Temperature-dependent ontogeny of bird thermoregulation and growth

Persson, Elin

2026

Document Version:
Publisher's PDF, also known as Version of record

Link to publication

Citation for published version (APA):
Persson, E. (2026). *Temperature-dependent ontogeny of bird thermoregulation and growth*. Lund University.

Total number of authors:
1

LUND UNIVERSITY

PO Box 117
221 00 Lund
+46 46-222 00 00

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ELIN PERSSON
DEPT. OF BIOLOGY | FACULTY OF SCIENCE | LUND UNIVERSITY

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Temperature-dependent ontogeny of bird thermoregulation and growth

Elin Persson

DOCTORAL DISSERTATION

Doctoral dissertation for the degree of Doctor of Philosophy (PhD) at the Faculty of Science at Lund University to be publicly defended on the 5th of June at 09.00 in the Blue Hall, Department of Biology, Ecology building, Kontaktvägen 10, Lund

Faculty opponent
Prof. Cameron Ghalambor

NTNU - Norwegian University of Science and Technology, Trondheim, Norway

Organization: LUND UNIVERSITY

Document name: Doctoral dissertation **Date of issue:** 2026-06-05

Author(s): Elin Persson

Title and subtitle: Temperature-dependent ontogeny of bird thermoregulation and growth

Abstract:

This thesis investigates the ontogeny of thermoregulation and growth in birds, to improve the understanding of how prevailing environmental temperature affects physiology and morphology, and to examine whether body size influences thermoregulation. My focus has been on temperature effects emerging after hatching, which are poorly understood compared to effects of variation in embryonic developmental temperature. In addition, there is limited empirical evidence for how morphology actually influences thermoregulatory capacity, despite such links being a popular explanation for extant size declines in birds.

First, I studied short- and long-term effects of cold or warm post-hatch developmental temperatures on thermoregulatory traits (metabolic rate, evaporative water loss, and cold- and heat tolerance; Papers I and II). The results showed that birds that grew up in high developmental temperatures had lower metabolic heat production but increased evaporative water loss, rendering them better able to tolerate both submaximal and maximal warm temperatures. Cold developmental temperatures, on the other hand, increased the cold tolerance limit and maximal cold-induced metabolic rate, but did not alter thermoregulation at submaximal temperatures. When the birds were measured again after a period without thermal challenges, no lasting effects were observed. In the second part of the thesis, I investigated how body size affected thermoregulation (Papers III and IV). I found that body size had limited effects on the thermoregulatory capacity, such that only large deviations in body mass and appendage length exceeding allometric expectations altered patterns of heat loss. Lastly, I tested theory arising from the captive studies in nature, where animals may struggle more to balance the costs of thermal challenges on account of resource limitations. Specifically, I investigated whether experimentally increased nest temperatures would limit growth and alter thermoregulatory responses in blue tits nestlings (Paper V). The results showed that high temperature during postnatal development caused a trade-off between thermoregulation and growth. Nestlings in heated nests incurred higher body temperature and decreased metabolic heat production as a compensatory response. However, this compensation was only partial, because body mass decreased in heated nests and more so the higher the nestling body temperature.

Taken together, this thesis shows that the effects of post-hatch developmental temperature on thermoregulatory traits may be costly in terms of growth and water balance but that they reflect phenotypic flexibility. In addition, decreasing body size has negligible effects on thermoregulation overall, but it may be meaningful under certain circumstances and for birds at the extreme ends of size distributions. While my work suggests that there might be potential to buffer effects of post-hatch heat exposure, birds developing under such conditions could still be maladapted if reversal of effects is slow, or if inheritance of thermoregulatory competence, leads to mismatches between phenotype and environment

Key words: bird, development, thermoregulation, growth, heat tolerance, cold tolerance, metabolic rate, evaporative cooling, extreme weather event, conservation physiology, climate change, life history

Language: English **Number of pages**: 66

ISBN (print): 978-91-90202-02-9 **ISBN (electronic):** 978-91-90202-03-6

Signature Date 2026-04-12

Temperature-dependent ontogeny of bird thermoregulation and growth

Elin Persson

LUND
UNIVERSITY

Cover illustration by Fredrik Herrmann

Published by:
Department of Biology
Faculty of Science
Lund University

ISBN: 978-91-90202-02-9 (print)
ISBN: 978-91-90202-03-6 (electronic)

Printed in Sweden by Media-Tryck, Lund University,
Lund, 2026

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Abstract

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Populärvetenskaplig sammanfattning

Syftet med denna avhandling var att undersöka omgivningstemperaturens påverkan på utvecklingen av förmågan att kontrollera kroppstemperaturen och tillväxt hos fåglar, samt att undersöka hur kroppsstorleken påverkar kroppstemperaturreglering.

