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Variation and flexibility of metabolic performance in birds

Ecological significance and physiological constraints

Engert, Elana Rae

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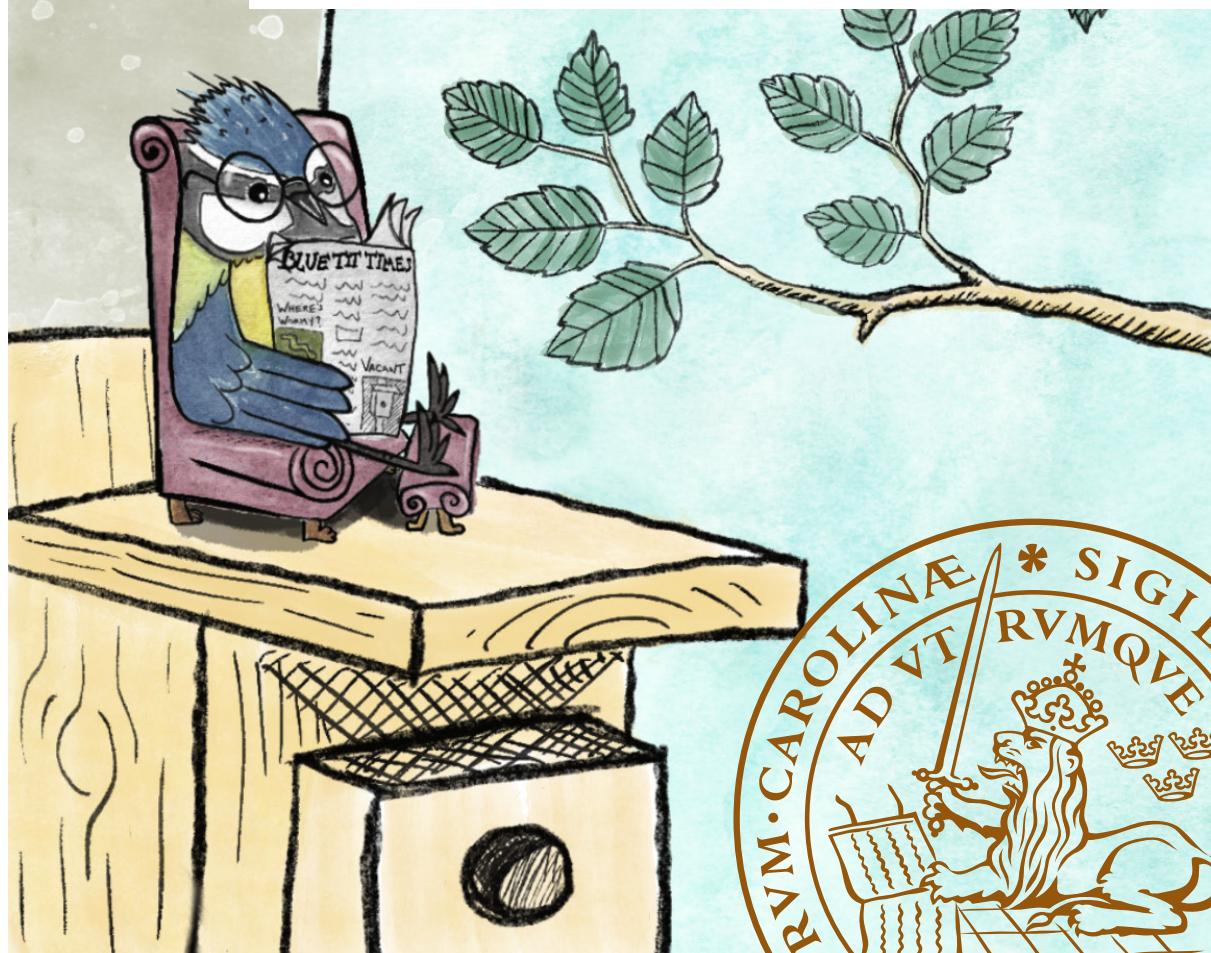


Variation and flexibility of metabolic performance in birds

Ecological significance and physiological constraints

ELANA RAE ENGERT

DEPARTMENT OF BIOLOGY | FACULTY OF SCIENCE | LUND UNIVERSITY



Variation and flexibility of metabolic performance in birds:
Ecological significance and physiological constraints

Variation and flexibility of metabolic performance in birds

Ecological significance and physiological constraints

Elana Rae Engert



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DOCTORAL DISSERTATION

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Abstract:

The rate of energy turnover in an animal, metabolic rate, is fundamental to life and determines the energy available for growth, reproduction, and survival. Thus, metabolic rate has been proposed as a mechanism linking physiology to broader ecological patterns. Numerous adaptive frameworks have been proposed to explain how selection acts on metabolic rate, how it relates to life histories, and the ecological significance of variation in metabolic rate. However, questions remain about how metabolic rate is determined, what constrains or limits metabolic rate, and how metabolic rate is connected to fitness. I aimed to understand how phenotypic variation and flexibility of metabolic rates manifest in both wild and captive birds, and to identify potential mechanisms and implications of those patterns. First, I investigated how the early environment affects the developmental trajectory of metabolic rate. Second, I measured the lower and upper limits to metabolic rates within individuals to determine if these traits were phenotypically correlated and to describe variation among individuals. Third, I measured the upper limit to metabolic rate at different points in time and in different environmental and ecological contexts, to determine if individual variation was consistent or flexible over time, or a combination of both. Fourth, I asked what sets the upper limits to metabolic rate. Fifth and finally, I investigated how individual variation in metabolic rates was associated with performance and fitness in different contexts. In this thesis, I show that the nest environment affects the development of metabolic rate. I found that minimal and maximal metabolic rates co-varied, although some of these patterns were also explained by variation in body mass. Maximum metabolic rate was both individually consistent between seasons and flexible, responding to changing environmental conditions and workload. During exercise, aerobic capacity was limited by increased air temperature, suggesting that the upper limits to metabolic rate shift depending on environmental conditions. As for links between metabolic performance and fitness, my results suggest that associations between metabolic phenotypes and fitness were dependent on the ecological and environmental context. Taken together, this thesis shows that metabolic traits can be phenotypically correlated, flexible, and repeatable, but their upper limits and links to fitness depend on the physiological and environmental context. Going forward, knowledge of physiological constraints, ecological consequences, and life history theory of metabolic rates could be leveraged to gain a better understanding of their ecological significance and how fitness outcomes could change in the context of the environment.

Key words: birds, ecophysiology, fitness, life-history, metabolic rate, natural selection, phenotypic flexibility, thermoregulation, exercise capacity, seasonality

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MADE IN SWEDEN 

*This thesis is dedicated to George, the
poet, scholar, naturalist, oyster farmer,
and national-park-inhabitant who taught
me that I could do anything in life*

“Imagination is more important than knowledge. For knowledge is limited, whereas imagination embraces the entire world, stimulating progress, giving birth to evolution. It is, strictly speaking, a real factor in scientific research.”

– Albert Einstein, 1931



Ryn Sullivan '20

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Abstract

The rate of energy turnover in an animal, metabolic rate, is fundamental to life and determines the energy available for growth, reproduction, and survival. Thus, metabolic rate has been proposed as a mechanism linking physiology to broader ecological patterns. Numerous adaptive frameworks have been proposed to explain how selection acts on metabolic rate, how it relates to life histories, and the ecological significance of variation in metabolic rate. However, questions remain about how metabolic rate is determined, what constrains or limits metabolic rate, and how metabolic rate is connected to fitness. I aimed to understand how phenotypic variation and flexibility of metabolic rates manifest in both wild and captive birds, and to identify potential mechanisms and implications of those patterns. First, I investigated how the early environment affects the developmental trajectory of metabolic rate. Second, I measured the lower and upper limits to metabolic rates within individuals to determine if these traits were phenotypically correlated and to describe variation among individuals. Third, I measured the upper limit to metabolic rate at different points in time and in different environmental and ecological contexts, to determine if individual variation was consistent or flexible over time, or a combination of both. Fourth, I asked what sets the upper limits to metabolic rate. Fifth and finally, I investigated how individual variation in metabolic rates was associated with performance and fitness in different contexts. In this thesis, I show that the nest environment affects the development of metabolic rate. I found that minimal and maximal metabolic rates co-varied, although some of these patterns were also explained by variation in body mass. Maximum metabolic rate was both individually consistent between seasons and flexible, responding to changing environmental conditions and workload. During exercise, aerobic capacity was limited by increased air temperature, suggesting that the upper limits to metabolic rate shift depending on environmental conditions. As for links between metabolic performance and fitness, my results suggest that associations between metabolic phenotypes and fitness were dependent on the ecological and environmental context. Taken together, this thesis shows that metabolic traits can be phenotypically correlated, flexible, and repeatable, but their upper limits and links to fitness depend on the physiological and environmental context. Going forward, knowledge of physiological constraints, ecological consequences, and life history theory of metabolic rates could be leveraged to gain a better understanding of their ecological significance and how fitness outcomes could change in the context of the environment.

Popular science summary

Birds are perhaps best known for their migratory feats, crossing oceans and continents on the wing. Here, in the cold dark winter of Sweden, an even more impressive feat is happening right under our noses. Outside, in the rain, snow and wind, there is a tiny bird, the size of a *chokladboll*, surviving in the cold. The small bird in winter faces an immense challenge to find food and to stay warm. Because of its small body size, it loses body heat much faster than larger animals and generates heat by shivering. In winter, small birds put on fat and change their body composition, increasing metabolic rates to become a “shivering machine”. Fast forward to spring, when the days are finally getting warmer and longer. The bird has survived the winter, and such a high metabolic rate is not needed, but now comes a new challenge, the nesting season. The nestlings grow fast, and they need a lot of food to be brought to the nest. Feeding the nestlings is a bit like running a marathon, flying back and forth hundreds of times per day, from dawn until dusk. The birds body composition and metabolic rate changes again, trimming down body mass and fat to become a lean “feeding machine”. Now, the problem isn’t the cold but the heat. Imagine that you are in the forest on a summer night, it’s bit chilly so you put on a sweater. Now imagine that the sun comes out, but you can’t take off your sweater, and now you have to run a race in the heat of the day. As opposed to in winter, when metabolic performance served to generate the heat needed for survival, now the bird’s metabolic performance could be limited by heat dissipation while feeding the nestlings. In this thesis, I investigated why small birds vary in their metabolic performance for both shivering and exercise, and if their metabolic strategy remains consistent between different seasons. I also wondered, if a bird has a high or low metabolic rate, what does this mean for the bird? I found that some birds have higher metabolism than others in both winter and summer. Birds with low metabolic rates were more likely to breed earlier and have heavier nestlings than those with high metabolic rates. On the other hand, birds with high metabolic rates during the breeding season were slightly more likely to survive and return to breed the following year. Birds might vary in their metabolic strategies because their chances of success are context dependent. For example, in a harsh winter, a high metabolic rate might be the winning strategy to stay alive, but in a mild winter, a low metabolic rate could be a good strategy if it means a higher reproductive success. I also found that warm temperatures can set the limit to metabolic performance during exercise. In a rapidly changing world, only time will tell how this might affect the metabolic strategies of small, resident birds.

