresponding discriminant functions with birds of known sex were used in the willow and coal tits (Koivula & Orell 1988, Brotons & Broggi, 2003) (I).

2.4 Measuring fat and body mass

Subcutaneous fat was estimated according to an index with three classes (Class 1, from no visible fat to a wide wedge of fat, covering less than half of the furcular (intraclavicular) depression and with small patchy traces or stripes of fat not wider than 1 mm in the abdominal area; Class 2, from a wide wedge to the complete covering of the furcular depression, its shape strongly concave, the abdomen presenting bands of fat, and the area between intestinal loops completely filled; Class 3, from a completely covered furcular depression and a small pad in the abdomen, with still two or three visible intestinal loops, to the connection of both areas and the complete covering of flight muscles (Rogers 1991, Kaiser 1993) (I).

Willow tits in Oulu were weighed without being captured and body masses were measured by visual readings from an electronic balance Sartorius 1002 MP9, (Goettingen, Germany) with an accuracy of 0.1g. The balance was used as a feeding tray where a small piece of solid porcine fat was placed over the weighing plate.

Birds were previously color-marked and trained to respond to a specific signal so that whenever birds heard it and were motivated to feed, they came to the observer in all parts of their territory (for a detailed description of the training procedure see Koivula *et al.* 1995) (II).

In all other studies, body mass of captured birds was measured by means of electric balances or Pesola (Baar, Switzerland) spring-scales (to the closest 0.05g) (I,III,V,VI).

2.5 Measuring Metabolic Rate

Resting MR was measured in open-circuit respirometers as the average minimal oxygen consumption under post absorptive digestive conditions during the night on resting, non-growing, non-reproductive animals. Basal MR was considered to be the resting MR at thermoneutrality (25°C) and measured in ml of oxygen per minute (McNab 1997). The energetic cost of thermoregulation (ECT) was measured as the difference between resting MR at a temperature below thermoneutrality and basal MR and represents the additional MR necessary for thermoregulation (III).

The respirometer in Lund consisted of a four-channel set with a flow of 200 ml/min, and is described in (Lindström *et al.* 1999, Nilsson & Råberg 2001) (III,V,VI). The Oulu respirometer consisted of a two-channel set, and one oxygen analyzer Servomex 1440 (U.K.) that received air samples of 600 ml/min through a valve system. Dried outdoor air was pumped to both metabolic chambers through mass-flow controllers Bronkhorst Hi-Tec F201C (Netherlands) and then dried again before analysis. The valve system switched between channels and outdoor air in periods of 30 min. Readings were recorded every minute, and later on minimum night averages were extracted over three-hour periods between 23:00 and 04:00 h for every bird (III).

From 2002 onwards, the respirometer in Oulu was rebuilt into a four channel set up following the same principles as before. The valve system was changed accordingly switching in periods of 12 min between channels and outdoor air. Further, flow was reduced from 600ml/min to 300ml/min and the oxygen analyzer and flow controllers

were changed to S-3A Ametek (USA) and FMA-A2407, Omega Engineering, Inc. (USA) respectively. Appropriate calibrations were performed and readings from 2002 onwards were comparable to previous ones (V,VI).

The closest outdoor-air reading was used as a reference in order to control for any possible analyzer drift. In Lund, CO₂ was measured, whereas in Oulu it was removed from inlet and outlet air, as CO₂ was not measured. Appropriate equations for each of these conditions were used according to (Hill 1972).

Appropriate calibrations were performed in order to make sure that measurements were comparable between respirometers. In order to calibrate both respirometer set-ups, 100 ml/min of N₂, measured by exactly the same mass-flow controller Bronkhorst Hi-Tec F201C (Netherlands), was injected to both systems between the respective mass-flow controller and the oxygen analyzer of each respirometer. The calculated consumption of oxygen differed by 2.18 %, Lund readings being higher than in Oulu. Such a difference was minimal as compared to the observed difference, and in any case opposite to the resulting trends in all papers (III,V) thus making our results conservative. All procedures were conducted in agreement with the local ethical committees.

2.6 Measuring feather structure

A few feathers from the side of the breast of great tits (between the shoulder and the black breast stripe) were plucked from each individual (IV). From each feather, the division between the plumulaceous and non-plumulaceous sections of the feather was determined and both types of barbs counted (2X); the total length of the feather not including the calamus and the length of the plumulaceous barb zone were measured at (0.6X). The amount of barbules on one barb of each different section (plumulaceous and non-plumulaceous) was counted in a 30 mm section of the barb, starting 9 mm from the rachis (7X). All the feather measurements were done by means of a stereoscopic microscope with an ocular grid following (Middleton 1986). Further, we repeated measurements on different feathers to test for within individual repeatability.

2.7 Aviaries and the “common garden” experiment

The outdoor aviaries consisted of 12,8 m² surface and 2,2 m high cages made of metallic mesh. Several nestboxes placed inside were available for roosting, and food during winter months consisted of a mixture of peanuts, sunflower seeds and animal fat provided *ad libitum* both in Lund and Oulu. Freshly cut spruce, pine and birch branches were provided regularly and placed inside each aviary. Snow accumulated on the floor assured water availability during winter, while fresh water was supplied daily during the rest of the season (III,VI).

For the “common garden” experiment (VI) we collected eggs from Oulu and Lund. The eggs from Lund were brought to Oulu, so that environmental conditions during growth would be equal for eggs from both origins (see Soler *et al.* 2003, Wikelski *et al.*

2003, Aday *et al.* 2003, de Neve *et al.* 2004, Kawecki & Ebert 2004 for similar approaches).

Great tit eggs from Lund were removed from different nests (two eggs per nest) before the clutch was complete and stored at +4°C and then brought to Oulu by plane. Another 30 eggs were gathered from nests in the study area in Oulu (65°N, 25°30'E) and stored under same conditions. All eggs were then distributed to foster females, replacing their original clutches, two days after the start of incubation. Thus, foster females incubated homogeneous clutches either from Oulu or Lund. Alive larvae of the fly *Calliphora sp.* and mealworms *Tenebrio molitor* were supplied to the parents beside the nests, so they got used to this food.

Just before fledging, nestboxes with the chicks were moved inside aviaries together with one of the parents. Parents continued to feed the chicks during the first weeks after fledging inside the aviaries, and after a few weeks chicks were able to feed themselves. Fly larvae and mealworms were provided *ad libitum* as well as fresh water with dissolved commercial vitamin-complex for the whole experiment. Ant pupae *Formica rufa s.l.* and moth caterpillars *Orthosia gothica*, *O. incerta* and *Cerastis rubricosa* were collected and grown during the summer months and provided once a week. In late summer a food mixture (tuna fish, baked cereals, beans and eggs, carrots and apples) was included in the diet, together with sunflower seeds, peanuts, and pork fat.

3 Results

3.1 Management of internal energy reserves in hoarding species

Daily reserve acquisition patterns were studied in two species of hoarding tits from two different locations, but with similar climate. Special emphasis was put on the study of the effects of social dominance and residence status on short- and long-term internal reserve acquisition.

In paper I we found coal tits in Coll de Pal to modulate their level of fat reserves according to the time of the day, residence status and ambient temperature. All residence classes increased fat levels throughout the day and with decreasing temperatures. No seasonal differences were detected. Transients showed a higher level of reserves over juvenile residents and adult residents, which were the leanest throughout the day.

In paper II we found willow tits in Oulu to increase their morning mass according to their sex and age, and also their wing length and snow depth. Dominance rank, which is largely determined by sex and age, was the most important predictor of both morning mass variation and daily mass increase, with most dominant classes showing higher body masses overall. Only adult males, i.e. most dominant, increased their morning body mass with winter progression. Further, both juvenile and adult females, the most subordinate classes, were affected by interannual variations, in addition to snow depth and wing length.

3.2 Interpopulation differences in winter energy management

The metabolic response to experimentally varying temperatures, and to natural conditions throughout the non-breeding season, in two populations of great tit i.e. Oulu (northern Finland) and Lund (southern Sweden) were studied. The possible mechanisms underlying the differences observed were further studied.

In paper III we found that great tits from the two studied populations increased their resting MR with decreasing experimental temperatures. Birds from Oulu maintained higher levels of expenditure at all treatments but also experienced higher costs of thermoregulation, i.e. resting MR- basal MR, at the lowest temperature (-10 °C).

In paper IV we found great tits from both populations studied (III) to differ in plumage structure. Feathers from Oulu birds were denser, shorter and had a lower proportion of plumulaceous barbs than their counterparts in Lund.

In paper V we found Oulu birds maintained a higher basal MR than in Lund, despite responding to sources of variation in a similar way. Basal MR from Oulu great tits was negatively affected by temperature and date but otherwise showed the same pattern as in Lund, with increasing basal MR with mass and decreasing with day length, size and age. Further, Lund birds showed an interannual variation in basal MR.

In paper VI we found birds that originated from Oulu and Lund, but hatched and grew under the same conditions in Oulu, to still differ in their basal MR in the following non-breeding season. Basal MR was higher in birds originating from Lund compared to the ones from Oulu, contrary to previous results (III,V). The results suggest that birds from both of these populations are locally adapted to react differently to different environmental conditions. Additionally, we found an age decline in basal MR, in agreement with the “rate of living theory” on aging and senescence

4 Discussion and concluding remarks

4.1 Long-term vs. short-term winter energy management.

Long-term energy management can be considered to be a strategic response to anticipate the worsening of conditions that come with winter, and to prevent situations when immediate responses would be impossible, either due to a lack of resources or the time available to develop a response. For small birds living at high altitudes or latitudes, long-term energy management has been claimed to be essential for winter survival (Grubb Jr. & Pravosudov 1994, Pravosudov & Grubb Jr. 1997).