Alla levande organismer påverkas av omgivningstemperaturen. Konsekvenserna av snabba förändringar i temperatur, till exempel under värmeböljor och köldknäppar, är ofta allvarliga och kan påverka allt från kroppsvikt och reproduktionsförmåga till överlevnad. På många platser i världen är det faktiskt vanligt att vilda djur dör när de drabbas av värmeböljor och torka. Vid ökande eller minskande omgivningstemperaturer ökar risken för överhettning eller nedkylning och djuren måste anpassa sig genom att förändra sitt beteende eller sin fysiologi. För att minska risken för skador i kroppen, som minskar chansen att överleva, måste djur alltså kontrollera sin kroppstemperatur. I den här avhandlingen har jag därför undersökt vad det är som bestämmer hur bra ett djur blir på att reglera sin kroppstemperatur.

Tidigare studier har visat att fåglar från ägg som ruvats vid höga eller låga temperaturer är bättre på att hantera värme och kyla långt efter kläckningen. Under utvecklingen kan fåglars temperaturreglerande egenskaper alltså programmeras utifrån miljön. Vi vet däremot nästan ingenting om vad som händer när temperaturändringarna sker efter kläckning. Fåglar som växer upp under en värmebölja borde producera mindre värme och samtidigt bli bättre på att kyla ned sig jämfört med fåglar från milda förhållanden, och tvärt om hos fåglar anpassade till kalla temperaturer.

I den första delen av avhandlingen studerade jag kort- och långvariga effekter av att växa upp under kalla eller varma temperaturer i en kontrollerad laboratoriemiljö och om dessa effekter beror på permanent ”programmering” eller reversibla förändringar. Detta gjorde jag genom att mäta både hur mycket värme unga och vuxna japanska vaktlar producerar och hur bra de är på att kyla ner sig. Fåglar som växte upp i varma temperaturer minskade på värmeproduktionen och ökade avkylningsförmågan. Därför kunde fåglarna hantera både varma och maximalt tolererbara höga temperaturer bättre. De blev alltså blev bättre anpassade till sin miljö. Kalla temperaturer under utvecklingen ledde däremot bara till att fåglarna blev bättre anpassade till extremt låga temperaturer. Efter en period under milda förhållanden fanns inga effekter av uppväxttemperaturen kvar. Det tyder på att effekterna av uppväxtmiljön inte är stora nog för att påverka fåglarna som vuxna.

Flera studier visar att fåglar och andra djur blir mindre och mindre. Eftersom denna storleksminskning sammanfaller med global uppvärmning, har många forskare föreslagit att fåglar krymper eftersom små fåglar skulle klara sig bättre i ett varmare klimat. En liten fågel har nämligen större avkylningsyta i förhållande till sin kroppsvolym och skulle därför kunna öka sin värmeförlust. Eftersom det kan gynna värmeförlusten att vara liten, medan att vara stor kan underlätta att hålla värmen, skulle en minskning i kroppsstorlek ha fördelar i ett allt varmare klimat. I avhandlingens andra del undersökte jag därför om kroppsstorleken påverkar förmågan att producera eller avge värme genom att studera olika stora japanska vaktlar. Kroppsstorleken visade sig ha minimal betydelse för förmågan att reglera kroppstemperaturen. Skillnaderna i kroppsvikt måste vara extremt stora – större än vad som ryms inom den naturliga variationen i naturen – för att ge upphov till några meningsfulla förbättringar.

Till sist studerade jag också vilda fåglar. Det var nödvändigt, eftersom fåglar i fångenskap alltid lever ett enklare liv än fåglar i naturen, bland annat eftersom de har fri tillgång till mat och vatten. Därför är det möjligt att effekterna av varma och kalla temperaturer ser olika ut inomhus och i naturen. Till exempel är det möjligt att fågelungar som måste lägga en större del av näringen från maten på temperaturreglering inte kan växa lika snabbt. Jag testade därför om det finns kostnader av höga temperaturer under utvecklingen hos vilda blåmesar, genom att studera förhållandet mellan regleringen av kroppstemperatur och tillväxten. Jag gjorde ett experiment för att höja temperaturen i vissa holkar genom att hänga in små handvärmare inuti holken. Det höjde holktemperaturen under den första veckan efter kläckning med ungefär 8 grader. Blåmesungar i uppvärmda holkar hade högre kroppstemperatur än ungar från holkar med naturliga temperaturer – de blev överhettade – men de producerade också mindre värme, troligen för att undvika att bli ännu varmare. Trots det växte de värmda ungarna sämre än ungarna från naturliga holkar. Åtta dagar efter att uppvärmningen avslutats fanns inga effekter av den tidigare uppvärmningen kvar på varken förmågan att temperaturreglera eller på kroppsstorleken. De värmda ungarna kunde alltså växa i kapp den vikt de förlorade på grund av värmningen.