List of papers

- I. **Engert, E. R.**, Andreasson, F., Nord, A., & Nilsson, J-Å. (2025). Using metabolic data to investigate the role of brood size in the development of endothermy. *Journal of Avian Biology*, 2025: e03301. <https://doi.org/10.1111/jav.03301>
- II. **Engert, E. R.**, Grange, M., Nord, A., Andreasson, F., Nilsson, J-Å. Fitness and flexibility of metabolic phenotypes in a temperate resident bird. *Functional Ecology*. *In press*.
- III. **Engert, E. R.**, Nord, A., Andreasson, F., Nilsson, J-Å. (2026). Flexibility of exercise capacity during nestling feeding in blue tits. *Journal of Experimental Biology*, 229(7), jeb251043. <https://doi.org/10.1242/jeb.251043t>
- IV. **Engert, E. R.**, Nord, A., Andreasson, F., Nilsson, J-Å. Body temperature is repeatable and related to cold tolerance and exercise-induced hyperthermia in a passerine bird. *Submitted*
- V. **Engert, E. R.**, Nilsson, A., Nord, A., Andreasson, F., Nilsson, J-Å. Air temperature limits aerobic capacity and scope in active birds. *Submitted*
- VI. **Engert, E. R.**, Andreasson, F., Nilsson, J-Å. Thermoregulatory constraints to activity: applying biophysical models in birds. *Manuscript*

Additional published papers not included in the thesis

Engert, E. R., Hellström, M., Åkesson, S. (2023). Autumn fueling behavior in passerines in relation to migratory distance and daylength. *Ecology and evolution*, 2023(13), e9571. <https://doi.org/10.1002/ece3.9571>

Author contributions

- I.** Conceptualization: E.R.E., F.A., A.No., J-Å.N.; Methodology: E.R.E., F.A., A.No., J-Å.N.; Investigation: E.R.E., F.A., A.No., J-Å.N.; Formal analysis: E.R.E. Visualization: E.R.E. Writing – original draft: E.R.E. Writing – review and editing: all authors; Resources: A.No., J-Å.N; Supervision: F.A., A.No., J-Å.N.
- II.** Conceptualization: E.R.E., J-Å.N.; Methodology: E.R.E., F.A., A.No., J-Å.N.; Investigation: E.R.E., M.G., F.A., A.No., J-Å.N.; Formal analysis: E.R.E. Visualization: E.R.E. Writing – original draft: E.R.E. Writing – review and editing: all authors; Resources: A.No., J-Å.N; Supervision: F.A., A.No., J-Å.N.
- III.** Conceptualization: E.R.E., J-Å.N.; Methodology: E.R.E., F.A., A.No., J-Å.N.; Investigation: E.R.E., F.A., A.No., J-Å.N.; Formal analysis: E.R.E. Visualization: E.R.E. Writing – original draft: E.R.E. Writing – review and editing: all authors; Resources: A.No., J-Å.N; Supervision: F.A., A.No., J-Å.N.
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Authors

Fredrik Andreasson (F.A.), Elana Rae Engert (E.R.E), Marion Grange (M.G.), Ammeli Nilsson (A.Ni.), Jan-Åke Nilsson (J-Å.N.), Andreas Nord (A.No.)

General Introduction

Metabolic rate, the rate of energy turnover in an organism (Box 1, Figure 1), is a defining feature of life, controlling the energy available for animals to do everything that they do. It is central to evolutionary and life history theories that relate to how animals grow, reproduce, live and die. Thus, metabolic rate is hypothesized to be a physiological mechanism explaining larger ecological patterns (Ricklefs & Wikelski, 2002). However, the ecological and evolutionary significance of metabolic rate can be difficult to determine, as it can be both genetically and environmentally determined and is tightly linked with other physiological traits (Metcalf et al., 2023). Metabolic rate varies between individuals, changes with the seasons and is also highly variable from moment to moment. Despite widely accepted protocols to standardize measures of metabolic rate and controlling for variation in body mass, there is considerable residual intraspecific variation in metabolic rate (Speakman et al., 2004; White & Kearney, 2013) as well as intraindividual variation (Konarzewski & Książek, 2013). The sources and significance of this variation have been the subject of much debate resulting in successive theories in the fields of evolutionary biology, life history and ecology (Burton et al., 2011; Speakman et al., 2004).

The diversity that we observe today, or lack thereof, is a snapshot that can tell us a story of how macroevolutionary patterns came to be and how selection might work at a microevolutionary level. It goes to show that unexplained phenotypic variation is interesting, especially if there is a reason to believe that said variation is ecologically important (Schwieterman et al., 2026). But it is also a great challenge to uncover the causes and consequences of an exceedingly complex and multidimensional phenotype such as metabolic rate, in the context of a perhaps even more complex, variable, and multi-layered environment. The challenge is exacerbated for ecologists who are interested in real-world implications for free-living animals, because in a natural setting, a myriad of conditions affect metabolic rate, which is difficult to measure precisely in the field. I approach the topic of this thesis – the ecological significance of variation and flexibility in metabolic rate – with three assumptions: (1) an individual's metabolic rate, when measured in a standardized way, is a physiological characteristic of that individual, (2) variation in metabolic rate among individuals reflects differences in physiological function and (3) metabolic rates could be consequential for fitness and variation as such could be ecologically significant.

Box 1. The study of metabolic rate

What is metabolic rate? – Metabolic rate (MR) the rate of energy turnover within an organism, the engine that converts chemical energy (food) into useable energy (ATP) and heat (Figure 1). The organismal metabolic rate is the sum of all cellular respiration occurring within the mitochondria. Some tissues are more metabolically active than others and explain the most variation in metabolic rate. The liver, brain, kidney, heart, muscle, and digestive tract are particularly important contributors to organismal metabolic rate (Barceló et al., 2017; Daan et al., 1990; McKechnie & Swanson, 2010; Swanson, 2010).

How do you measure metabolic rate? – Energy is defined as the capacity to do work. We see, hear, and feel the effects of energy as light, heat, sound, and motion. Energy is somewhat abstract because it cannot be seen or measured directly, but the amount and flow of energy can be inferred from its effects on other physical properties. Since the rate of O_2 consumption is proportional to energy turnover, this can be used as an fairly accurate approximation of metabolic rate. Respirometry, the measure of O_2 and CO_2 flux, is commonly used as an indirect measurement of metabolic rate.

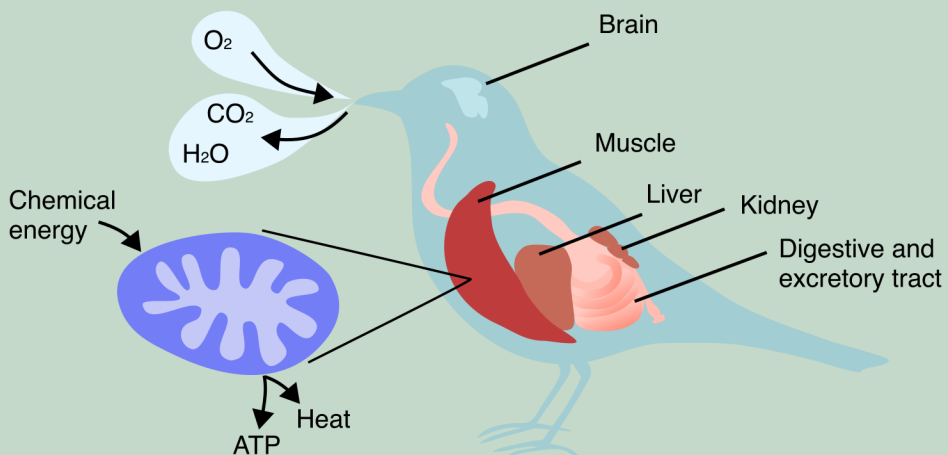


Figure 1. Schematic drawing of metabolically important muscles and organs in a bird and the main inputs (O_2 , chemical energy) and outputs (CO_2 , H_2O , ATP, and heat) of cellular respiration.

Aims of the thesis

The overarching aim of this thesis was to describe patterns in phenotypic variation of metabolic rates within bird populations and to identify potential mechanisms and implications of those patterns. I was interested in the determinants of individual variation in metabolic rates, including the developmental environment, parental effort, and challenging environmental conditions. I aimed to identify potential constraints to metabolic rates, both in the strict sense, as in hard physiological or environmental limits, but also in the broad sense, as in phenotypic correlations or energy management strategies that trade-off different aspects of fitness. I was also interested in the consequences of individual variation in metabolic rates for performance in different contexts. The specific research questions addressed in this thesis are described below.

1. What is the role of brood size in the development of metabolic rate and endothermy?

In altricial birds, birds that care for and brood their young in the nest until they fully develop, brood size is predicted to affect both the nutritional (via sibling competition) and thermal environment (via thermal inertia of the brood) for individual nestlings, which could influence the development of thermoregulation. In **Paper I**, I manipulated brood size to determine the possible role of sibling competition and/or thermal inertia of the brood in the timing of ontogeny of endothermy and the potential trade-off between growth and development of endothermy.

2. How does variation in multiple aspects of metabolic rate manifest in a population?

Minimal and maximal standardized measures of metabolic rates could be expected to vary in a correlated or independent way within individuals, which could have implications for what phenotypes are available for natural selection. The pattern of variation could be expected to differ in a wild population with fluctuating conditions and unpredictable food resources versus in a captive population where conditions are mild and stable where food is provided *ad libitum*. In **Papers II** and **IV**, I investigated if and how minimal and maximal standardized metabolic rates co-vary

in a wild population of birds (**Paper II**) and a captive population of birds (**Paper IV**) to determine if certain phenotypes are more likely to occur than others and if individuals could be characterized by metabolic syndromes.

3. Does individual variation in metabolic rate remain consistent or fluctuate across different time scales?

Basal metabolic rate (BMR) has been shown to be flexible and repeatable in birds, but comparatively little is known about how maximum exercise-induced metabolic rate (MMR) responds in different environmental and ecological contexts. I investigated the flexibility and repeatability of MMR in wild birds between seasons in **Paper II**, and depending on nestling feeding demand within a breeding season in **Paper III**. In **Paper IV**, I investigated the short-term repeatability of captive birds body temperature and MMR. To better understand environmental constraints to MMR, in **Paper V**, I measured the repeatability and flexibility of MMR in captive birds when manipulating air temperature.

4. What sets the limit to maximum metabolic rate and what are the potential consequences?

Maximum metabolic rate could be associated with overall aerobic capacity (i.e. maximum sustainable metabolic rate, SusMR and endurance) and could intuitively be important for activities that increase fitness such as nestling provisioning. In **Paper III**, I manipulated brood size in wild birds to determine if MMR was responsive to workload and if the capacity to adjust MMR was associated with parental investment (i.e., feeding frequency) and performance (i.e., nestling mass). In **Paper V**, I investigated if aerobic performance, measured as MMR and endurance, is constrained by increased air temperatures in birds. In **Paper VI**, I was interested in how biophysical models could be applied to active birds and if they could be leveraged to predict the effects of environmental temperature on the scope for activity.

5. How is individual variation in metabolic rates associated with fitness in the ecological and environmental context?

If there are fitness consequences of individual variation in metabolic rates, it could be positive, negative or context dependent. In **Paper II**, I aimed to determine if there were associations between metabolic rates and predictors of fitness (survival or reproductive success) in free-living birds in the contexts of season (winter or spring), life stage (breeding or non-breeding), and which standardized metabolic rate was considered (BMR, MMR, or M_{sum} ; Box 2).

Background

The determinants of metabolic rate and its ecological and evolutionary significance have been a subject of debate for nearly a century (Kleiber, 1932). Both adaptive and non-adaptive explanations abound, and variation in basal metabolic rate continues to perplex and provoke scientists across disciplines (Metcalf et al., 2023; Swanson et al., 2017). After correcting for body mass, which scales allometrically with basal metabolic rate (BMR, Box 2), the main factors that determine interspecific variation in metabolic rates are climate, geography, and ecology, and the determinants of intraspecific variation in metabolic rates are the genetic background, body composition, developmental plasticity, phenotypic flexibility, and the environmental, physiological and behavioral context.