As a general response, birds increased the level of their reserves with winter progression (II, V), although this should not be considered a long-term strategy but rather a seasonal change in daily energy management, since storing internally for future use over long periods of time is not an option for small passerines (see 1.1). “True winter fattening”, understood as an increase in morning and daily mass increase (Lehikoinen 1987) was not detected in the studied willow tit population. The result that only the most dominant birds had a slight increase in morning mass with season implies that energy is managed on a daily basis rather than seasonally (II). Further, in the coal tit population studied, fat reserves did not change from autumn to winter when time of day, residence status and environmental temperature was controlled for (I), indicating that reserves are managed on a short-term basis. Since body mass was not analyzed in this study, but only the level of fat reserves, it is difficult to compare results from the two studies (see 4.5.1). Beside the reasons discussed earlier (see introduction in paper II), the fact that both tit species hoard suggests that, in contrast to small granivorous birds, external food hoards may decrease the need for winter fattening (see 4.3).

On the other hand, although we did not specifically test for the seasonality in body mass variation (V), great tits most probably increased the level of reserves, together with basal MR as shown by a positive and strong partial correlation, between both variables (V). Several lines of evidence have shown that the great tit currently engages in winter fattening (Halttunen *et al.* 1974, Gosler 1996, Gosler & Carruthers 1999, Gosler 2002). Nevertheless, the fact that body mass varies seasonally together with basal MR (V) could be because they are part of the same response, namely the need for increased thermogenesis and consequently bigger physiological machinery that requires more energy resources as conditions deteriorate (Dawson & Marsh 1988). Thus, rather than a

strategic increase in energy reserves to cope with unpredictable food resources, winter fattening could be understood as part of a wider energetic strategy where thermogenic capacity and endurance is increased (Swanson, in press), and so are the energy reserves to fuel such changes (Pravosudov & Grubb Jr. 1997).

As energy expenditure can be modulated relatively fast (III), and large changes involving adjustments in basal MR can be achieved as quickly as in a few days (Swanson & Olmstead 1999), long-term management of energy expenditure would seem unnecessary. However, we do not know whether such differences in speed during adjustments in basal MR imply different costs. Nevertheless, birds change their basal MR strategically, when responding to long-term environmental cues such as changes in photoperiod as well as more immediate clues such as previous days' temperatures (see 4.2) (V).

Since plumage in tits is only moulted once a year, before the non-breeding season (Jenni & Winkel 1994), long-term modulation of energy conservation is thus fixed by the plumage characteristics. Further, short-term regulation of heat loss is limited, as plumage ptiloerection is usually at its maximum insulating capacity when birds start producing heat for thermoregulation (Hohtola *et al.* 1980). Thus, modulation can only occur behaviorally through the choice of an appropriate microhabitat or by means of reduced body temperature i.e. FNH.

In paper (III) we obtained indirect evidence of the possible use of facultative nocturnal hypothermia in great tits. Similarly, in paper (II), willow tits appeared to maintain a steady morning body mass throughout the season despite changing environmental conditions, probably due to saving energy through FNH.

However, in both cases birds appeared reluctant to use FNH and probably became hypothermic when other mechanisms were not sufficient for coping with the situation. This suggests, in line with previous studies, that there may be costs associated with using such a strategy, see 1.3.1 (Grubb Jr. & Pravosudov 1994, Reinertsen 1996, McKechnie & Lovegrove, 2002). Altogether it appears that more empirical evidence is needed, both from laboratory and field studies, to fully understand the role played by FNH in overall energy management in wintering small passerines (McKechnie & Lovegrove 2002).

Nevertheless, regulation of energy management through changes in the conservation of heat seems to either be regulated on a long-term basis, as fixed by the plumage characteristics, or as a short-term emergency solution like FNH, when other mechanisms fail to fulfill energetic needs.

The development of highly plastic strategies in both acquisition and storage of energy (Koivula *et al.*, 2002) allows these species to respond to energetic challenges by regulating acquisition and expenditure in daily cycles rather than seasonally. Overall, birds seem to be highly adapted to endure winter conditions by managing energy reserves mostly on a short-term rather than on a long-term basis (I, II, III) (see 4.3).

4.2 Environmental effects on winter energy management.

Environmental conditions dictate the energetic needs for survival, e.g. the lower the temperature, the more energy is required to stay homeothermic. Likewise, short days and

thick snow cover reduce food predictability for small passerines like tits (see 4.3). Birds from all three species studied appeared to respond to environmental variables (I, II, III, V), although the different species and populations differed in their sensitiveness to these variables. The two hoarding species studied appeared to be affected mostly by immediate environmental cues e.g. minimum temperature or snow cover (I, II). Whereas in the great tit, long-term variables e.g. day length and calendar date had a stronger effect than short-term environmental conditions (V). Although it is possible that such a relationship is seen partly because the measured parameters, basal MR vs. internal reserves, differ in their sensitivity to environmental variables.

Some studies have shown that environmental cues can be used to anticipate future changes in weather conditions and develop the appropriate strategies (Carey & Dawson 1999). But the same environmental conditions could also constrain the development of such strategies, when certain limits are exceeded or changes are too sudden (Gosler 2002). Great tits from the two populations reacted similarly to environmental variables (V), the only difference being with temperature (see 4.5.2). Lund birds appeared to be constrained by minimum temperature, although this result should be considered with caution, as the sample distribution may be biased by two few measurements at low temperatures (V).

Besides the immediate or long-term effects that environmental conditions may have on adult birds, birds may use environmental cues during early development in order to develop certain capabilities that will allow them to later react to environmental conditions in an optimal way (VI). In that sense, phenotypic plasticity allows individuals to develop different capabilities depending on growth conditions, and also due to processes of acclimatization later in adulthood that ultimately allow individuals to persist in a wide range of environmental conditions (Via *et al.* 1995). Nevertheless, the nature of such clues triggering the expression of different phenotypes, such as characters involved in winter acclimatization, remain largely unknown.

4.3 Effects of food predictability on winter energy management

The general pattern that emerges (I,II,V) is that the level of internal reserves, and probably expenditure, vary a lot depending on food predictability. Since we only have indirect evidence of the effects of food predictability on the management of energy reserves, and proper tests or experimental data are missing, I can only address some general conclusions.

In willow tits, dominant birds that probably enjoy higher food predictability than subordinates (see 4.4) kept overall higher levels of reserves and daily mass gain than subordinates. On the other hand, coal tits in Coll de Pal show the opposite trend as resident individuals maintain lower reserve levels than transients, which would presumably face lower food predictability due to inferior dominance status and knowledge of the environment. These results suggest that natural food conditions were plentiful, and allowed most subordinate individuals to increase their reserve levels over most dominant individuals, which in turn could avoid carrying extra weight.

Verhulst & Hogstad (1996) suggested a model to explain the effects of social dominance and predation risk on the level of internal reserves in order to explain some previous results (Ekman & Lilliendahl 1993, Koivula *et al.* 1995). According to their model, differences between populations could be explained by the relative importance of predation risk and food predictability. In our case, food predictability rather than predation could account for the different patterns observed between species, as it appears that forests in Coll de Pal may provide much higher food predictability than in Oulu. Again, comparisons between these studies may have to be treated cautiously, since reserve levels were estimated in different ways (see 4.5.1).

Hoarding behavior is supposed to enhance local food predictability, either on a long-term basis, buffering seasonal changes in food availability, or on a short-term basis by allowing birds to minimize predation risk by postponing reserve acquisition to the later part of the day. The relative importance of hoarding on winter energy management strategies is again hard to evaluate since direct information on hoarding and retrieval effort and reward is missing. In fact, hoarding does not appear to have any important effect on a long-term scale in neither coal nor willow tits, as there is little seasonal or daily variation in the levels of reserves between resident or social classes (I,II). On the other hand, as we compare hoarding with non-hoarding species, we found that the great tit most likely changes its body mass with season (see 4.1), suggesting that although hoarding may not be as important to show differences between social or resident classes within species, it may be important enough to buffer dramatic changes in food predictability that presumably happen with season.

There is an important between-year variation in the internal reserve levels (I,II), which are even more accentuated between social classes, the lowest ranks suffering from the strongest fluctuations (II). The reasons behind such fluctuations are probably related to environmental conditions such as between-year climatic differences that may cause fluctuations in food supply and/or predation risk (see 4.3). Many small mammal species, e.g. small rodents and shrews, show cyclic fluctuations in numbers that are paralleled by their common predators. Such fluctuations are known to induce changes in predation risk for small birds, which is known as the “alternative prey hypothesis” (Dunn 1977, Norrdahl & Korpimäki 2000) since they are used as alternative prey during low population phases of the main prey species. Interestingly, subordinate willow tits, which are more exposed to predation than dominants (Koivula *et al.* 1994) and that presumably face lower food predictability, were most sensitive to interannual variations (II). Likewise, the great tits from the Lund population experienced stronger interannual fluctuations in the levels of basal MR than great tits from Oulu (V). Probably because Lund birds rely on natural food sources, unlike birds in Oulu, which spend the winter near human settlements with a much more stable food resource (Orell 1989, Gosler 1993).

4.4 Effects of individual characteristics on winter energy management

In social species such as tits, individuals organize themselves in a social hierarchy which is often stable and is based on dominance relationships. As a common rule, resident individuals within a territory dominate transients, males dominate females, older over young and bigger and in best condition over smaller and weaker individuals. Such dominance relationships imply, by definition, priority of access to resources such as food, and thus result in higher food predictability for higher ranked individuals (Koivula 1994). Social status can therefore be crucial for individual energy management (see 1.1.2).

In both willow and coal tits, where non-breeding social hierarchies are known to be stable, dominance appeared to significantly influence the management of reserves (I,II). Morphology played a marginal role and was only important within social classes of the willow tit or within populations of the great tit (I,II,V). Such differences are probably due to an underlying dominance hierarchy. Likewise, gender was marginally significant, and the differences observed between sexes are most probably due to differences in size rather than gender *per se* (II). Further, age and sex, which are intimately linked to dominance rank, also played a role in explaining variation in internal reserves (see 4.3) (I, II).

Interestingly, great tits decreased their basal MR with age (V). Two non-exclusive explanations could account for this finding. First, individuals could decrease their basal MR as they age. Second, birds with lower basal MR could live longer and thus become more common at older ages. Both possibilities are in line with the “rate of living theory”. The theory suggests that aging and lifespan are regulated by energy metabolism and predicts that basal MR should decrease with age (Hulbert & Else 2000, Barja 2002). In any case, the decreasing basal MR with age suggests an interesting scenario, since the energetic strategy of an individual may determine, at least partly, its lifespan and thus life-history (see 4.5.3).

4.5 Integrated approach to winter energy management

4.5.1 *Integrated approach on an individual level*

The individual’s energy budget may be characterized in terms of energy inputs and outputs, the difference between these being the total energy content in the body (Ricklefs 2005). To understand energetics in an evolutionary context, it is important to consider how changes in energy management affect an individual’s fitness. Therefore, research on the evolutionary significance of energy management requires an integrated approach. It is thus necessary to consider all aspects involved in the acquisition-storage, expenditure and conservation of energy in order to understand the ecological and evolutionary significance of such strategies.

For example, dynamic optimization models provide an important tool for behavioral ecologists and rely on the assumption that the characters being managed e.g. internal

reserves, are under natural selection and thus should be optimized (Houston *et al.* 1988). The “small-bird-in-winter dilemma” has been a popular topic for dynamic optimization modeling (see Pravosudov & Grubb Jr. 1997 for a review). Nevertheless, such models have often failed to find empirical support for e.g. the “lean-is-safe” (see 1.1.3), or for the hoard vs. fat (see 1.1.4) models. One possibility for such mismatch between theoretical predictions and empirical data is that models are being built assuming that single characters, for example body mass, are uniquely optimized. In reality, other correlated characters may also play a role in the system and not necessarily in the same direction as the focal character.

For example, although it is well-known that metabolic rate and body mass are strongly and positively correlated, most studies on body mass have not considered the possibility that patterns of variation in body mass might be partly due to the strategic regulation of metabolic rate. A small bird facing a predation-starvation risk dilemma would get leaner (and MR would decrease) under good food conditions, if body mass was the only character to be optimized. In that way, the bird would optimize maneuverability to escape and time exposed to predators. On the other hand, if MR was to be optimized, the bird should increase the MR (and body mass would increase) in order to be more reactive to external stimuli and have a higher potential for energy expenditure. We certainly need to integrate most important aspects of energy management in order to understand how birds cope with each particular situation.

Another factor that should be accounted for is the precision of measurements and repeatability of the variables being measured. For example, despite the common knowledge of the high variability in basal MR (V), little effort has been dedicated to explore the sources of this variability and use standardized and corrected data to make different studies comparable. Further, problems in comparing studies may arise when fat reserves and body mass are used as estimates of internal energy reserves. In the first case precision is often reduced because estimates of fat are difficult to standardize due to certain subjectivity in the scales used (Rogers 1991). In the second case, the problems arise because the increases in fat reserves imply increases in body mass but the opposite is not necessarily true. As the increase in body mass may not only reflect increases in energy reserves (mostly fat) but also changes in other tissues like muscle or changes in organ sizes like the digestive tract (Rogers 2003). This highlights the importance of considering individual body composition when inferring MR from body mass or vice versa. Fat reserves have a relatively low mass specific metabolic rate compared to other tissues (Blem 1990). Thus, individuals with the same body mass, but different body composition, may have very different rates of metabolism (Piersma *et al.* 1996).

Thus, to gain a complete picture of how energy is managed, the level of reserves, body temperature and energy expenditure should be measured or estimated at the same time.

4.5.2 Differences between populations

Populations of the same species that are distributed over wide geographical ranges and which are exposed to different conditions may develop different strategies that allow them to survive at different locations. Such differences may depend on local adaptations

but are normally reversible plastic modulations of the phenotype known as acclimatization (Ricklefs & Wikelski 2002). However, the reaction norm of this plasticity may also be locally adapted (VI).

The differences between the two populations of great tit in the length and the structure of the contour feathers (IV) do not seem to explain the observed contrast in the ECT (III). Plumage quality would require a deeper analysis, including not only plumage structure but also overall feather density and core body temperature measurements at varying temperatures. These, together with the overall energy expenditure, would allow a proper determination of the plumage insulation characteristics. Instead, the differences in ECT between populations were probably due to a lowered body temperature in Lund birds when exposed experimentally to -10 °C, since the increase in MR over basal MR is low as compared with other studies (see paper III for discussion).

Nevertheless, both populations not only face contrasting winter energy requirements, but also may experience a different trade-off between breeding and moulting, which could explain the differences found in their plumage structure (VI).

One interesting issue that remains poorly explored is the relationship between social dominance on one side and energy reserves and metabolism on the other. The level of energy reserves, and thus the relative differences in food predictability and predation risk, are known to vary between social classes depending on the population studied (see 4.4 for discussion). Furthermore, MR is known to play a role (see 1.2.2) in determining the dominance hierarchies established in a social group. Thus, it would be very interesting to explore such a scenario by comparing the MR and body mass relationships between social classes from populations known to differ in their food predictability and /or predation risk (see 1.1.2). Considering the positive and linear relationship between body reserves and basal metabolism, I would predict differing relationships between rank and MR or between body mass and MR between the studied populations (see 4.5.1).

Great tits appeared to be locally adapted to winter conditions, in a situation where previous studies from the breeding season suggested that gene flow from southern populations prevented local adaptations to arise in the north (Rytkönen & Orell 2001). Our findings suggest that characters involved in winter acclimatization may be selected for whereas others such as the clutch size may not be due to the overriding effect of the gene-flow (VI). Such a scenario has been termed adaptation-with-gene-flow (Smith *et al.* 1997, Blondel *et al.* 1999) and provides an interesting opportunity to study how microevolutionary processes are shaping populations at the limits of their distributions (Hoffmann & Blows 1994).

Further, from a biogeographical perspective, the study of different populations can provide important insights on what determines the distributions of populations and how populations may react to changes in climate or respond to the colonization of new habitats.

The distribution of species is ultimately determined by individuals' ability to reproduce in an area, and specifically whether reproductive output compensates for mortality in a population. Therefore, the physiological link between the abiotic factors and mortality at the edge of these distributions is crucial to understanding how distributions may change. Further, from knowledge on these abiotic factors, one could predict physiological limits for the distributions that may not necessarily match the observed ones (Kanda & Fulle 2005). The study of differences in energy management

between populations at the limits of their distributions can provide important information on how these limits are shaped. The great tit is an especially interesting study object since it is rapidly expanding north (Koskimies 1989). Further, the fact that human provided-food may be pushing the demographic distribution limit closer to the physiological limit provides a unique opportunity to study how both distribution limits are shaped.

4.5.3 Implications on individual life-history

Winter survival is known to be a crucial aspect shaping life histories of homeotherms remaining sedentary in temperate and boreal regions throughout the year. Nevertheless, studies on avian ecological energetics have traditionally considered the breeding period as the main energetic bottle-neck on the individual's life history. Despite the knowledge that winter survival is a key factor in several boreal passerines species (Lahti 1997, Orell *et al.* 1999), little effort has been put into considering winter energy management in the context of the individual's life history.

In the studied great tit populations, it seems that the characters involved in winter acclimatization have probably been under stronger selective pressure than other characters directly related to fitness like clutch size (VI). This underlines the idea that winter survival is a key episode shaping the life history of boreal tits.

Moreover, it is interesting to consider the implications that a given energetic strategy an individual has adopted to withstand the winter may have on the individual's life history. Further, since winter conditions vary across the latitudinal distribution of the species, life history strategies may differ between populations depending on the distance to the edge of the distribution.

On one hand there may be physiological costs that may impose trade-offs between life-history episodes i.e. winter vs. breeding energy management. Considering the fact that energy-demanding periods have long-term physiological costs for the individual in the form of oxidative stress (Wiersma *et al.* 2004), individuals that keep high levels of expenditure throughout the winter may thus accumulate higher levels of oxidative stress than others with a more restricted budget. In line with this, as changes in basal MR do occur with aging (V), individuals maintaining different levels of energy expenditure are expected to have different optimal life histories.

On the other hand, the existing trade-off between breeding and moulting leads to the expectation that these traits are traded differently (IV).

Comparisons on how energy is managed during the winter and how characters such as plumage quality change between populations exposed to different time and energy constraints may shed light on the evolution of life-histories, especially as a result of changes in climate or colonization of new areas.

5 Final remarks and questions for further studies

In this thesis I have shown that energy management strategies vary a lot between species, and among populations and individuals of the same species. Such differences may depend on several environmental factors, food predictability and individual characteristics. Birds from the studied populations appear to react on a short-term basis and in a highly flexible way to energetic challenges. In the great tit, despite such flexibility, populations appear to be locally adapted to endure winter conditions. Such results may have important implications on their life-history and distribution range.

Several questions arise that, in my opinion, deserve further studies. In general, I think that some effort should be dedicated to the acquisition of empirical data from more species and populations, especially at their distribution limits, and approaching the subject by integrating all possible aspects involved in energy management (see 4.5.1).

Further, most studies on energy management have focused on the daily regulation either of energy expenditure, acquisition or accumulation, whereas little effort has been placed on the study of night-time regulation of energy conservation. In that sense, it would be very interesting to acquire more information on the factors determining variation in night-time heat loss in small passerines.