Evidence for macro-evolutionary patterns

After correcting for body mass, which scales allometrically with basal metabolic rate (BMR, Box 2), inter-specific variation in endotherms has been attributed to evolutionary history and phylogeny, characteristics of the species, as well as ambient temperature, geography and climate (White & Kearney, 2013). Birds are endothermic homeotherms, meaning they produce heat endogenously through metabolism to regulate their body temperature within a certain range. Selection for high aerobic capacity in the ancestors of modern birds and mammals may have led to correlated selection for high BMR and body temperature, an idea that has been termed the aerobic capacity model (Bennett & Ruben, 1979). Birds have relatively high basal metabolic rates and normothermic body temperatures for their body size compared to mammals (King & Farner, 1961; McNab, 2009; Prinzinger et al., 1991). Flying birds also have twice the aerobic capacity of running mammals of similar size (Bishop & Butler, 2015). Passerines in particular have high mass-specific BMR compared to other taxonomic groups (McNab, 2009). In birds, BMR is correlated with environmental temperature, geography, and climate (White & Kearney, 2013), and tends to be higher in polar, temperate, and mountain ecosystems than in tropical, arid, and lowland ecosystems (McNab, 2009).

Box 2. Standardized measures of metabolic rate

Organismal metabolic rate is highly variable and changes depending on the time of day, temperature, activity, feeding, growth and reproductive status. Thus, standardized measures of metabolic rates contextualize results and allow for meaningful comparisons between individuals, species, and taxa (McNab, 1997). Basal metabolic rate **BMR**, is the energy expenditure required for basic functions when resting in thermoneutrality, and not digesting, growing or actively reproducing (McNab, 1997). Resting metabolic rate **RMR** is also a standardized measure of minimum metabolic rate, but is used when the animal is not fasted and thus does not meet the strict requirements for BMR. **M_{sum}**, the cold-induced summit metabolic rate and **MMR**, the maximum exercise-induced metabolic rate are widely used as measures of upper limits to metabolic rate (McKechnie & Swanson, 2010). **SusMR** is the maximum metabolic rate that can be sustained for

days to weeks and field metabolic rate **FMR** is measured in free-living animals that are exhibiting normal behaviors (Peterson et al., 1990). Metabolic rate can also be written as metabolic scope, which is expressed as multiples of basal metabolic rate.

Ecological relevance – Animals rarely meet the strict requirements of BMR, **M_{sum}** or **MMR** in the wild (Figure 2). However, BMR is always running in the background, adding to the total cost of living (Swanson et al., 2017). BMR could also reflect the maintenance cost of organs and muscles that influence energy assimilation and metabolic capacity (Daan et al., 1990). As for the upper limits to metabolic rate, maximal metabolic rates (**M_{sum}** and **MMR**) tend to reflect the overall capacity for sustained activity (i.e., endurance, **SusMR**; Swanson & McKechnie, 2010). **M_{sum}** also has clear implications for survival in the cold whereas **MMR** could affect short burst performance, such as escaping predators.

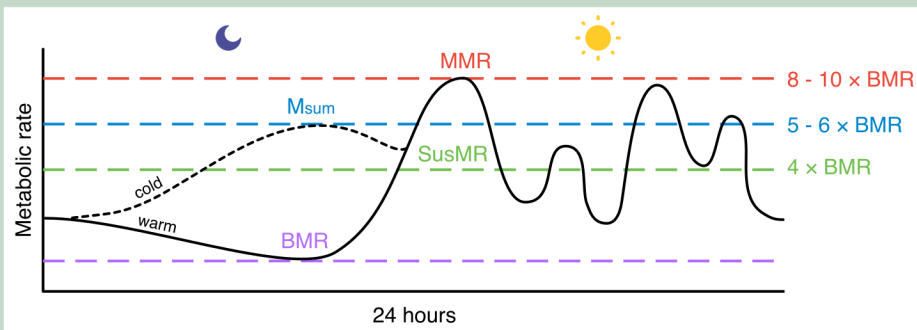


Figure 2. Schematic of variation in metabolic rate over a 24-hour period in a free-living bird with examples of standardized metabolic rates BMR, **M_{sum}**, **MMR**, and **FMR**.

Life-history theory and metabolic rate

Energy can be seen as a currency that is budgeted for the competing interests of growth, self-maintenance, and reproduction in a way that maximizes fitness (i.e., lifetime reproductive success). Fitness, measured as lifetime reproductive success, is the combined outcome of all aspects of life-history; survival, lifespan, the timing and frequency of breeding attempts, fecundity and recruitment. The evolution of life-histories is hypothesized to be constrained by trade-offs, resulting in a distinct set of possible life-history strategies (Roff, 1992). Examples of classic theoretical trade-offs in life-history theory are growth versus reproduction, current versus future reproduction, and number versus quality of offspring (Stearns, 1998).

Metabolic rate and the pace of life

Species vary along a “fast” – “slow” continuum that reflect fundamental life history trade-offs in growth, reproduction, and survival (Gaillard et al., 1989). “Fast” species mature early, are small-bodied, have a short lifespan, and have many offspring with lower investment per offspring, whereas “slow” species are characterized by the opposite. Phenotypic traits that co-vary with life history traits have been further categorized into pace-of-life syndromes (POLS), which have also been proposed to include hormonal, immunity, and personality traits (Réale et al., 2010). Because metabolic rate is related to the rates of biological processes, it has been suggested as a mechanism that sets the pace of life. The metabolic theory of ecology proposes that metabolic rate, determined by universal scaling relationships between mass and temperature, dictates the flow of energy at all levels, from individuals to entire ecosystems (Brown et al., 2004).

Determinants of individual variation in metabolic rate

Genetic background

Phylogenetic evidence shows that metabolic rate has been shaped by evolutionary history. For metabolic rate to continue to evolve there must be heritable genetic variation. There is growing evidence that BMR is a heritable trait in both captive (Mathot et al., 2013; Rønning et al., 2007; Tieleman et al., 2009a; Tieleman et al., 2009b) and wild bird populations (Bushuev et al., 2012; Nafstad et al., 2023; Nilsson et al., 2009). BMR is usually, but not always, found to be repeatable within and between years (Broggi et al., 2009; Bushuev et al., 2011; McFarlane et al., 2021), although repeatability declines with time between measurements (Cortés et al., 2015). Artificial selection experiments have also confirmed the heritability of maximal exercise-induced metabolic rate (MMR, Box 2) in rodents (Wone et al., 2015), but the heritability of MMR in birds has not yet been investigated. Similarly,

maximum cold-induced metabolic rate (M_{sum} , Box 2) has been found to be heritable in rodents, but has not been investigated in birds (White & Kearney, 2013). M_{sum} appears to be repeatable within individual birds when conditions are constant (Swanson & King, 2013). Thus, some variation in metabolic rates seems to have a heritable component.

Body composition

Body mass explains a substantial amount of variation in metabolic rates, so metabolic rates are often presented or compared as mass-independent residuals of allometric regressions (the pros and cons of which are discussed in Box 3). BMR consumes a large portion of the energy budget in endotherms, ranging from 30 – 50% (Swanson et al., 2017), so basic functions consume a substantial component of the energy budget. The size of the central organs, especially those associated with the digestive and excretory systems, are positively associated with BMR both within and between species (Barceló et al., 2017; Daan et al., 1990). M_{sum} is achieved through shivering thermogenesis, where heat is produced through rapid contraction of the skeletal muscles, which implicates an increase in metabolic rate. Skeletal muscle mass is positively related to M_{sum} (Petit & Vézina, 2014a), and increases with cold-training (Zhang et al., 2015b). MMR is positively related to both flight muscle mass and heart mass (Chappell et al., 1999; Zhang et al., 2015b). Cross-training experiments have shown that MMR and M_{sum} share mechanistic components, in the flight muscles (Petit & Vézina, 2014a; Zhang et al., 2015b), oxygen transport (Bury et al., 2019; Petit & Vézina, 2014a), and lipid catabolism (Zhang et al., 2015a). The metabolic intensity of different tissues can also vary independently of body mass (Barceló et al., 2017).

Developmental plasticity

Another possible determinant of metabolic rate is the conditions experienced in the peri- and neonatal stages of development (Nord & Giroud, 2020; Page et al., 2022; Tabh & Nord, 2023). Nord and Nilsson (2011) showed that blue tit nestlings incubated at lower temperatures had a higher RMR before fledging. Broggi et al. (2022) found that the effects of ambient temperature during incubation may last into the first winter in a wild population of great tits. Thermal conditions experienced after hatching may also influence the metabolic rate of birds. In Japanese quail, chicks exposed to a simulated heatwave had thermoregulatory and metabolic advantages to withstand heat stress as juveniles, but the effects did not persist into adulthood when the temperature stressor had been removed (Persson et al., 2024). Thermal and nutritional conditions during the nestling period may also affect the development of cold tolerance (Andreasson et al., 2016) and endothermy in wild altricial birds.

Box 3. Body mass and metabolic rate

BMR, MMR and M_{sum} all scale allometrically with body mass, complicating comparisons of whole-animal metabolic rates among individuals or species that differ in size. To account for this, many studies present residuals from allometric regressions alongside absolute metabolic rates. However, treating covariation in metabolic rate and body mass simply as a confounding effect may discount biologically meaningful variation in metabolic rates. BMR, MMR and M_{sum} are phenotypically flexible and can change in association with variation in the mass of organs and muscles that contribute disproportionately to metabolic rate (Barceló et al., 2017; Vézina et al., 2006), potentially resulting in steeper scaling relationships with body mass (McKechnie et al., 2006). Thus, covariation in body mass and metabolic

rate may arise in part as a shared response to the same stimulus, making them difficult to separate. Comparisons of whole-animal metabolic rates can therefore be informative (Swanson et al., 2012), particularly when variation in structural body size is relatively small. Absolute metabolic rates reflect not only the overall metabolic capacity, but also potential costs associated with maintaining and fuelling the metabolic machinery, which could indicate differences in energy-management strategies. Conversely, residual metabolic rate can provide information about metabolic intensity for a given body mass, which could stem from variation in mitochondrial density or body composition. Ultimately, absolute and residual metabolic rates contain different information and can be informative in different contexts.

Phenotypic flexibility

Metabolic rate evolves within the context of the environment and varies with climate and geography. However, the environmental conditions experienced by individuals are seldom constant. Many birds breeding in temperate regions avoid seasonal fluctuations by migrating (Ruegg et al., 2021; Zurell et al., 2018). For temperate residents, birds contend with large fluctuations in temperature between seasons and sometimes between day and night. While some variation in metabolic phenotypes may be explained by genetics and developmental plasticity, the ability of adult birds to adjust their metabolic machinery in a matter of days to weeks to match environmental conditions and energy demand is well documented (for a review see McKechnie and Swanson, 2010; Figure 3). Body composition shifts between summer and winter, with larger fat stores (Pravosudov & Grubb, 1997), and enlarged skeletal and visceral organs (Liknes & Swanson, 2011; O'Connor, 1995; Swanson, 1991; Vézina et al., 2006; Zheng et al., 2014) in cold-acclimated birds. BMR, M_{sum} , and cold tolerance are all generally elevated in winter in small resident

birds . Due to the high demands of thermoregulation, they generally have the highest FMR in winter compared to other seasons (Swanson, 2010).

The breeding season is another energy-demanding phase of the annual cycle (Swanson 2010). Egg laying, incubation, and chick rearing all require a high parental investment. Altricial birds feed their young while they develop in the nest which entails making frequent foraging trips, up to once per minute, between dawn and dusk. This commonly coincides with a decrease in fat stores and body mass, which could lower the costs of both maintenance and locomotion (Swanson, 2010). However, RMR has been found to increase during reproduction in female great tits, relative to winter BMR (Nilsson & Råberg, 2001). Comparatively little is known about seasonal variation in MMR, but MMR is also phenotypically flexible, as confirmed by flight training experiments (Zhang et al., 2015b). One might predict MMR to increase during the breeding season, at least during the peak of chick feeding, due to the high flight requirements of feeding offspring (Yu et al., 2024).