Finally, this thesis has highlighted the variability in energy expenditure found in the great tit. However evidence from other studies suggests that such results may be widespread among other sedentary passerines species living in temperate and boreal areas. In order to understand how these different energetic strategies affect individual life-histories and determine species distributions, it is crucial to relate such strategies to an individual's fitness to be able to uncover the microevolutionary patterns that have shaped them.

References

- Aday DD, Wahl DH & Philipp DP (2003) Assessing population-specific and environmental influences on bluegill life histories: a common garden approach. *Ecology* 84: 3370-3375.
- Alexander RM (1999) Energy for animal life. Oxford University Press, Oxford.
- Barja G (2002) Rate of generation of oxidative stress-related damage and animal longevity. *Free Radical BiolMed* 33: 1167-1172.
- Barluenga M, Barbosa A & Moreno E (2001) Differences in daily mass gain between subordinate species are explained by differences in ecological plasticity. *Ecoscience* 8: 437-440.
- Bautista LM & Lane SJ (2000) Coal tits increase evening body mass in response to tawny owl calls. *Acta Ethol* 2: 105-110.
- Bautista LM, Tinbergen JM, Wiersma P & Kacelnik A (1998) Optimal foraging and beyond: How starlings cope with changes in food availability. *Am Nat* 152: 543-561.
- Bech C, Langseth I & Gabrielsen GW (1999) Repeatability of basal metabolism in breeding female kittiwakes *Rissa tridactyla*. *Proc R Soc Lond B* 266: 2161-2167.
- Beckman KB & Ames BN (1998) The free radical theory of aging matures. *Physiol Rev* 78: 547-581.
- Bednekoff PA & Houston AI (1994a) Avian daily foraging patterns: effects of digestive constraints and variability. *Evol Ecol* 8: 36-52.
- Bednekoff PA & Houston AI (1994b) Optimizing fat reserves over the entire winter: a dynamic model. *Oikos* 71: 408-415.
- Bednekoff PA & Krebs JR (1995) Great tit fat reserves: effects of changing and unpredictable feeding day length. *Funct Ecol* 9: 457-462.
- Biebach H (1996) Energetics of winter and migratory fattening. In: Carey C (ed) *Avian energetics and nutritional ecology*. Chapman & Hall, New York 280-323.
- Blem CR (1990) Avian energy storage. *Current Ornithol* 7: 59-113.
- Blem CR & Shelor MH (1986) Multiple regression analyses of midwinter fattening of the white-throated sparrow. *Can J Zool* 64: 2405-2411.
- Blondel J, Dias PC, Perret P, Maistre M & Lambrechts MM (1999) Selection-Based Biodiversity at a Small Spatial Scale in a Low-Dispersing Insular Bird. *Science* 285: 1399-1402.
- Brittingham MC & Temple SA (1988) Impacts of supplemental feeding on survival rates of black-capped chickadees. *Ecology* 69: 581-589.
- Brodin A (2000) Why do hoarding birds gain fat in winter in the wrong way? Suggestions from a dynamic model. *Behav Ecol* 11: 27-39.
- Brodin A (2001) Mass-dependent predation and metabolic expenditure in wintering birds: is there a trade-off between different forms of predation? *Anim Behav* 62: 993-999.
- Brodin A & Clark CW (1997) Long-term hoarding in the Paridae: A dynamic model. *Behav Ecol* 8: 178-185.
- Brodin A & Ekman J (1994) Benefits of food hoarding. *Nature* 372: 510.
- Brodin A & Lundborg K (2003) Rank-dependent hoarding effort in willow tits (*Parus montanus*): a test of theoretical predictions. *Behav Ecol Sociobiol* 54: 587-592.

- Brodin A, Lundborg K & Clark CW (2001) The effect of dominance on food hoarding: a game theoretical model. *Am Nat* 157: 66-75.
- Brooks WS (1968) Comparative adaptations of the alaskan redpolls to the arctic environment. *Wilson Bull* 80: 253-280.
- Brotons L (1997) Changes in foraging behaviour of the coal tit *Parus ater* due to snow cover. *Ardea* 85: 249-257.
- Brotons L (2000a) Individual food-hoarding decisions in a nonterritorial coal tit population: the role of social context. *Anim Behav* 60: 395-402.
- Brotons L (2000b) Winter spacing and non-breeding social system of the coal tit (*Parus ater*) in a subalpine forest. *Ibis* 142: 657-667.
- Brotons L & Broggi J (2003) Influence of morphology on winter residence and recruitment in juvenile coal tits (*Parus ater*) after the post-fledging period. *Ecoscience* 10: 273-282.
- Bryant DM & Newton AV (1994) Metabolic costs of dominance in dippers, *Cinclus cinclus*. *Anim Behav* 48: 447-455.
- Burns JG & Ydenberg RC (2002) The effects of wing loading and gender on the escape flights of least sandpipers (*Calidris minutilla*) and western sandpipers (*Calidris mauri*). *Behav Ecol Sociobiol* 52: 128-136.
- Buttemer WA, Astheimer LB, Weathers WW & Hayworth AM (1987) Energy savings attending winter-nest use by verdins (*Auriparus flaviceps*). *Auk* 104: 531-535.
- Calf K, Adams N & Slotow R (2002) Dominance and huddling behaviour in Bronze Mannikin *Lonchura cucullata* flocks. *Ibis* 144: 488-493.
- Carey C & Dawson WR (1999) A search for environmental cues used by birds in survival of cold winters. *Current ornithology* 15: 1-31.
- Carrascal LM, Diaz JA, Huertas DL & Mozetich I (2001) Behavioral thermoregulation by treecreepers: trade-off between saving energy and reducing crypsis. *Ecology* 82: 1642-1654.
- Carrascal LM & Polo V (1999) Coal tits, *Parus ater*, lose weight in response to chases by predators. *Anim Behav* 58: 281-285.
- Chaplin SB (1976) The physiology of hypothermia in the Black-capped chickadee, *Parus atricapillus*. *J Comp Physiol* 112: 335-344.
- Clark CW & Ekman J (1995) Dominant and subordinate fattening strategies: a dynamic game. *Oikos* 72: 205-212.
- Cooper SJ (1999) The thermal and energetic significance of cavity roosting in mountain chickadees and juniper titmice. *Condor* 101: 863-866.
- Cooper SJ (2002) Seasonal Metabolic Acclimatization in Mountain Chickadees and Juniper Titmice. *Physiol Biochem Zool* 75: 386-395.
- Cooper SJ & Gessaman JA (2005) Nocturnal hypothermia in seasonally acclimatized mountain chickadees and juniper titmice. *Condor* 107: 151-155.
- Cruz-Neto AP & Bozinovic F (2004) The Relationship between Diet Quality and Basal Metabolic Rate in Endotherms: Insights from Intraspecific Analysis. *Physiol Biochem Zool* 77: 877-889.
- Cuthill IC, Maddocks SA, Weall CV & Jones EKM (2000) Body mass regulation in response to changes in feeding predictability and overnight energy expenditure. *Behav Ecol* 11: 189-195.
- Dall SRX & Witter MS (1998) Feeding interruptions, diurnal mass changes and daily routines of behaviour in the zebra finch. *Anim Behav* 55: 715-725.
- Dawson WR & Carey C (1976) Seasonal acclimatization to temperature in cardueline finches. I. Insulative and metabolic adjustments. *J Comp Physiol* 112: 317-333.
- Dawson WR & Marsh RL (1986) Winter fattening in the american goldfinch and the possible role of temperature in its regulation. *Physiol Zool* 59: 357-368.
- Dawson WR & Marsh RL (1988) Metabolic acclimatization to cold and season in birds. In: Bech C & Reinertsen RE (eds) *Physiology of Cold adaptations in birds*. Plenum Press, New York 83-94.
- Dawson WR, Marsh RL, Buttemer WA & Carey C (1983) Seasonal and geographic variation of cold resistance in house finches *Carpodacus mexicanus*. *Physiol Zool* 56: 353-369.
- Dawson WR & O'Connor TP (1996) Energetic features of avian thermoregulatory responses. In: Carey C (ed) *Avian energetics and nutritional ecology*. Chapman & Hall, New York 85-123.