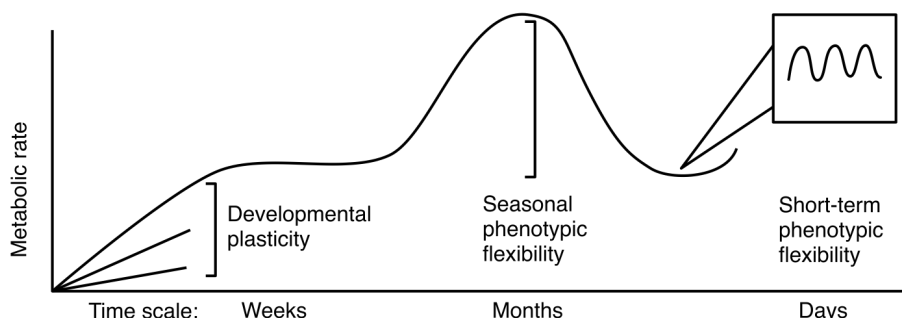


Figure 3. Representative drawing of the phenotypic trajectory determined by the genotype, developmental plasticity and reversible phenotypic flexibility developmental plasticity was investigated in **Paper I**, seasonal phenotypic flexibility was investigated in **Paper II**, and short-term phenotypic flexibility within a season was investigated in **Paper III**.

Environmental, physiological, and behavioral context

While life history theory is central to predictions of energetic trade-offs within animals, ecophysiology provides the context and scope of the energy budget with respect to environmental conditions. Birds are endothermic, meaning they produce heat endogenously to maintain a relatively high body temperature (Prinzinger et al., 1991). Keeping body temperature within the margins of safety is vital for maintaining normal function, performance and survival (Boyles et al., 2011). The amount of energy required to maintain a stable body temperature in a cold environment depends on air temperature, body temperature, and how fast body heat is lost to the environment (Box 4). Therefore, the energy budget is influenced greatly by environmental temperature and factors that influence heat dissipation (Scholander et al., 1950; Speakman & Król, 2010). As temperatures increase, the efficacy of dry heat loss diminishes, and birds actively increase heat dissipation rate

by leveraging the latent heat of vaporization of water. In songbirds, the only thermoregulatory pathway for evaporative heat loss is panting (McKechnie et al., 2021). In arid environments, maintaining water balance can become an issue in hot weather as evaporative cooling could lead to dehydration (Conradie et al., 2024). In many bird species, there is also a metabolic cost to panting, increasing the burden for heat dissipation and overall energy requirements (McKechnie et al., 2021).

Any increase in activity results in an increase in metabolic heat production (Box 4). In cold temperatures, activity substitutes for shivering heat production which ameliorates the need for facultative thermogenesis. In warm temperatures, however, heat production during activity can overwhelm the capacity for heat dissipation. Thus, the thermal niche for successful reproduction is likely to be narrower than that for survival (Nord et al., 2026), especially in highly active species.

Limits to metabolic rates

Limits to energy acquisition, assimilation, and expenditure

Life history theory contains the implicit assumption that animals are energy limited. Perhaps the most obvious limitation to the overall scope of the energy budget is resource availability, because food provides the fuel for metabolism. However, the capacity to convert food into useable energy could also limit the energy budget (central limitation hypothesis, Weiner, 1992), and this capacity could be positively related to BMR (Barceló et al., 2017). Animals can also be limited by the capacity for the muscles to perform work or the efficiency of oxygen delivery to the tissues (peripheral limitation hypothesis, Peterson et al., 1990), which could affect maximum aerobic capacity, MMR and M_{sum} . Drent and Daan (1980) proposed that a metabolic scope greater than $4 \times \text{BMR}$ cannot be sustained without causing damage that leads to reductions in survival or future reproductive success.

A more recent theory, the heat dissipation limit (HDL) theory, proposes that sustained energy expenditure can be limited by heat dissipation under certain conditions. A growing body of work has shown that birds use behavioral means of thermoregulation to avoid overheating, leading to costs related to missed opportunities in the wild (reviewed by Cunningham et al., 2021). Behavioral responses to overheating include shade-seeking and limiting activity during the hottest part of the day (Wiley & Ridley, 2016). In arid climates, this can constrain the time available for foraging (Goldstein, 1984) or foraging efficiency (du Plessis et al., 2012). Insufficient heat dissipation can also limit nestling provisioning during the breeding season and have negative consequences for body condition of the parents and nestling growth, even at temperatures that are considered mild in temperate climates (Nord & Nilsson, 2019; Silva et al., 2015; Tapper et al., 2020a).

Box 4. Biophysical models of thermoregulation

From first biophysical principles, the metabolic rate or evaporative heat loss required to maintain a stable core body temperature can be modelled as a function of air temperature (King & Farner, 1961). The U-shaped Scholander-Irving model was one of the first to predict the metabolic cost of thermoregulation in resting endotherms (Scholander et al., 1950; Fig 4, left). Forming the flat part of the curve is the thermoneutral zone (TNZ), where animals maintain normothermy by adjusting insulation and peripheral circulation, which affects thermal conductance (C). Below the lower critical temperature (LCT) endotherms actively produce heat by increasing metabolic rate, for example by

shivering. Above the upper critical temperature (UCT), heat dissipation is actively increased through evaporative cooling, which can also incur a metabolic cost. One limitation of such models is that they apply only to inactive animals. Activity causes metabolic rate to increase, shifting the balance between heat production and dissipation. Rezende and Bacigalupe (2015) proposed an "expanded" Scholander-Irving model based on the same principles, which predicts the rate of dry heat loss during activity, and thus at what temperature threshold evaporative heat loss would need to increase to maintain activity at the maximum sustainable level, SusMR (Fig 4, right).

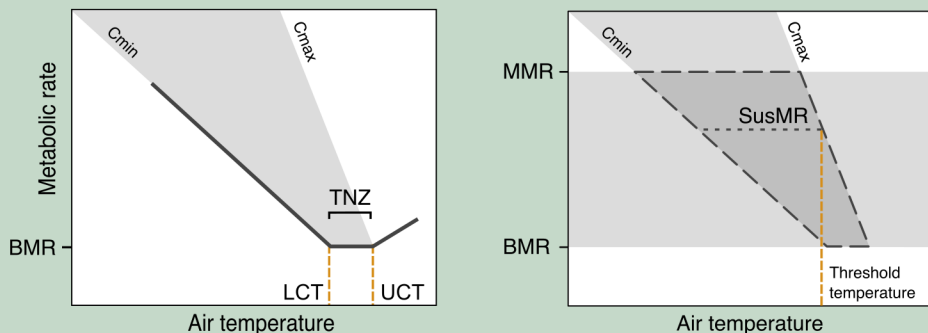


Figure 4. Left: A heat balance model predicts the metabolic rate required to maintain a stable core body temperature as a function of air temperature. Within the thermoneutral zone (TNZ), body temperature is maintained by adjusting thermal conductance. Below the lower critical temperature (LCT), metabolic rate must increase at a rate as dry heat loss, determined by the minimal thermal conductance (C_{min}). The upper critical temperature (UCT) marks the threshold where thermal conductance cannot be increased further (C_{max}), and heat must be dissipated via evaporative cooling. Right: An expanded model that incorporates activity. Metabolic heat production must be reduced or evaporative heat loss increased at the same rate that dry heat loss diminishes, which is determined by C_{max} . The threshold temperature marks where increased evaporative heat loss would be necessary to maintain the maximum sustained metabolic rate (SusMR; modified from Rezende & Bacigalupe., 2015 and O'Connor et al., 2022).

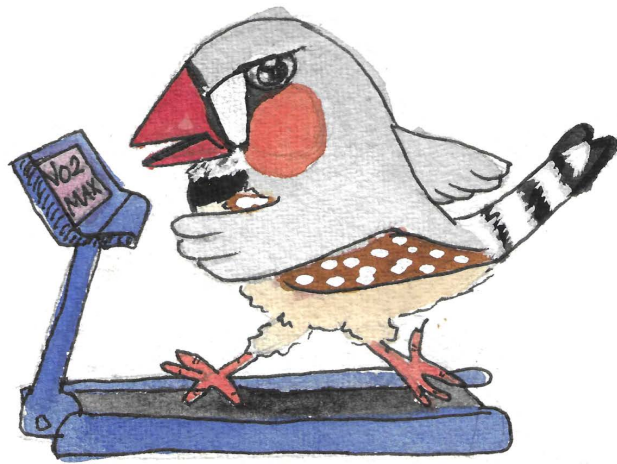
Phenotypic constraints

Individual variation in metabolic rates could be shaped by phenotypic, functional, or genetic correlations within and between minimal and maximal metabolic rates, or other physiological traits. M_{sum} generally increases in the winter in temperate residents, along with body mass, and BMR (Swanson, 2010). However, the positive relationship between BMR and M_{sum} is most likely explained by a phenotypic correlation as BMR and M_{sum} seem to have different mechanistic underpinnings (Swanson et al., 2012). In line with this, some studies show a temporal decoupling between BMR and M_{sum} in the wild (Barceló et al., 2017; Le Pogam et al., 2020; Petit et al., 2013). A phenotypic link between maximal metabolic rates and BMR might be expected if an increase in basal metabolic rate is needed to support a higher rate of overall energy expenditure in the organ and muscle systems involved in energy supply and demand (Suarez & Darveau, 2005). Cold-acclimation is generally associated with a higher FMR and a higher food intake is associated with a higher BMR (Petit et al., 2013; Vézina et al., 2006). Along the same line of reasoning, one might also expect a positive phenotypic correlation between MMR and BMR. The few empirical studies in birds show mostly positive (Careau et al., 2014; Chappell et al., 1999; Wiersma et al., 2007) but also no correlation (Swanson et al., 2012) within individuals. In captive house sparrows, BMR decreased and MMR increased when subjected to exercise training (Zhang et al., 2015b). Since performance in MMR and M_{sum} have similar physiological foundations, one might expect that they would be positively correlated. Results from cross-training experiments (Zhang et al., 2015b) and that birds in migratory disposition have an elevated M_{sum} (Chappell et al., 1999; Swanson, 1995; Swanson & Dean, 1999; Vézina et al., 2007), suggest that MMR and M_{sum} can respond in parallel to the same training or environmental stimuli.

Fitness of metabolic rates

Metabolic rates are hypothesized to be consequential for fitness, but logical arguments can be made for either positive, negative selection, or no selection. How selection may act on basal metabolic rate has been described by three different energy-management models (summarized in Burton et al., 2011). BMR could be expected to be positively related to fitness if an increased capacity to perform work – such as parental care, or shivering thermogenesis – requires a higher capacity for energy assimilation, and thus a higher cost of maintaining the metabolic machinery (“performance” or “increased-intake” model). Alternatively, BMR could be negatively related to fitness if energy invested in self-maintenance trades off with energy that can be allocated to other energy-demanding tasks (“allocation” model). The “context-dependence” model posits that the performance model applies when resources are not limited, while the allocation model applies when resources are

limited, so the relationship between metabolic rate and fitness could depend on the environmental context. Context-dependent selection could also offer a possible explanation for the maintenance of individual variation in metabolic rate within a population (Nilsson & Nilsson, 2016). Studies of captive birds have found support for the allocation hypothesis (Koetsier & Verhulst, 2011; Nudds & Bryant, 2001; Zhang et al., 2015b), while studies of wild birds have shown conflicting results (Nilsson, 2002; Nilsson & Nilsson, 2016; Tinbergen & Wiersma, 2003; Visser et al., 2019).



Ryn Sullivan

Unresolved questions

Metabolic rate has been contemplated and studied for over two centuries, leading to a wealth of theory and knowledge of the various potential sources and ecological significance of variation in metabolic rate among species and populations. Due to the relatively complex determination and variable nature of metabolic rate, there continues to be unanswered questions about how and why variation is maintained within populations. We lack knowledge of which environmental and physiological factors limit aerobic capacity (MMR , M_{sum}) and sustainable metabolic rate ($SusMR$) in different contexts. Little is known about how patterns may be shaped by the possible interrelatedness and constraints within and among minimal, maximal, and sustained metabolic rates. Comparatively little is known to what degree interindividual differences in metabolic rates represent consistent individual strategies or flexible responses to the environment. This could have implications for long-term individual performance, particularly when fitness outcomes are expected to differ within the context of seasons and life-cycle stages.

General methodology

Study area

The field experiments were conducted around Stensoffa ecological field station in an area of about 60 square kilometers encircling Lake Krankesjön in southernmost Sweden (55°42'N, 13°28'E). Southern Sweden is characterized by a temperate climate. Historically, southern Sweden was dominated by broad-leaf deciduous forests interspersed with wetlands but has been converted over time to mostly agricultural land use. The field site is now comprised of grasslands that are grazed by cattle, with patches of secondary deciduous and planted coniferous forest. In this area, around 500 nest boxes have been monitored each breeding season since 1983. The nest boxes are constructed from wood, have an entrance hole (26 mm diameter) that is large enough for blue tits (*Cyanistes caeruleus*) and marsh tits (*Poecile palustris*), but too small for sympatric great tits (*Parus major*).



The road to Stensoffa ecological field station

Study species

Blue tits (*Cyanistes caeruleus*, Figure 5) are small, hole-nesting passerine birds that are widespread and common in much of continental Europe. They are partially migratory in the northern part of their range, but most adult birds stay in the breeding area and defend territories throughout the year (Smith, 1987). They readily nest in nestboxes, which makes them a convenient study species because nests can be easily monitored. They are relatively small birds, weighing around 11 g. They lay a clutch size of 8-15 eggs and have a nestling period of about 3 weeks (Nilsson, 2000). After nestlings hatch, both male and female parents feed their young with caterpillars or other invertebrates, which they bring to the nest. Blue tits were used in all field experiments, in **Papers I, II, and III** in this thesis.

Zebra finches (*Taeniopygia guttata*, Figure 5) are small (ca 14 g) social, colonial-nesting passerine birds that are widespread across Australia. Their social tendencies mean they are easily kept in groups in captivity, and they have become a model species for lab-based biological research. They are normally fed on a diet of seeds in captivity (Griffith et al., 2021). A captive population of zebra finches were kept in outdoor aviaries at Stensoffa ecological field station during my doctoral studies and were used in lab experiments in **Papers IV and V** in this thesis.



Figure 5. Species studied in this thesis. Left: zebra finches (*Taeniopygia guttata*, left; Pixabay) were used in **Papers IV and V**. Right: blue tits (*Cyanistes caeruleus*, right) were used in **Papers I, II, and III**.

Field methods

Nesting phenology and reproductive success

The nestbox population has been monitored each year since the long-term study was established in 1983. The mean laying date for the two tit species breeding in nestboxes in the study area is from mid to late April (Andreasson et al., 2023). Starting in April, nestboxes were checked for signs of nest-building and eggs. Birds lay one egg every 24 hours, and blue tits generally have a clutch of more than 7 eggs. Thus, to determine the date that the first egg was laid, each nestbox was visited once every 7 days, and laying date was calculated by subtracting the number of eggs from the date. One day before the predicted hatching date, the nest was checked each day for signs of hatching to record the precise hatching date, which was considered as day 0 for nestling age. On day 14, both parents were caught in the nestbox, and they were aged, sexed, ringed and measurements of their wing length, tarsus length and body mass were taken. Nestlings (Figure 6) were also ringed and measured on day 14, when they can be handled without risk of premature fledging.

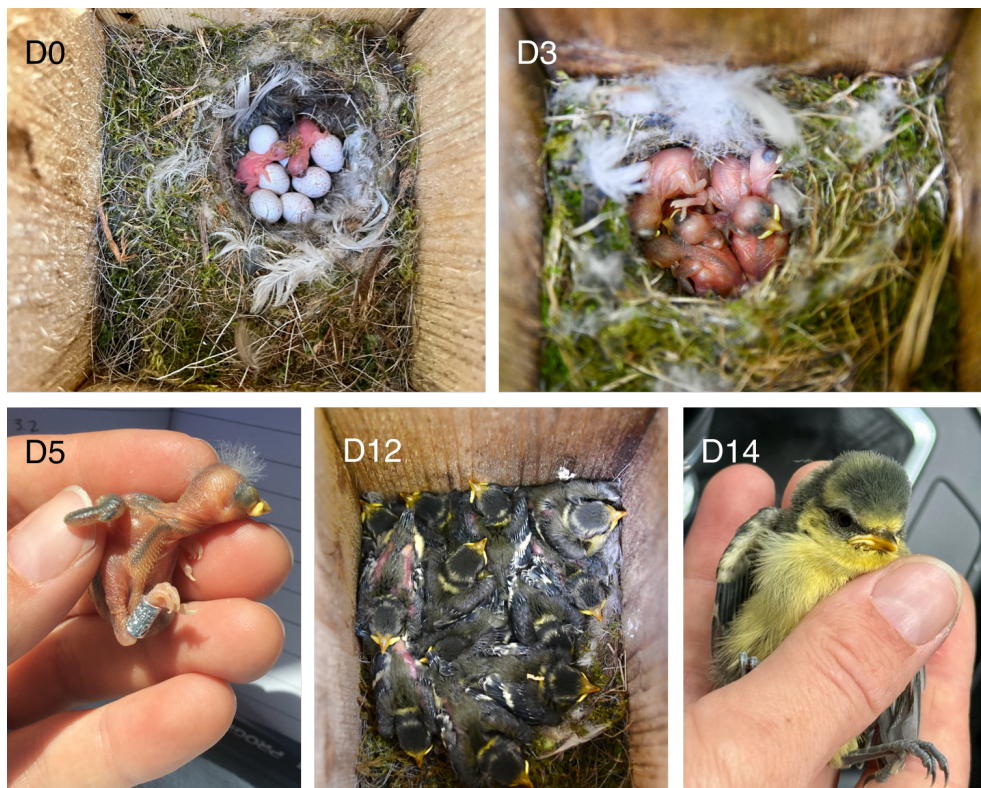


Figure 6. Blue tit nestlings at different ages (in days). Nestlings were ringed on day 14, or earlier if they were in a brood size manipulation experiment. Biometric measurements were taken on day 14.

Brood size manipulations

In **Papers I and III**, I was interested in the effect of parental workload on metabolic rates of both nestlings and parents. With the aim of influencing parental investment, I manipulated brood size by transferring nestlings from one nest to another, forming two experimental groups: reduced and enlarged broods. Nestlings were handled in the same way in a third, control group, but I did not remove or add nestlings from these nests. I moved nestlings rather than eggs to separate the effects of sibling competition or parental work rate from possible carryover effects of incubation (Monaghan & Nager, 1997). Brood size manipulations usually, but not always, influence parental effort, as parents generally increase feeding frequency when they have more mouths to feed (Nilsson, 2002; Nur, 1984; Visser et al., 2019), and feeding frequency has been found to be positively correlated with daily energy expenditure (Bryant, 1997; Nilsson, 2002; Visser et al., 2019). However, parents usually do not fully compensate for the increased brood size, and enlarged nests often end up with lighter and less-developed nestlings compared to control and reduced broods (Burness et al., 2000; Nilsson & Gårdmark, 2001; Nilsson & Nord, 2017; Nur, 1984).

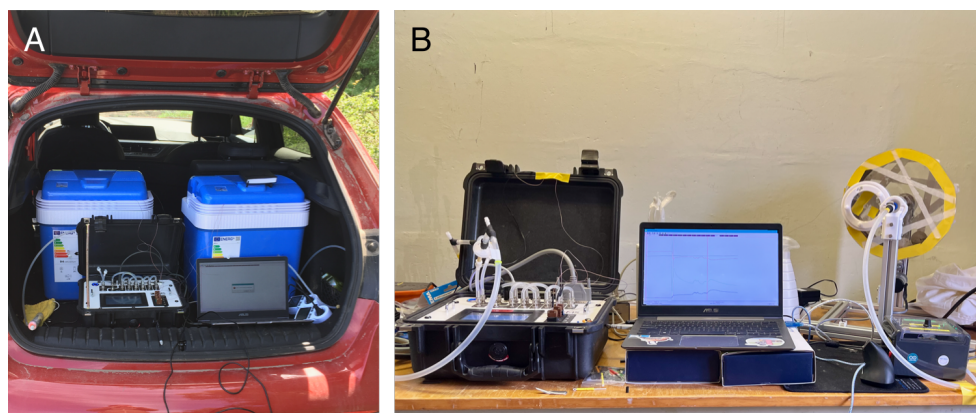


Figure 7. Field respirometry lab setup. A: Mobile lab in the trunk of the car with FMS and climate chambers used in **Paper I**. B: Lab setup at Stensoffa field station with FMS and hop-flutter wheel, used in **Paper III**.

Lab methods

Animal housing facility

Zebra finches were transported from their outdoor holding aviaries at Stensoffa to an indoor, temperature and humidity-controlled animal housing facility at Lund University with a 12-hour light-dark cycle (07:00 to 19:00) at least 2 weeks before metabolic rate was measured. They were kept in one room with six cages (each 120

× 84 × 100 cm, l x w x h) with four to six birds in each cage. Birds were provided with food and water *ad libitum* (tropical finch mix with vitamins and mineral supplements), grit, cuttlebone and water for bathing.

Respirometry

I measured oxygen consumption to estimate metabolic rate, using flow-through respirometry (see Box 1 in *General Introduction*, Figure 7-8). Oxygen consumption and carbon dioxide production was measured by pulling or pushing air at a known rate into an airtight chamber with an animal enclosed inside. The gas flowing out of the chamber was then measured to determine the difference in concentration from the incurrent air. I used gas analyzers in various configurations to measure the fractional concentrations of O₂, CO₂, water vapor pressure (WVP), gas flow rate (FR), and barometric pressure (BP) simultaneously. The rate of oxygen consumption, expressed in ml min⁻¹ was then derived from the change in fractional concentrations of O₂ and CO₂ (Lighton, 2018) and converted to the energy equivalent expressed in Watts (Lighton et al., 1987).

Metabolic rates

BMR was measured throughout the night to ensure that birds were resting and in a post-absorptive state when the minimum metabolic rate was recorded. Birds were placed in the respirometry chamber inside of a climate cabinet at dusk and were kept in the dark and at a constant temperature within the thermoneutral zone for each species (zebra finch: 35°C; blue tit: 25°C) and were removed at sunrise. Data recordings were taken each hour, and the minimum metabolic rate of all recordings was taken as BMR.

I used a sliding cold exposure experiment to elicit M_{sum}, where the ambient temperature is lowered incrementally at regular intervals in a helox (79 % helium, 21% oxygen) environment until metabolic rate reached a maximal level (Swanson et al., 1996). Helox allows for M_{sum} to be reached at higher air temperatures due to its higher thermal conductivity, which causes a higher rate of heat loss from the bird to the environment (Thomas et al., 1998). This is more practical than using extremely low temperatures and reduces the risk of freezing cold injury to the bird. The test was terminated when metabolic rate started to steadily decrease, indicating that M_{sum} had been reached. Cold endurance was recorded as the total amount of time the test lasted.

I used a hop-flutter wheel to induce birds to exercise continuously until exhaustion (Chappell et al., 1996). The wheel was constructed as a cylindrical, airtight plexiglass cylinder with an air inlet and outlet at the points of rotation. The wheel was connected to a motor, which controlled the speed of the wheel. Three ping-pong balls were placed at the bottom of the wheel which stayed at the bottom when the wheel was rotating. The bird was placed into the wheel and allowed a period of acclimation in dimmed lighting or with a sheet covering the wheel. When the test

began, the wheel started to turn at a low speed, and the bird was induced to hop and flutter its wings to maintain its position in the wheel. The test continued until the bird could no longer maintain its position in the wheel. Endurance was measured as the time to exhaustion. After the test, birds showed signs of exhaustion such as panting, closing their eyes, and resting their belly on the floor of the wheel. Birds recovered after several minutes of rest.