- de Neve L, Soler JJ, Pérez-Contreras T & Soler M (2004) Genetic, environmental and maternal effects on magpie nestling-fitness traits under different nutritional conditions: a new experimental approach. *Evol Ecol Res* 6: 415-431.
- Deerenberg C, Overkamp GJF, Visser GH & Daan S (1998) Compensation in resting metabolism for experimentally increased activity. *J Comp Physiol B* 198: 507-512.
- Dolby AS, Temple JG, Williams LE, Dilger EK, Stechler KM & Davis VS (2004) Facultative rest-phase hypothermia in free-ranging white-throated sparrows. *Condor* 106: 386-390.
- Downs CT & Brown M (2002) Nocturnal heterothermy and torpor in the Malachite Sunbird (*Nectarinia famosa*). *Auk* 119: 251-260.
- Dunn E (1977) Predation by weasels (*Mustela nivalis*) on breeding tits (*Parus* spp.) in relation to the density of tits and rodents. *J Anim Ecol* 46: 633-652.
- Dutenhoffer MS & Swanson DL (1996) Relationship of basal to summit metabolic rate in passerine birds and the aerobic capacity model for the evolution of endothermy. *Physiol Zool* 69: 1232-1254.
- Ekman J (1989) Ecology of non-breeding social systems of *Parus*. *Wilson Bull* 101: 263-288.
- Ekman J & Lilliendahl K (1993) Using priority to food access: fattening strategies in dominance-structured willow tit (*Parus montanus*) flocks. *Behav Ecol* 4: 232-238.
- Evans PR (1969) Winter fat deposition and overnight survival of yellow buntings (*Emberiza citrinella* L.). *J Anim Ecol* 38: 415-423.
- Ferguson JWH, Nijland MJM & Bennett NC (2002) Simple roost nests confer large energetic savings for sparrow-weavers. *J Comp Physiol B* 172: 137-143.
- Frappell PB & Butler PJ (2004) Minimal metabolic rate, what it is, its usefulness, and its relationship to the evolution of endothermy: A brief synopsis. *Physiol Biochem Zool* 77: 865-868.
- Gavrilov VM (1999) Comparative energetics of passerine and non-passerine birds: Differences in maximal, potential productive and normal levels of existence metabolism and their ecological implication. In: Adams NJ & Slotow RH (eds) *Proceedings of the 22nd International Ornithological Congress Birdlife South Africa*, Durban 338-369.
- Geiser F & Ruf T (1995) Hibernation versus daily torpor in mammals and birds: Physiological variables and classification of torpor patterns. *Physiol Zool* 68: 935-966.
- Geluso K & Hayes JP (1999) Effects of Dietary Quality on Basal Metabolic Rate and Internal Morphology of European Starlings (*Sturnus vulgaris*). *Physiol Biochem Zool* 72: 189-197.
- Gentle LK & Gosler AG (2001) Fat reserves and perceived predation risk in the great tit, *Parus major*. *Proc R Soc Lond B* 268: 487-491.
- Gillooly JF, Brown JH, West GB, Savage VM & Charnov EL (2001) Effects of size and temperature on metabolic rate. *Science* 293: 2248-2251.
- Gosler AG (1993) *The Great Tit*. Paul Hamlyn Ltd, London.
- Gosler AG (1996) Environmental and social determinants of winter fat storage in the great tit *Parus major*. *J Anim Ecol* 65: 1-17.
- Gosler AG (2002) Strategy and constraint in the winter fattening response to temperature in the great tit *Parus major*. *J Anim Ecol* 71: 771-779.
- Gosler AG & Carruthers T (1999) Body reserves and social dominance in the Great tit *Parus major* in relation to winter weather in southwest Ireland. *J Avian Biol* 30: 447-459.
- Gosler AG, Greenwood JJD & Perrins C (1995) Predation risk and the cost of being fat. *Nature* 377: 621-623.
- Grubb Jr. TC & Pravosudov VV (1994) Toward a general theory of energy management in wintering birds. *J Avian Biol* 25: 255-260.
- Haftorn S (1972) Hypothermia of tits in the arctic winter. *Ornis Scand* 3: 153-166.
- Haftorn S (1989) Seasonal and diurnal body weight variation in titmice, based on analyses of individual birds. *Wilson Bull* 101: 217-235.
- Haftorn S (1992) The diurnal body weight cycle in titmice *Parus* spp. *Ornis Scand* 23: 435-443.
- Haftorn S (1999) Dominance and daily activity during the winter in Willow tits *Parus montanus*, Marsh tits *P. palustris* and Great tits *P. major*. *Ornis Norvegica* 22: 43-52.
- Haftorn S (2000) Rank-dependent winter fattening in the Willow Tit *Parus montanus*. *Ornis Fenn* 77: 49-56.

- Hake M (1995) Adaptive control of starvation risk in greenfinches (*Carduelis chloris*). PhD Thesis, University of Gothenburg.
- Hake M (1996) Fattening strategies in dominance-structured greenfinch (*Carduelis chloris*) flocks in winter. *Behav Ecol Sociobiol* 39: 71-76.
- Halttunen E, Helle P & Kauppinen V (1974) On the winter body weight of the great tit in central Finland. *Lintumies* 2: 33-39.
- Hammond KA, Chappell MA, Cardullo RA, Lin R & Johnsen TS (2000) The mechanistic basis of aerobic performance variation in red junglefowl. *J Exp Biol* 203: 2053-2064.
- Harrap S & Quinn D (1996) Tits, nuthatches & treecreepers. Christopher Helm, London.
- Hill RW (1972) Determination of oxygen consumption by use of a paramagnetic oxygen analyzer. *J Appl Physiol* 33: 261-263.
- Hill RW, Beaver DL & Veghte JH (1980) Body surface temperatures and thermoregulation in the black-capped chickadee (*Parus atricapillus*). *Physiol Zool* 53: 305-321.
- Hitchcock CL & Houston AI (1994) The value of a hoard: not just energy. *Behav Ecol* 5: 202-205.
- Hoffmann AA & Blows MW (1994) Species borders: ecological and evolutionary perspectives. *Trends Ecol Evol* 9: 223-227.
- Hogstad O (1987) It is expensive to be dominant. *Auk* 104: 333-336.
- Hohtola E, Hissa R, Pyörnilä A, Rintamäki H & Saarela S (1991) Nocturnal hypothermia in fasting Japanese quail: the effect of ambient temperature. *Physiol Behav* 49: 563-567.
- Hohtola E, Pyörnilä A & Rintamäki H (1994) Fasting endurance and cold resistance without hypothermia in a small predatory bird: the metabolic strategy of Teggmalm's owl, *Aegolius funereus*. *J Comp Physiol B* 164: 430-437.
- Hohtola E, Rintamäki H & Hissa R (1980) Shivering and piloerection as complementary cold defense responses in the pigeon during sleep and wakefulness. *J Comp Physiol* 136: 77-81.
- Hohtola E & Stevens ED (1986) The relationship of muscle electrical activity, tremor and heat production to shivering thermogenesis in Japanese Quail. *J Exp Biol* 125: 119-135.
- Horak P, Saks L, Ots I & Kollist H (2002) Repeatability of condition indices in captive greenfinches (*Carduelis chloris*). *Can J Zool* 80: 636-643.
- Houston AI, Clark C, McNamara JM & Mangel M (1988) Dynamic models in behavioural and evolutionary ecology. *Nature* 332: 29-34.
- Houston AI & McNamara JM (1993) A theoretical investigation of the fat reserves and mortality levels of small birds in winter. *Ornis Scand* 24: 205-219.
- Houston AI, McNamara JM & Hutchinson JMC (1993) General results concerning the trade-off between gaining energy and avoiding predation. *Phil Trans R Soc Lond B* 341: 375-397.
- Houston AI, Welton NJ & McNamara JM (1997) Acquisition and maintenance costs in the long-term regulation of avian fat reserves. *Oikos* 78: 331-340.
- Hulbert AJ & Else PL (2000) Mechanisms underlying the cost of living in animals. *Annu Rev Physiol* 62: 207-235.
- Hurly TA (1992) Energetic reserves of Marsh tit (*Parus palustris*): food and fat storage in response to variable food supply. *Behav Ecol* 3: 181-188.
- Jansson C, Ekman J & Von Brömssen A (1981) Winter mortality and food supply in tits *Parus* spp. *Oikos* 37: 313-322.
- Jenni L & Jenni-Eiermann S (1987) Body weight and energy reserves of bramblings in winter. *Ardea* 75: 271-284.
- Jenni L & Winkel R (1994) Moulting and aging of European passerines. Academic Press, London.
- Johnson MS, Thomson SC & Speakman JR (2001) Limits to sustained energy intake: II. Interrelationships between resting metabolic rate, life-history traits and morphology in *Mus musculus*. *J Exp Biol* 204: 1937-1946.
- Kaiser A (1993) A new multi-category classification of subcutaneous fat deposits of songbirds. *J Field Ornithol* 64: 246-255.
- Kanda LL & Fulle TK (2005) Demographic responses of Virginia opossums to limitation at their northern boundary. *Can J Zool* 82: 1126-1134.
- Karpouzou H, Hernandez AM, MacDougall-Shackleton EA & MacDougall-Shackleton SA (2005) Effects of day-length and food availability on food caching, mass and fat reserves in black-capped chickadees (*Poecile atricapillus*). *Physiol Behav* 84: 465-469.