Body temperature

Zebra finches were implanted intraperitoneally with a temperature sensitive PIT tags ($L \times W$: 12×2.1 mm, LifeChip bio-thermo, Destron Fearing, DFW Airport, TX USA) weighing 0.26 g, 1 – 2% of the birds' body mass. Body temperature was recorded continuously during metabolic measurements or in the animal housing facility using HPR Plus data loggers and antennae, Biomark, Boise, ID, USA).

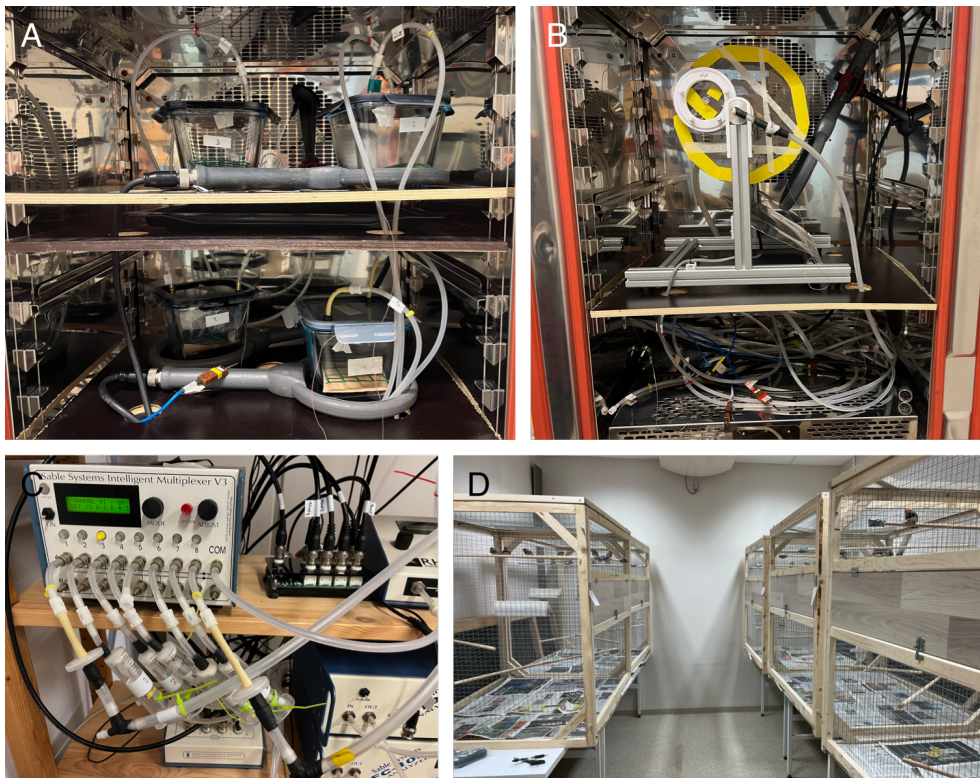


Figure 8. A: Respirometry chambers for measuring BMR and M_{sum} inside of a climate cabinet. B: Hop-flutter wheel for measuring MMR inside of a climate cabinet. C: Lab equipment used for respirometry measurements in **Paper V**. D: Zebra finch housing at Lund University

Contributions to the field

Brood size may affect metabolic rate in early life

In **Paper I**, I found that the development of a metabolic response to cooling tended to proceed at a faster rate when brood size was experimentally reduced, compared to when broods were experimentally enlarged (Figure 9). As I did not find a difference in growth rate or nestling mass between enlarged and reduced broods, individuals in reduced broods could have prioritized the development of thermogenic tissues at the expense of overall growth. However, body mass was a strong predictor of metabolic rate and the metabolic response to cooling overall, especially as nestlings grew older. These results strengthen previous evidence (Andreasson et al., 2016) that brood size influences the ontogeny of endothermy in altricial nestlings. I did not measure the metabolic response of nestlings after day 8, so more research is needed to determine if these differences were permanent or reversible, and if this could affect individuals into adulthood. Previous research has shown that the environment during incubation can affect adult metabolic rate until at least the first winter in wild great tits (Broggi et al., 2022). The effects of environmental conditions during the

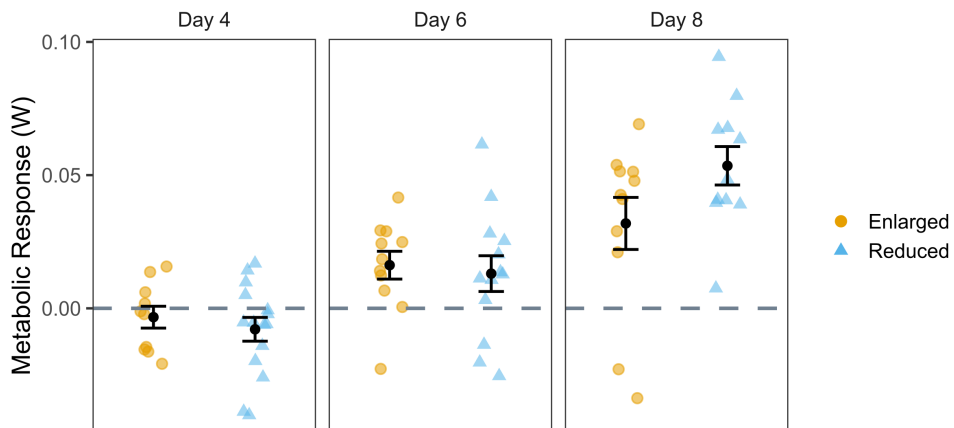


Figure 9. Blue tit nestlings' metabolic response to a cold challenge (measured as the difference from a baseline at nest temperature) at 4, 6, and 8 days after hatching. Adapted from Figure 5 in **Paper I**.

nestlings period, however, may not last after reaching maturity (Persson et al., 2024). Nonetheless, I show that the environment experienced by nestlings during early development may affect their developmental trajectory of incipient endothermy and metabolic rate in the nest. If the environment during development permanently affects metabolic rates, this could have implications for phenotypic matching or mismatching with the environment in adulthood (Nord & Giroud, 2020). Flexibility, on the other hand may buffer the effects of environmental fluctuations during development.

Evidence for phenotypic correlations between three standardized measures of metabolic rate

In Papers II and IV, I found evidence for phenotypic correlations between minimal and maximal metabolic rates, which were attributable to variation in body mass. Interestingly, I found nearly the same result in both free-living blue tits and in captive zebra finches even though I assume they differed markedly in the stability of environmental conditions and resource availability. BMR was significantly, positively correlated with MMR and Msum, but not when accounting for variation in body mass. Given that BMR, Msum, and MMR have all been found to scale allometrically with body mass (McKechnie & Swanson, 2010) the correlations between metabolic rates found here could be explained by size differences between individuals. This is similar to patterns found in other passerine species where correlations between minimal and maximal metabolic rates were explained by variation in body mass (Swanson et al., 2012), or were decoupled in winter (Petit et al., 2013). However, a larger body mass may not only reflect a proportional upscaling of body size, but also the different organs and muscles that contribute disproportionately to BMR, MMR or Msum, respectively (Daan et al., 1990) or fat mass, which has low metabolic activity (Scott & Evans, 1992). One could also speculate that variation in mass could be related to energy management strategies, for example if individuals with high metabolic rates could be dominant to others and maintain a comparatively higher body condition in winter. Thus, it may not be straightforward to determine the relative importance of mass for individual metabolic phenotypes, and how co-variation of mass with metabolic rate should be interpreted within a population. Ultimately, if minimal and maximal metabolic rates are phenotypically correlated, individuals with higher metabolic rates as a whole may use more energy at rest to maintain their metabolic machinery, increasing the overall cost of living. There may also be a connection between maximal metabolic rates and FMR via effects of cold or exercise acclimation (Zhang et al., 2015b). Without information about FMR, however, these notions are only speculative, as BMR, FMR and maximal metabolic rates could also vary independently (Barceló et al., 2017).

Although minimal and maximal absolute metabolic rates co-varied, there was considerable residual variation, but more so in blue tits ($R^2 = 0.08 - 0.09$) than in zebra finches ($R^2 = 0.27 - 0.28$), meaning that whole minimal and maximal metabolic rates were not tightly correlated and can also vary independently. This aligns with evidence for differences in mechanistic underpinnings of minimal and maximal MRs, as BMR is mostly attributed to the digestive organs while MMR and M_{sum} are related to skeletal muscle mass and systems related to oxygen transport. In line with this, the two maximal metabolic rates, M_{sum} and MMR, were significantly, positively correlated even when accounting for variation in body mass, meaning that individuals with a high MMR for their body mass also had a high residual M_{sum} . This was true in both blue tits and zebra finches, despite differences in the stability of environmental conditions between these study animals. The mass-independence of this relationship could be explained by mitochondrial function and the relatively high metabolic intensity of muscles by weight, both of which may contribute to M_{sum} and MMR (Norin & Metcalfe, 2019) independently of body mass (Barceló et al., 2017). In **Paper IV**, I investigated relationships between body temperature and metabolic rates. I found that body temperature measured throughout the day in undisturbed, captive male zebra finches seems to vary independently of both raw and mass-independent BMR and MMR, which suggests that individuals vary in their rate of heat dissipation. However, median body temperature was related to the degree of hyperthermia during exercise and may have also been positively related to M_{sum} and cold tolerance.

The theory that variation in life-histories co-vary with metabolic rate along a “slow” – “fast” continuum has primarily been applied to higher level taxonomic comparisons, on the level of species, families and orders. However, recent evidence has shown that life histories can co-evolve with metabolic rate according to pace-of-life syndromes within species and between populations, suggesting that microevolutionary processes can mirror macroevolutionary patterns in common garden experiments (Auer et al., 2018; Pettersen et al., 2016). My results provide tentative support for phenotypic correlations which could constrain co-variation in different aspects of metabolic rates, body mass, and body temperature representing physiological syndromes along a slow – fast continuum.

Interindividual differences in maximum metabolic rate remain consistent across seasons

In this thesis, I present evidence that MMR is a repeatable and flexible trait in two passerine species. This was true across time intervals ranging from days to months, and in both wild and captive birds (Figure 10). In **Paper II**, MMR in male blue tits showed seasonal flexibility similar to what has been found in BMR and M_{sum} in

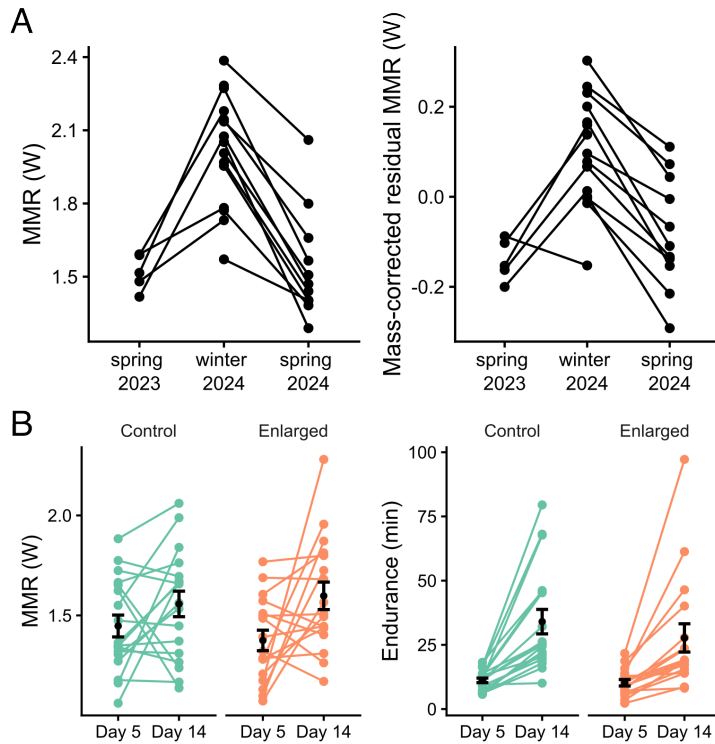


Figure 10. A: Maximum exercise-induced metabolic rate (MMR, left) and mass-corrected residual MMR (right) of free-living blue tits measured in spring 2023, winter 2024, and spring 2024. Lines connect individuals. Adapted from Figure 3 in **Paper II**. B: Effect of brood size manipulation and nestling age on exercise capacity of male blue tits on the day of brood size manipulation (day 5) and 9 days after (day 14). Each individual bird is represented by one line. Black points and error bars show group means and s.e.m. Adapted from Figure 2 in **Paper III**.

other free-living temperate songbirds. I found that MMR was higher in winter than in summer, which aligns with evidence that MMR increases with cold-acclimation, a phenomenon that has previously described as “cross-training” (Zhang et al., 2015b). That MMR did not reach as high in the breeding season compared to winter was unexpected, as the breeding season is predicted to be a period of high energy expenditure due to parental investment. One possible explanation for this is that MMR could be constrained in the spring in ways that it would not be in winter, for instance due to heat dissipation constraints or reductions in body mass. Alternatively, a higher aerobic capacity may be more important for

thermoregulation in winter than for nestling provisioning in spring, assuming that these are the main priorities in winter and spring, respectively, evidence by FMR being the highest in winter in small bird resident in cold climates (Swanson, 2010). I found high repeatability of both raw MMR and residual MMR between seasons, suggesting that individuals have flexible metabolic phenotypes, but remain

consistent relative to one another, at least within a year. This supports the hypothesis that individuals vary in metabolic strategies, in alignment with pace of life syndromes (Nilsson & Nilsson, 2016). However, repeatability generally declines if measured over longer time periods (White et al., 2013) could vary among years or seasons, suggesting that patterns could be driven by environmental conditions rather than individual strategies (Cortés et al., 2015).

In **Paper III**, I measured repeatability and flexibility of MMR in male blue tits within breeding season, both early and late in the nestling provisioning period and with manipulated parental workload via brood size manipulations. Blue tits showed short-term flexibility of MMR over a period of 9 days, but in this case, MMR was not individually repeatable (Figure 10). Thus, individuals showed varied metabolic responses to the progression of nestling age and differences in brood size. Endurance, however, increased and was highly repeatable during the nestling period. One potential explanation is that individuals may respond more consistently in endurance than in metabolic capacity to changes in parental effort. This would be plausible if endurance is a better indicator of work performed in the preceding days at sub-maximal levels (SusMR), or if MMR is more constrained than endurance during the spring and summer (Peterson et al., 1990). For example, in elite human athletes, MMR normally plateaus whereas endurance can continue to improve over an athlete's career, due to changes in lactate threshold and efficiency of energy conversion to power output (Płoszczyca et al., 2019).

In **Paper IV**, MMR (2 measurements on consecutive days) and body temperature (over two weeks) were repeatable in captive zebra finches in stable, indoor housing. This strengthens evidence that MMR and body temperature are individually consistent individual traits in this particular set of conditions. Individuals also showed flexibility in body temperature during the day and the median and maximum daytime body temperature (T_b) were positively correlated. Individuals with a higher median daytime T_b also reach a higher T_b when they were exercising. In **Paper V**, I found that MMR decreased and T_b increased in response to increased air temperature during exercise. MMR and T_b were also repeatable with changing air temperatures, pointing to individual intercepts of reaction norms. This points to there being consistent individual differences reflecting a pattern of more general constraints at the population level.

Evidence for physiological, ecological, and environmental determinants of performance

In **Paper III**, I present evidence that MMR is flexible within a breeding season at the population level, potentially in response to the interactive effects of parental workload and individual experience, in wild male blue tits. I found that exercise

performance, measured as MMR and endurance, increased with nestling age. If nestling provisioning involves natural behaviours that are analogous experimental flight training in birds (Zhang et al., 2015b), these changes in exercise capacity could reflect a training or acclimation effect of increased workload. Further supporting my hypothesis, I found an age-dependent effect of experimentally enlarged brood size (i.e., experimentally increased workload) on MMR and MR measured immediately before exercise, but not endurance. First-year breeders with enlarged broods showed an increase in MMR and pre-exercise MR, while older

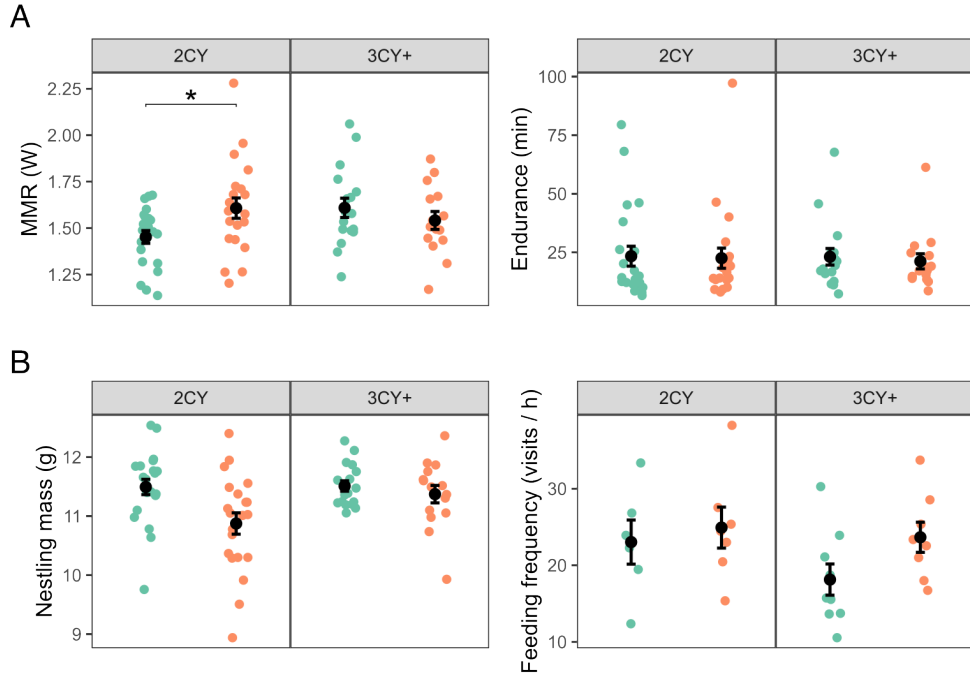


Figure 11. Effect of brood size manipulation and age on (A) exercise capacity and (B) measures of performance in male blue tits. Maximum metabolic rate (MMR), endurance, nestling mass and feeding frequency were measured on day 14 after chicks hatched, 9 days after brood size manipulation (control or enlarged). Birds were grouped by age as 2nd calendar year (2CY) or 3rd or greater calendar year (3CY+). Black points and error bars represent means and standard error. Asterisks indicate significance of pairwise comparisons of emmeans using the Tukey method (* $P < 0.05$, ** $P < 0.01$). Adapted from Figure 3 and Figure 5 in **Paper III**.

birds did not. However, feeding frequency did not increase significantly in birds with enlarged broods, and nestlings were lighter in enlarged broods. Thus, individuals seem to differ in their response to increased workload exemplified by the lack of repeatability (Figure 11). Therefore, the links between exercise capacity, parental investment, and reproductive success are less clear, and could involve other factors such as age, experience, and access to resources.

In **Paper IV**, I investigated the relationship between body temperature, thermoregulation, and aerobic performance in captive male zebra finches. Body temperature measured during the day was positively related to M_{sum} , cold endurance and hyperthermia during exercise, but was not related to MMR or endurance. In **Paper V**, I expand on this to show that the ceiling for aerobic capacity can also be set by environmental conditions. In captive, male zebra finches, MMR was limited at air temperatures well within the thermoneutral zone, while T_b and evaporative water loss increased to near maximal levels (Figure 12). This could indicate that even mild air temperatures constrain energy expenditure during intense activity. If these effects

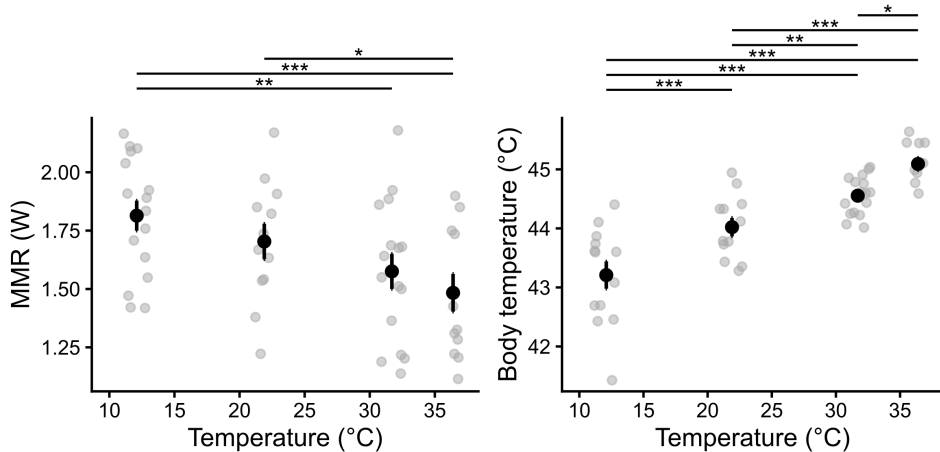


Figure 12. Effect of air temperature on physiological parameters during exercise in captive Zebra Finches. Raw data for individual is shown as gray points and mean $\pm$ se are shown as black points and error bars. Significant pairwise comparisons of estimated marginal means from a linear mixed model with cage and ID included as random factors are shown. Adapted from Figure 2 in **Paper V**.

are generalizable to wild birds in natural conditions, this could have broad ecological implications for free-living birds. For example, if MMR and maximum metabolic scope are associated with breeding success in the warm spring and summer months, thermoregulatory constraints during activity could lead to reduced fitness due to missed opportunity costs in conditions that are not conventionally expected to cause heat stress in resting birds.

Biophysical models can be used to predict the metabolic rate required to remain in energy and mass balance depending on environmental conditions. In **Paper VI**, I discuss the applicability of a relatively recent thermoregulatory polygon model, introduced by Rezende and Bacigalupe (2015), to active birds based on empirical data collected in **Paper V**. I compare the assumptions of the polygon model to the zebra finch data and discuss its potential strengths and weaknesses when applied to

birds in real-world conditions. In zebra finches, the relatively high rates of evaporative water loss during exercise at all temperatures, and the prevalence of hyperthermia with increasing air temperature, suggest that a polygon model including the possibility for hyperthermia and evaporative heat loss may be more representative of the thermoregulatory capacities of active birds than a model assuming a constant body temperature and restricted to dry heat loss.

Metabolic rates show weak but consistent associations with predictors of fitness

In **Paper II**, I develop a conceptual framework for how metabolic rates could be expected to relate to fitness in different contexts (Figure 13). Individuals could consistently vary in metabolic strategies (Figure 13A), or individuals could vary in how flexible they are, (Figure 13B). This will affect how selection could act on metabolic rates in different contexts. If individuals are consistent, antagonistic selection in different contexts could maintain variation in metabolic rates (Figure 13 C). Overall, I found that metabolic rates were weakly but consistently associated with fitness-related traits in a wild population of blue tits. Male birds with higher MMR in spring were more likely to return and breed in the area the following summer. On the other hand, high metabolic rates were consistently negatively associated with clutch size (MMR) and nestling mass (MMR, BMR and M_{sum}) and positively associated with laying date (M_{sum} and BMR). A later laying date is generally associated with lower reproductive success in the study population, while a lower clutch size leads to fewer offspring and lighter nestlings generally have lower chances of recruitment. These results suggest that birds with higher metabolic rates in winter may have lower reproductive success in spring, while birds with higher MMR were more likely to be re-sighted, which could indicate a higher probability of survival or lower likelihood of dispersal. Previous studies in the same study system have found that apparent survival probability was positively related to BMR in a harsh winter and negatively related in a mild winter (Nilsson & Nilsson, 2016). Taken together, it is plausible that metabolic rate is associated with fitness antagonistically in different contexts, in alignment with the scenario in Figure 13 D. It is plausible that both of these strategies could be beneficial at different times in the context of an environment where conditions fluctuate between years. However, they do not necessarily align with predictions from pace of life theory, where one would expect a “fast” strategy to be beneficial for reproductive output and a “slow” strategy to benefit survival. Thus, it may be important to consider how trade-offs may function within the specific ecological and environmental context of a species or population.