- Kawecki TJ & Ebert D (2004) Conceptual issues in local adaptation. *Ecol Letters* 7: 1225-1241.
- King JR (1972) Adaptive periodic fat storage by birds. *Proc XV Internat Ornithol Congress*, 200-217.
- King JR & Mewaldt LR (1981) Variation of body weight in gambel's white-crowned sparrows in winter and spring: latitudinal and photoperiodic correlates. *Auk* 98: 752-764.
- Koivula K (1994) Social dominance in willow tit (*Parus montanus*) flocks. PhD Thesis, University of Oulu.
- Koivula K, Lahti K, Rytönen S & Orell M (1994) Do subordinates expose themselves to predation? Field experiments on feeding site selection by Willow tits. *J Avian Biol* 25: 178-183
- Koivula K Orell M, 1988. Social rank and winter survival in the Willow tit *Parus montanus*. *Ornis Fenn* 65: 114-120.
- Koivula K, Orell M & Lahti K (2002) Plastic daily fattening routines in willow tits. *J Anim Ecol* 71: 816-823.
- Koivula K, Orell M, Rytönen S & Lahti K (1995) Fatness, sex and dominance: seasonal and daily mass changes in wintering Willow tits. *J Avian Biol* 26: 209-216.
- Koskimies P (1989) Distribution and numbers of Finnish breeding birds. In: Anonymous (ed) Suomen Lintuatlas. Finnish Ornithological Society (SLY), Lintutieto Oy, Helsinki.
- Krams I (1998) Rank-dependent fattening strategies of Willow tit *Parus montanus* and Crested tit *Parus cristatus* mixed flock members. *Ornis Fenn* 75: 19-26.
- Krams I (2000) Length of feeding day and body weight of great tits in a single- and a two-predator environment. *Behav Ecol Sociobiol* 48: 147-153.
- Krams I (2002) Mass-dependent take-off ability in wintering great tits (*Parus major*): comparison of top-ranked adult males and subordinate juvenile females. *Behav Ecol Sociobiol* 51: 345-349.
- Ksiazek A, Konarzewski M & Lapo IB (2004) Anatomic and energetic correlates of divergent selection for BMR in laboratory mice. *Physiol Biochem Zool* 77: 890-899.
- Kullberg C (1998) Behaviour under predation risk in birds. PhD Thesis, University of Stockholm.
- Kullberg C, Houston DC & Metcalfe NB (2002a) Impaired flight ability - a cost of reproduction in female blue tits. *Behav Ecol* 13: 575-579.
- Kullberg C, Jakobsson S, Kaby U & Lind J (2005) Impaired flight ability prior to egg-laying: a cost of being a capital breeder. *Funct Ecol* 19: 98-101.
- Kullberg C, Metcalfe NB & Houston DC (2002b). Impaired flight ability during incubation in the pied flycatcher. *J Avian Biol* 33: 179-183.
- Labocha MK, Sadowska ET, Baliga K, Semer A & Koteja P (2004) Individual variation and repeatability of basal metabolism in the bank vole, *Clethrionomys glareolus*. *Proc R Soc Lond B* 271: 367-372.
- Lahti K (1997) Social status and survival strategies in the willow tit *Parus montanus*. PhD Thesis, University of Oulu.
- Lahti K (1998) Social dominance and survival in flocking passerines birds: a review with an emphasis on the Willow tit *Parus montanus*. *Ornis Fenn* 75: 1-17.
- Lahti K, Koivula K & Orell M (1997) Dominance, daily activity and winter survival in willow tits: detrimental cost of long working hours? *Behaviour* 134: 921-939.
- Lahti K, Koivula K, Rytönen S, Mustonen T, Welling P, Pravosudov VV & Orell M (1998a) Social influences on food caching in willow tits: a field experiment. *Behav Ecol* 9: 122-129.
- Lahti K, Orell M, Rytönen S & Koivula K (1998b) Time and food dependence in willow tit winter survival. *Ecology* 79: 2904-2916.
- Lampila S, Orell M, Belda, E & Koivula K (2006) Importance of adult survival, local recruitment and immigration in a declining boreal forest passerine, the willow tit *Parus montanus*. *Oecologia* 148: 405-413.
- Laurila M & Hohtola E (2005) The effect of ambient temperature and simulated predation risk on fasting-induced nocturnal hypothermia of pigeons in outdoor conditions. *J Thermal Biol* 30: 392-399.
- Laurila M, Hohtola E, Saarela S & Rashotte ME (2003) Adaptive timing of digestion and digestion-related thermogenesis in the pigeon. *Physiol Behav* 78: 441-448.
- Laurila M, Pilo T & Hohtola E (2005) Testing the flexibility of fasting induced hypometabolism in birds: effect of photoperiod and repeated food deprivations. *J Thermal Biol* 30: 131-138.

- Lehikoinen E (1987) Seasonality of the daily weight cycle in wintering passerines and its consequences. *Ornis Scand* 18: 216-226.
- Liknes ET, Scott SM & Swanson DL (2002) Seasonal acclimatization in the american goldfinch revisited: to what extent do metabolic rates vary seasonally? *Condor* 104: 548-557.
- Lilliendahl K (1997) The effect of predator presence on body mass in captive greenfinches. *Anim Behav* 53: 75-81.
- Lilliendahl K (1998) Yellowhammers get fatter in the presence of a predator. *Anim Behav* 55: 1335-1340.
- Lilliendahl K (2000) Daily accumulation of body reserves under increased predation risk in captive Greenfinches *Carduelis chloris*. *Ibis* 142: 587-595.
- Lilliendahl K (2002) Daily patterns of body mass gain in four species of small wintering birds. *J Avian Biol* 33: 212-218.
- Lilliendahl K, Carlson A, Welander J & Ekman JB (1996) Behavioural control of daily fattening in great tits (*Parus major*). *Can J Zool* 74: 1612-1616.
- Lima SL (1986) Predation risk and unpredictable feeding conditions: determinants of body mass in birds. *Ecology* 67: 377-385.
- Lind J (2001) Escape flight in moulting tree sparrows (*Passer montanus*). *Funct Ecol* 15: 29-35.
- Lind J, Fransson T, Jakobsson S & Kullberg C (1999) Reduced take-off ability in robins (*Erithacus rubecula*) due to migratory fuel load. *Behav Ecol Sociobiol* 46: 65-70.
- Lindström Å (1997) Basal metabolic rates of migrating waders in the Eurasian arctic. *J Avian Biol* 28: 87-92.
- Lindström Å, Klaassen M & Kvist A (1999) Variation in energy intake and basal metabolic rate of a bird migrating in a wind tunnel. *Funct Ecol* 13: 352-359.
- Lovegrove BG (2000) The zoogeography of mammalian basal metabolic rate. *Am Nat* 156: 201-219.
- Lovegrove BG & Smith GA (2003) Is 'nocturnal hypothermia' a valid physiological concept in small birds?: a study on Bronze Mannikins *Spermestes cucullatus*. *Ibis* 145: 547-557.
- Lucas JR (1994) Regulation of cache stores and body mass in Carolina chickadees (*Parus carolinensis*). *Behav Ecol* 5: 171-181.
- Lucas JR & Zielinski DL (1998) Seasonal variation in the effect of cache pilferage on cache and body mass regulation in Carolina chickadees: what are the trade-offs? *Behav Ecol* 9: 193-200.
- Lundborg K & Brodin A (2003) The effect of dominance rank on fat deposition and food hoarding in the Willow Tit *Parus montanus*- an experimental test. *Ibis* 145: 78-82.
- Lustick S, Adam M & Hinko A (1980) Interaction between posture, color, and the radiative heat load in birds. *Science* 208: 1052-1053.
- Lustick S, Battersby B & Kelty M (1978) Behavioural thermoregulation: orientation toward the sun in herring gulls. *Science* 200: 81-83.
- Matthysen E (1990) Nonbreeding social organization in Parus. *Current Ornithol* 7: 209-249.
- McKechnie AE & Lovegrove BG (2002) Avian facultative hypothermic responses: a review. *Condor* 104: 705-724.
- McNab BK (1988) Food habits and the basal rate of metabolism in birds. *Oecologia* 77: 343-349.
- McNab BK (1997) On the utility of uniformity in the definition of basal rate of metabolism. *Physiol Zool* 70: 718-720.
- McNab BK (2002) Short-term energy conservation in endotherms in relation to body mass, habits, and environment. *J Thermal Biol* 27: 459-466.
- McNamara JM, Ekman J & Houston AI (2004) The effect of thermoregulatory substitution on optimal energy reserves of small birds in winter. *Oikos* 105: 192-196.
- McNamara JM & Houston AI (1987) Starvation and predation as factors limiting population size. *Ecology* 68: 1515-1519.
- McNamara JM & Houston AI (1990) The value of fat reserves and the trade off between starvation and predation. *Acta Biotheor* 38: 37-61.
- McNamara JM, Houston AI & Krebs JR (1990) Why hoard? The economics of food storing in tits, *Parus* spp. *Behav Ecol* 1: 12-23.
- McNamara JM, Houston AI & Lima SL (1994) Foraging routines of small birds in winter: A theoretical investigation. *J Avian Biol* 25: 287-302.

- Meijer T, Möhring FJ & Trillmich F (1994) Annual and daily variation in body mass and fat of starlings *Sturnus vulgaris*. *J Avian Biol* 25: 98-104.
- Metcalf NB, Taylor AC & Thorpe JE (1995) Metabolic rate, social status and life-history strategies in Atlantic salmon. *Anim Behav* 49: 431-436.
- Metcalf NB & Ure SE (1995) Diurnal variation in flight performance and hence potential predation risk in small birds. *Proc R Soc Lond B* 261: 395-400.
- Middleton ALA (1986) Seasonal changes in plumage structure and body composition of the American goldfinch, *Carduelis tristis*. *Can Field-Nat* 100: 545-549.
- Morrison ML, Ralph CJ, Verner J & Jehl Jr. JR (1988) Avian foraging: theory, methodology, and applications. *Studies in Avian Biology* 13. Cooper Ornithological Society, Allen Press Inc, Lawrence.
- Mueller P & Diamond J (2001) Metabolic rate and environmental productivity: Well-provisioned animals evolved to run and idle fast. *Proc Natl Acad Sci USA* 98: 12550-12554.
- Nilsson J-Å (2002) Metabolic consequences of hard work. *Proc R Soc Lond B* 269: 1735-1739.
- Nilsson J-Å & Råberg L (2001) The resting metabolic cost of egg laying and nestling feeding in great tits. *Oecologia* 128: 187-192.
- Nolan Jr. V & Ketterson ED (1983) An analysis of body mass, wing length, and visible fat deposits of dark-eyed juncos wintering at different latitudes. *Wilson Bull* 95: 603-620.
- Norrdahl K & Korpimäki E (2000) Do predators limit the abundance of alternative prey? Experiments with vole-eating avian and mammalian predators. *Oikos* 91: 528-540.
- Novoa FF, Bozinovic F & Rosenmann M (1994) Seasonal changes of thermal conductance in *Zonotrichia capensis* (Emberizidae), from central Chile: the role of plumage. *Comp Biochem Physiol* 107A: 297-300.
- Nudds RL & Bryant DM (2001) Exercise training lowers the resting metabolic rate of Zebra Finches. *Funct Ecol* 15: 458-464.
- Orell M (1989) Population fluctuations and survival of Great tits *Parus major* dependent on food supplied by man in winter. *Ibis* 131: 112-127.
- Orell M, Lahti K & Mäler J (1999) High survival rate and site fidelity in the Siberian Tit *Parus cinctus*, a focal species of the taiga. *Ibis* 141: 460-468.
- Peters RH (1983) The ecological implications of body size. Cambridge University Press, Cambridge.
- Piersma T, Bruinzeel L, Drent R, Kersten M, VanderMeer J & Wiersma P (1996) Variability in basal metabolic rate of a long-distance migrant shorebird (Red Knot, *Calidris canutus*) reflects shifts in organ sizes. *Physiol Zool* 69: 191-217.
- Piersma T, Gessaman JA, Dekinga A & Visser GH (2004) Gizzard and other lean mass components increase, yet basal metabolic rates decrease, when red knots *Calidris canutus* are shifted from soft to hard-shelled food. *J Avian Biol* 35: 99-104.
- Piersma T & Lindström Å (1997) Rapid reversible changes in organ size as a component of adaptive behaviour. *Trends Ecol Evol* 122: 134-138.
- Pilastro A, Bertorelle G & Marin G (1995) Winter fattening strategies of two passerine species: environmental and social influences. *J Avian Biol* 26: 25-32.
- Pinowski J & Myrcha A (1970) Winter fat deposition in the tree sparrow (*Passer m. montanus* L.). *Bulletin de L'académie polonaise des sciences CL II XVIII*: 457-462.
- Piper WH & Wiley RH (1990) The relationship between social dominance, subcutaneous fat, and annual survival in wintering white-throated sparrows (*Zonotrichia albicollis*). *Behav Ecol Sociobiol* 26: 201-208.
- Polo V & Bautista LM (2002) Daily body mass regulation in dominance-structured coal tit (*Parus ater*) flocks in response to variable food access: a laboratory study. *Behav Ecol* 13: 696-704.
- Polo V & Carrascal LM (1997) El ciclo diario de ganancia de peso durante el invierno en una población silvestre de *Parus cristatus* en el centro de España. *Ardeola* 44: 215-224.
- Pravosudov VV & Grubb Jr. TC (1997) Energy management in passerine birds during the nonbreeding season. A review. *Current Ornithol* 14: 189-234.
- Pravosudov VV & Grubb Jr. TC (1998a) Body mass, ambient temperature, time of day and vigilance in tufted titmice. *Auk* 115: 221-223.