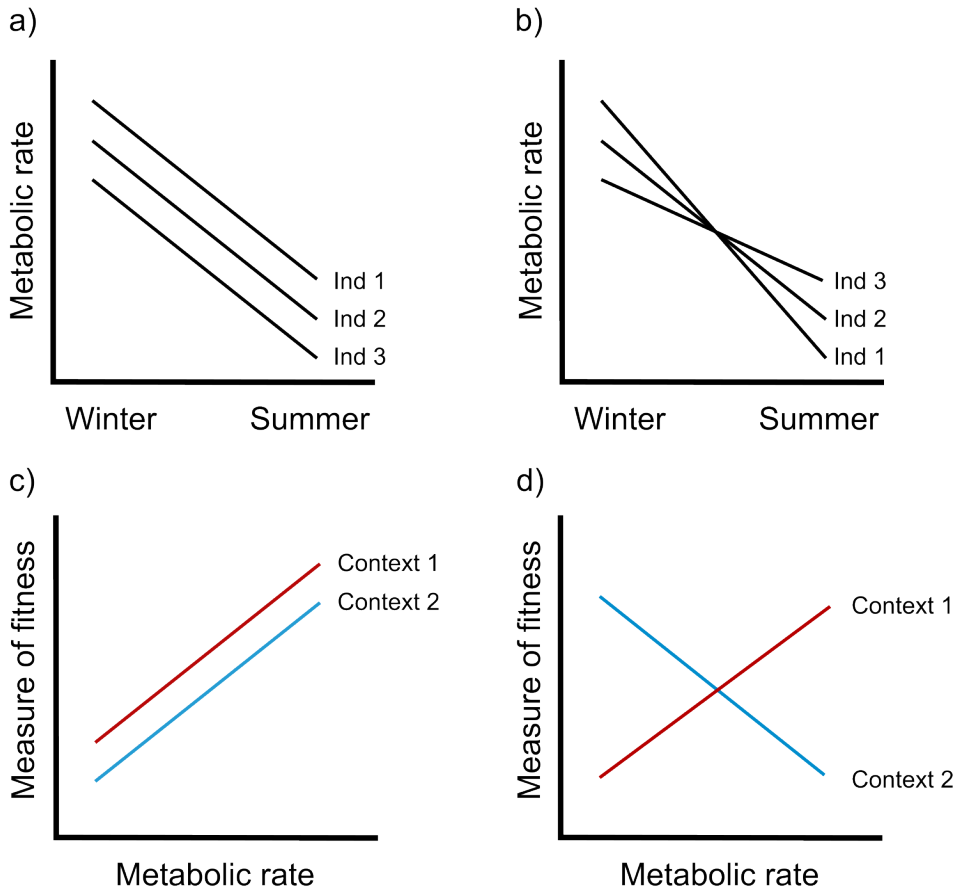


Figure 13. Panels a and b: Hypotheses for how individual variation in reaction norms may vary in the intercept only (a) or in both intercept and slope (b) between seasons. Panels c and d: metabolic rates can be predicted to be related to fitness synergistically (c) or antagonistically (d) depending on the context of season, severity of winter conditions or life stage (breeding or non-breeding). The expected relationship can also differ depending on the measure of fitness (i.e., survival or reproduction), and the standardized measure of metabolic rate (i.e., BMR, M_{sum} , or MMR) used in associations. Adapted from Figure 1 in **Paper II**.

Conclusions and future directions

Evidence for co-variation in metabolic rates and physiological syndromes

In this thesis, I found evidence for co-variation between minimal and maximal metabolic rates. This was true in both free-living birds and captive birds, showing that phenotypic correlations persist in both unpredictable and predictable environments. Similarly to other studies, the correlation between minimal (BMR) and maximal (MMR, M_{sum}) metabolic rates was attributable to co-variation in body mass. Whether this variation reflects differences in structural body size, a proportional increase in metabolically important organs and muscles, or differences in body condition is more difficult to determine. I argue that variation in raw organismal metabolic rate within a population is ecologically and physiologically relevant, because total energy turnover is what ultimately determines both the energy intake needs for self-maintenance and the upper limits to metabolic rate, both of which could conceivably have consequences for fitness. On the other hand, metabolic intensity, which could be inferred from residual variation in metabolic rates after correcting for body mass, could be informative in that it could reflect differences in body composition or metabolic adaptations that could also reflect performance. How different components of body mass contribute to intraindividual and intrapopulation variation in metabolic rate is an area that could be developed with future research using non-invasive methods such as quantitative magnetic resonance (QMR). For instance, knowledge of how the mass of different organs and muscles scale with metabolic rate, or the degree to which metabolic intensity can vary independently of body mass within and among individuals would contribute to our understanding of traits that could potentially be integrated within a physiological syndrome.

Repeatable yet flexible individual variation – evidence for consistent metabolic strategies

At the population level, BMR and M_{sum} increase during winter and decrease during summer in small resident birds in seasonal climates. However, the individual patterns of flexibility and whether they are consistent or vary in magnitude are not as well-understood. I found that MMR is repeatable among seasons, adding to evidence that individuals can, in some cases, show flexible yet consistent metabolic strategies (Broggi et al., 2009; Cortés et al., 2015; Petit & Vézina, 2014b). This phenotypic flexibility was most likely a response to seasonal variation in air

temperature (Swanson, 2010), as aerobic capacity for exercise (MMR) was correlated with the cold-induced metabolic rate (M_{sum}) in wild blue tits. Within the breeding season, however, individuals varied in their response to an increase in workload. This suggests that metabolic flexibility in response to seasonal environmental fluctuations may be more consistent among individuals than metabolic flexibility in response to changing demands for parental investment. Individuals could potentially buffer the demand for nestling provisioning by modulating their behavioral response, foraging efficiency, or the feeding habits of the co-parent. However, it is difficult to draw conclusions about the links between nestling demand, parental effort, exercise capacity, and ultimately, reproductive success without knowing the actual amount of work that was performed. Feeding frequency is an imperfect measure of parental effort, because individuals can differ in foraging trip duration, distance and load size. In the future, it would be ideal to measure energy expenditure more precisely throughout the nestling period to determine if there is a true training effect on metabolic capacity, and if this can be linked to reproductive success. This could be done in the future by tracking activity with accelerometers.

Consequences of variation in metabolic strategies - potential implications for fitness and natural selection?

While I did not find strong evidence that metabolic rates are associated with apparent survival or reproductive success, there were some limitations of the study, including small sample sizes and taking measurements late in winter, which may have affected the results. A previous study in the same system has found evidence for context-dependent selection for BMR depending on the severity of conditions (Nilsson & Nilsson, 2016). My results suggest that MMR could be positively related to apparent survival in male blue tits and that metabolic rates could be negatively associated with reproductive success in both males and females, which could be mediated by a delayed breeding phenology in birds with higher metabolic rates. In synthesizing the results of this thesis, I propose a framework of context-dependent selection leading to new hypotheses for why high individual variation in metabolic rates persist in populations. In this framework, individuals with a “slow” strategy are favored in warm winters and during the breeding season in terms of both survival and reproductive success whereas individuals with a “fast” strategy are favored in cold winters. If individuals show consistent metabolic strategies across seasons (i.e., MMR in **Paper II**), this could result in the direction of selection to switch depending on the context, resulting in antagonistic selection for metabolic rates. This could lead to selection for lower metabolic rates as winters become milder with climate change, or the maintenance of variation if climate change leads to greater unpredictability of conditions and more frequent of extreme weather events. However, if individuals vary in flexibility (Cortés et al., 2015) or show low variation in both slopes and intercepts of reaction norms (Petit & Vézina, 2014b), they may

be able to mitigate changing selection pressures through reversible phenotypic flexibility.

Ecological implications for environmental limits to aerobic capacity and scope

Knowledge of thermal tolerance limits of animals is important to understand how populations might respond to climate change. However, most of our knowledge of thermal tolerance is pertains to resting animals. Few studies have investigated thermoregulatory constraints in active birds, and this thesis provides novel insights into how birds may respond to heat stress during exercise. I found that the evaporative cooling capacity of active birds is insufficient to offset high metabolic heat production, leading to lower thermal tolerance in active birds than in resting birds. This could provide a physiological explanation for recent evidence showing that increased temperature constrains parental investment in free-living birds.

According to the “context-dependence” hypothesis, if there are limits to energy acquisition or expenditure during the breeding season, one might expect to see a negative association between BMR and fitness (Burton et al., 2011). Previously, life-history theory has primarily considered energy limitation as constraints to energy supply, either set by food availability, assimilation efficiency, or aerobic capacity (Speakman & Król, 2010). The work in this thesis has shown that MMR can also be limited by the maximum capacity for heat dissipation during intense exercise, even in mild temperatures, in alignment with the heat dissipation limit (HDL) theory (**Paper V**). Heat dissipation constraints to reproductive effort have also been shown experimentally in free-living birds (Nord & Nilsson, 2019; Tapper et al., 2020b) meaning that SusMR might be constrained by high temperatures during the breeding season. The mechanisms for upper limits to metabolic rates may shift from constraints to energy supply (i.e. food availability or aerobic capacity) to heat dissipation constraints depending on environmental conditions. Thus, higher metabolic rates, assuming they reflect overall capacity for sustained exercise, might be favored only when temperatures are cooler during the breeding season and when food is abundant. The limits to MMR and SusMR in different contexts could be investigated experimentally in future studies by manipulating food availability, workload, and heat dissipation to determine if these factors interact to determine how metabolic rates are associated with reproductive success in different contexts.

In conclusion, this thesis advances our understanding of phenotypic correlations, flexibility, and repeatability of metabolic rates, and the context-dependence of their upper limits and links to fitness. However, this thesis only scratches the surface of understanding how metabolic rates are determined and how they might respond to selection with rising global temperatures. A logical next step would be to determine how environmental conditions affect aerobic capacity and scope in free-living birds. Biophysical models offer the potential to generate predictions for how environmental temperature might constrain activity, and thus reproductive success, in breeding birds. These predictions could be compared with real-world

physiological data to determine how these models perform when predicting thermoregulatory responses to heat during periods of high activity. Simultaneous measurement of activity and body temperature have recently become possible due to the miniaturization of accelerometers and body temperature loggers. If used during breeding, these data could be used to connect thermoregulatory constraints during activity with reproductive success of individuals. This way, missed opportunities could be quantified as predicted reductions in the scope for activity, and associated reductions in reproductive success, as a function of environmental temperature.

More work is needed to determine the genetic, environmental, physiological and ecological mechanisms underlying these patterns. Previous work in birds shows that RMR is phenotypically and genetically correlated with body mass (Nilsson et al., 2009). Future studies involving long-term and quantitative genetic approaches, could distinguish between plastic and genetic responses, to draw conclusions about if metabolic traits can evolve independently or correlatively and if they co-evolve with life-history traits in birds. Life history theory could be further integrated with knowledge of heat dissipation constraints to generate new hypotheses for how environmental conditions may affect energy allocation trade-offs. This will expand on the contributions from this thesis and will be informative regarding the ecological significance of metabolic rates and how they might relate to the pace of life in the ever-changing context of the environment.



Stensoffa (stone sofa)



The Blue tit



The Zebra finch

Elsie Xiong
2026 August and

Illustration by Elsie (Ye) Xiong

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