- Pravosudov VV & Grubb Jr. TC (1998b) Management of fat reserves in tufted titmice (*Parus bicolor*): evidence against a trade-off with food hoards. *Behav Ecol Sociobiol* 42: 57-62.
- Pravosudov VV & Grubb Jr. TC (1998c). Management of fat reserves in tufted titmice *Baeolophus bicolor* in relation to to risk of predation. *Anim Behav* 56: 49-54.
- Pravosudov VV, Grubb Jr. TC, Doherty Jr. PF & Bronson CL (1999) Social dominance and energy reserves in wintering woodland birds. *Condor* 101: 880-884.
- Pravosudov VV & Lucas JR (2000a) The costs of being cool: a dynamic model of nocturnal hypothermia by small food-caching birds in winter. *J Avian Biol* 31: 463-472.
- Pravosudov VV & Lucas JR (2000b). The effect of social dominance on fattening and food-caching behaviour in Carolina chickadees, *Poecile carolinensis*. *Anim Behav* 60: 483-493.
- Pravosudov VV & Lucas JR (2001a) A dynamic model of short-term energy management in small food-caching and non-caching birds. *Behav Ecol* 12: 207-218.
- Pravosudov VV & Lucas JR (2001b) Daily patterns of energy storage in food-caching birds under variable daily predation risk: a dynamic state variable model. *Behav Ecol Sociobiol* 50: 239-250.
- Rands SA & Cuthill IC (2001) Separating the effects of predation risk and interrupted foraging upon mass changes in the blue tit *Parus caeruleus*. *Proc R Soc Lond B* 268: 1783-1790.
- Rashotte M, Saarela S, Henderson RP & Hohtola E (1999) Shivering and digestion-related thermogenesis in pigeons during dark phase. *Am J Physiol* 277: R1579-R1587
- Read AF (1988) Sexual selection and the role of parasites. *Trends Ecol Evol* 3: 97-102.
- Reinertsen RE (1982) Radio telemetry measurements of deep body temperature of small birds. *Ornis Scand* 13: 11-16.
- Reinertsen RE (1983) Nocturnal hypothermia and its energetic significance for small birds living in the arctic and subarctic regions. A review. *Polar Res* 1: 269-284.
- Reinertsen RE (1984) Seasonal and local variation of nocturnal hypothermia between lowland and highland willow tits in central Norway. *Fauna Norv Ser C, Cinclus* 7: 70-74.
- Reinertsen RE (1996) Physiological and ecological aspects of hypothermia. In: Carey C (ed) *Avian energetics and nutritional ecology*. Chapman & Hall, New York 125-157.
- Reinertsen RE & Haftorn S (1986) Different metabolic strategies of northern birds for nocturnal survival. *J Comp Physiol B* 156: 655-663.
- Reinertsen RE, Haftorn S & Thaler E (1988) Is hypothermia necessary for the winter survival of the goldcrest *Regulus regulus*? *J Ornithol* 129: 433-437.
- Rezende EL, Bozinovic F & Garland Jr T (2004) Climatic adaptation and the evolution of basal and maximum rates of metabolism in rodents. *Evolution* 58: 1361-1374.
- Ricklefs RE (2005) Avian Energetics, Ecology, and Evolution. In: Carey C (ed) *Avian Energetics and Nutritional Ecology*. Chapman & Hall, New York, 1-30.
- Ricklefs RE, Konarzewski M & Daan S (1996) The relationship between basal metabolic rate and daily energy expenditure in birds and mammals. *Am Nat* 147: 1047-1071.
- Ricklefs RE & Wikelski M (2002) The physiology/life-history nexus. *Trends Ecol Evol* 17: 462-468.
- Rogers CM (1987) Predation risk and fasting capacity: Do wintering birds maintain optimal body mass? *Ecology* 68: 1051-1061.
- Rogers CM (1991) An evaluation of the method of estimating body fat in birds by quantifying visible subcutaneous fat. *J Field Ornithol* 62: 349-356.
- Rogers CM (1995) Experimental evidence for temperature-dependent winter lipid storage in the Dark-Eyed Junco (*Junco hyemalis oregonus*) and Song Sparrow (*Melospiza melodia morphna*). *Physiol Zool* 68: 277-289.
- Rogers CM (2003) New and continuing issues with using visible fat classes to estimate fat stores in birds. *J Avian Biol* 34: 129-133.
- Rogers CM & Heath-Coss R (2003) Effect of experimentally altered food abundance on fat reserves of wintering birds. *J Anim Ecol* 72: 822-830.
- Rogers CM, Nolan Jr. V & Ketterson ED (1993) Geographic Variation in Winter Fat of Dark-Eyed Juncos: Displacement to a Common Environment. *Ecology* 74: 1183-1190.
- Rogers CM, Nolan Jr. V & Ketterson ED (1994) Winter fattening in the Dark-eyed Junco: plasticity and possible interaction with migration trade-offs. *Oecologia* 97: 526-532.

- Rogers CM & Reed AK (2003) Does avian winter fat storage integrate temperature and resource conditions? A long-term study. *J Avian Biol* 34: 112-118.
- Rogers CM & Rogers CJ (1990) Seasonal variation in daily mass and minimum body mass: a test of a recent model. *Ornis Scand* 21: 105-114.
- Rogers CM & Smith JNM (1993) Life-history theory in the nonbreeding period: Trade-offs in avian fat reserves? *Ecology* 74: 419-426.
- Rogers CM, Smith JNM, Hochachka WM, Cassidy ALEV, Taitt MJ, Arcese P & Schluter D (1991) Spatial variation in winter survival of Song Sparrows *Melospiza melodia*. *Ornis Scand* 22: 387-395.
- Root TL, O'Connor TP & Dawson WR (1991) Standard metabolic level and insulative characteristics of eastern house finches, *Carpodacus mexicanus* (Müller). *Physiol Zool* 64: 1279-1295.
- Rønning B, Moe B & Bech C (2005) Long-term repeatability makes basal metabolic rate a likely heritable trait in the zebra finch (*Taeniopygia guttata*). *J Exp Biol* 208: 4663-4669.
- Røskaft E, Järvi T, Bakken M, Bech C & Reinertsen RE (1986) The relationship between social status and resting metabolic rate in great tits (*Parus major*) and pied flycatchers (*Ficedula hypoleuca*). *Anim Behav* 34: 838-842.
- Rytkönen S & Orell M (2001) Great tits, *Parus major*, lay too many eggs: experimental evidence in mid-boreal habitats. *Oikos* 93: 439-450.
- Saarela S, Klapper B & Heldmaier G (1995) Daily rhythm of oxygen consumption and thermoregulatory responses in some european winter-or summer-acclimatized finches at different ambient temperatures. *J Comp Physiol B* 165: 366-376.
- Saarela S, Rintamäki H & Saarela M (1984) Seasonal variation in the dynamics of ptiloerection and shivering correlated changes in the metabolic rate and body temperature of the pigeon. *J Comp Physiol B* 154: 47-53.
- Senar JC, Domenech J, Carrascal LM & Moreno E (1997) A funnel trap for the capture of tits. *Bull GCA* 14: 17-24.
- Senar JC, Polo V, Uribe F & Camerino M (2000) Status signalling, metabolic rate and body mass in the siskin: the cost of being a subordinate. *Anim Behav* 59: 103-110.
- Sherry DF (1989) Food storing in the *Paridae*. *Wilson Bull* 101: 289-234.
- Smith TB, Wayne RK, Girman DJ & Bruford MW (1997) A role for ecotones in generating rainforest biodiversity. *Science* 276: 1855-1857.
- Soler JJ, Moreno J & Potti J (2003) Environmental, genetic and maternal components of immunocompetence of nestling pied flycatchers from a cross-fostering study. *Evol Ecol Res* 5: 259-272.
- Speakman JR (2005) Body size, energy metabolism and lifespan. *J Exp Biol* 18: 1717-1730.
- Speakman JR, Król E & Johnson MS (2004) The functional significance of individual variation in basal metabolic rate. *Physiol Biochem Zool* 77: 900-915.
- Speakman JR, Selman C, McLaren JS & Harper EJ (2002) Living fast, dying when? The link between aging and energetics. *J Nutr* 132: 1583S-1597S.
- Swanson DL (1991) Seasonal adjustments in metabolism and insulation in the dark-eyed junco. *Condor* 93: 538-545.
- Swanson DL (1993) Cold tolerance and thermogenic capacity in Dark-eyed juncos in winter: Geographic variation and comparison with american tree sparrows. *J Therm Biol* 18: 275-281.
- Swanson DL (in press) Seasonal metabolic variation in birds: functional and mechanistic correlates. *Current Ornithol*.
- Swanson DL & Olmstead KL (1999) Evidence for a proximate influence of winter temperature on metabolism in passerine birds. *Physiol Biochem Zool* 72: 566-575.
- Tieleman BI, Williams JB, Buschur ME & Brown CR (2003) Phenotypic variation of larks along an aridity gradient: are desert birds more flexible? *Ecology* 84: 1800-1815.
- Van der Veen IT (1999a) Effects of predation risk on diurnal mass dynamics and foraging routines of yellowhammers (*Emberiza citrinella*). *Behav Ecol* 10: 545-551.
- Van der Veen IT (1999b) Trade-off between starvation and predation: Weight-watching in yellowhammers. PhD Thesis, University of Uppsala.
- Van der Veen IT & Sivars LE (2000) Causes and consequences of mass loss upon predator encounter: feeding interruption, stress or fit-for-flight? *Funct Ecol* 14: 638-644.

- Vander Wall SB (1990) Food hoarding in animals. University of Chicago Press, Chicago.
- Veasey JS, Houston DC & Metcalfe NB (2001) A hidden cost of reproduction: the trade -off between clutch size and escape take-off speed in female zebra finches. *J Anim Ecol* 70: 20-24.
- Veasey JS, Metcalfe NB & Houston DC (1998) A reassessment of the effect of body mass upon flight speed and predation risk in birds. *Anim Behav* 56: 883-889.
- Verhulst S & Hogstad O (1996) Social dominance and energy reserves in flocks of Willow tits. *J Avian Biol* 27: 203-208.
- Vézina F & Thomas DW (2000) Social status does not affect resting metabolic rate in wintering dark-eyed junco (*Junco hyemalis*). *Physiol Biochem Zool* 73: 231-236.
- Vézina F & Williams TD (2005) The metabolic cost of egg production is repeatable. *J Exp Biol* 208: 2533-2538.
- Via S, Gomulkiewicz R, De Jong G, Scheiner SM, Schlichting CD & Van Tienderen PH (1995) Adaptive phenotypic plasticity: consensus and controversy. *Trends Ecol Evol* 10: 212-217.
- Von Schantz T, Bensch S, Grahn M & Hasselquist D (1999) Good genes, oxidative stress and condition-dependent sexual signals. *Proc R Soc Lond B* 266: 1-12.
- Waite TA (1991) Nocturnal hypothermia in Gray Jays *Perisoreus canadensis* wintering in interior Alaska. *Ornis Scand* 22: 107-110.
- Waite TA (1992) Winter fattening in Gray Jays: seasonal, diurnal and climatic correlates. *Ornis Scand* 23: 499-503.
- Walsberg GE (1986) Thermal consequences of roost site selection: the relative importance of three modes of heat conservation. *Auk* 103: 1-7.
- Walsberg GE (1988) Heat flow through avian plumages: the relative importance of conduction, convection, and radiation. *J Therm Biol* 13: 89-92.
- Welton NJ, Houston AI, Ekman J & McNamara JM (2002) A dynamic model of hypothermia as an adaptive response by small birds to winter conditions. *Acta Biotheor* 50: 39-56.
- White CR & Seymour RS (2004) Does basal metabolic rate contain a useful signal? Mammalian BMR allometry and correlations with a selection of physiological, ecological, and life-history variables. *Physiol Biochem Zool* 77: 929-941.
- Wiersma P, Selman C, Speakman JR & Verhulst S (2004) Birds sacrifice oxidative protection for reproduction. *Biol Lett* 271: 360-363.
- Wikelski M, Spinney L, Schelsky W, Scheuerlein A & Gwinner E (2003) Slow pace of life in tropical sedentary birds: a common-garden experiment on four stonechat populations from different latitudes. *Proc R Soc Lond B* 270: 2383-2388.
- Witter MS & Cuthill IC (1993) The ecological costs of avian fat storage. *Phil Trans R Soc Lond B* 340: 73-92.
- Witter MS Swaddle JP, 1995. Dominance, competition, and energetic reserves in the European starling, *Sturnus vulgaris*. *Behav Ecol* 6: 343-348.
- Witter MS, Swaddle JP & Cuthill IC (1995) Periodic food predictability and strategic regulation of body mass in the European starling, *Sturnus vulgaris*. *Funct Ecol* 9: 568-574.
- Wolf BO & Walsberg GE (1996) Thermal Effects of Radiation and Wind on a Small Bird and Implications for Microsite Selection. *Ecology* 77: 2228-2236.
- Wolf BO & Walsberg GE (2000) The Role of the Plumage in Heat Transfer Processes of Birds. *Am Zool* 40: 575-584.

Original papers

- I Broggi J & Brotons L (2001) Coal Tit fat-storing patterns during the non-breeding season: the role of residence status. *J Avian Biol* 32: 333-337.
- II Broggi J, Koivula K, Lahti K & Orell M (2003) Seasonality in daily body mass variation in a hoarding boreal passerine. *Oecologia* 137: 627–633.
- III Broggi J, Orell M, Hohtola E & Nilsson J-Å. (2004) Metabolic response to temperature variation in Great tit: An interpopulation comparison. *J Anim Ecol* 73: 967-972.
- IV Broggi J, Gamero A, Hohtola E, Orell M. & Nilsson J-Å (2005) Interpopulation differences in feather structure. (manuscript)
- V Broggi J, Hohtola E, Koivula K, Orell M, Thomson RL & Nilsson, J-Å (2005) Sources of variation in winter basal metabolic rate in the great tit *Parus major*. (manuscript)
- VI Broggi J, Hohtola E, Orell M & Nilsson J-Å (2005) Local adaptation to winter conditions in a passerine spreading north: a common garden approach. *Evolution* 59: 1600-1603.

Papers I, II, III and VI were reprinted with kind permission from the publishers.
Copyrights:

Papers I, III Blackwell Science Ltd (Osney Mead, Oxford, UK).

Paper II Springer Science and Business Media.

Paper VI The Society for the Study of Evolution (810E 10th Street, Lawrence, US).

Original articles are not included in the electronic version of the dissertation.

ACTA UNIVERSITATIS OULUENSIS
SERIES A SCIENTIAE RERUM NATURALIUM

452. Autio, Jyrki (2006) Environmental factors controlling the position of the actual timberline and treeline on the fells of Finnish Lapland
453. Rautiainen, Pirjo (2006) Population biology of the *Primula sibirica* group species inhabiting frequently disturbed seashore meadows: implications for management
454. Taskinen, Jukka (2006) Protein crystallographic studies of CoA-dependent proteins: new insight into the binding mode and exchange mechanism of acyl-CoA
455. Molin-Juustila, Tonja (2006) Cross-functional interaction during the early phases of user-centered software new product development: reconsidering the common area of interest
456. Thomson, Robert L. (2006) Breeding habitat selection and its consequences in boreal passerines. Using the spatial dispersion of predators and heterospecifics as a source of information
457. Iivari, Netta (2006) Discourses on 'culture' and 'usability work' in software product development
458. Vähäoja, Pekka (2006) Oil analysis in machine diagnostics
459. Mutanen, Marko (2006) Genital variation in moths—evolutionary and systematic perspectives
460. Bhaumik, Prasenjit (2006) Protein crystallographic studies to understand the reaction mechanism of enzymes: α -methylacyl-CoA racemase and argininosuccinate lyase
461. Korkalo, Tuomo (2006) Gold and copper deposits in Central Lapland, Northern Finland, with special reference to their exploration and exploitation
462. Pahnla, Seppo (2006) Assessing the usage of personalized web information systems
463. Puhakainen, Petri (2006) A design theory for information security awareness
464. Rytkönen, Anna (2006) The role of human replicative DNA polymerases in DNA repair and replication
465. Rönkä, Antti (2006) Dynamics, genetic structure and viability of a small and declining Temminck's stint (*Calidris temminckii*) population
466. Wäli, Piippa (2006) Environment and genetic background affecting endophyte-grass symbiosis

Book orders:
OULU UNIVERSITY PRESS
P.O. Box 8200, FI-90014
University of Oulu, Finland

Distributed by
OULU UNIVERSITY LIBRARY
P.O. Box 7500, FI-90014
University of Oulu, Finland

S E R I E S E D I T O R S

A
SCIENTIAE RERUM NATURALIUM
Professor Mikko Siponen

B
HUMANIORA
Professor Harri Mantila

C
TECHNICA
Professor Juha Kostamovaara

D
MEDICA
Professor Olli Vuolteenaho

E
SCIENTIAE RERUM SOCIALIUM
Senior Assistant Timo Latomaa

F
SCRIPTA ACADEMICA
Communications Officer Elna Stjerna

G
OECONOMICA
Senior Lecturer Seppo Eriksson

EDITOR IN CHIEF
Professor Olli Vuolteenaho

EDITORIAL SECRETARY
Publication Editor Kirsti Nurkkala

ISBN 951-42-8172-1 (Paperback)

ISBN 951-42-8173-X (PDF)

ISSN 0355-3191 (Print)

ISSN 1796-220X (Online)