Sammanfattningsvis visar min avhandling att temperaturer under utvecklingen efter kläckning påverkar förmågan att producera värme och att kyla ned sig, men att effekterna är flexibla och beroende på i vilket sammanhang fåglarna utsätts för värme. Temperaturer under utvecklingen programmerar inte förmågan att reglera kroppstemperaturen permanent, så det verkar inte som att fåglar som växer upp under värmeböljor drabbas av långvariga konsekvenser som påverkar dem längre fram i livet. Däremot läggs näring på att reglera kroppstemperaturen som i annat fall hade kunnat användas för tillväxt. Det leder till att ungarna behöver kompensera för den förlorade vikten genom att växa snabbare, vilket i sin tur kan påverka överlevnaden efter att de lämnat boet. Därutöver, underlättar inte en mindre kroppsstorlek regleringen av kroppstemperatur särskilt mycket. Min avhandling ger alltså inte stöd till teorin om att fåglar krymper i takt med klimatförändringen för att bli bättre på att hantera höga temperaturer. Sammantaget tyder resultaten på att fåglar har en buffert för att hantera varierande omgivningstemperaturer. I framtida forskningsarbeten är det viktigt att undersöka mekanismerna bakom detta, men även om förmågan att temperaturreglera går i arv eftersom ungarna då kan påverkas negativt om omgivningstemperaturen har ändrat sig från den föräldrarna upplevde.

List of papers

I. **Persson, E.**, Cuív, C. Ó., & Nord, A. (2024). Thermoregulatory effects of growing up during a heatwave or a cold snap in Japanese quail. *Journal of Experimental Biology*, 227(2), jeb246876. doi: 10.1242/jeb.246876

II. **Persson, E.**, Correia, M., & Nord, A. (2026). Postnatal temperature triggers predictable thermoregulatory shifts without a trade-off between heat- and cold tolerance. *Journal of Experimental Biology*. in press. doi: 10.1242/jeb.251867

III. Tabh, J. K. R., **Persson, E.**, Correia, M., Cuív, C. Ó., Thoral, E., & Nord, A. (2025). Limited evidence that body size shrinking and shape-shifting alleviate thermoregulatory pressures in a warmer world. *Communications Biology*, 8(1), 707. doi: 10.1038/s42003-025-08131-7

IV. **Persson. E.**, Tabh, J. K. R., Svensson, J., & Nord, A. Allometric correlates of heat tolerance in birds: A test using quail breeds with extreme size variation. Manuscript.

V. **Persson, E.**, Nilsson, J-Å., & Nord, A., Experimental evidence for a trade-off between growth and thermoregulation in blue tit nestlings. *Submitted.*

Author contributions

I. Conceptualization: A.N.; Methodology: E.P., A.N.; Investigation: E.P., C.Ó.C., A.N.; Data curation: E.P., C.Ó.C.; Formal analysis: E.P., A.N., C.Ó.C; Visualization: E.P.; Validation: E.P., A.N.; Writing - original draft: E.P.; Writing - review & editing: all authors. Resources: A.N.; Supervision: A.N.; Project administration: A.N.; Funding acquisition: A.N.

II. Conceptualization: A.N., E.P.; Methodology: E.P., M.C., A.N.; Investigation: E.P., M.C.; Data curation: E.P.; Formal analysis: E.P., A.N.; Visualization: E.P.; Validation: E.P., A.N., M.C.; Writing - original draft: E.P.; Writing - review & editing: all authors. Resources: A.N.; Supervision: A.N.; Project administration: A.N.; Funding acquisition: A.N., E.P.

III. Conceptualization: J.K.R.T., E.P., A.N.; Methodology: E.P., C.Ó.C., A.N., J.K.R.T.; Investigation: E.P., C.Ó.C., M.C., E.T., J.K.R.T., A.N.; Data curation: J.K.R.T., E.P., C.Ó.C., M.C.; Formal analysis: J.K.R.T.; Visualization: J.K.R.T.; Validation: J.K.R.T., A.N.; Writing - original draft: J.K.R.T.; Writing - review & editing: all authors. Resources: A.N.; Supervision: A.N.; Project administration: A.N.; Funding acquisition: A.N., J.K.R.T., E.P.

IV. Conceptualization: E.P., J.K.R.T., A.N.; Methodology: E.P., A.N.; Investigation: E.P., J.S.; Data curation: E.P., J.K.R.T.; Formal analysis: E.P., A.N., J.K.R.T.; Visualization: E.P., J.K.R.T.; Validation: E.P., A.N., J.K.R.T.; Writing - original draft: E.P., A.N.; Writing - review & editing: all authors. Resources: A.N.; Supervision: A.N.; Project administration: A.N.; Funding acquisition: A.N., E.P., J.K.R.T.

V. Conceptualization: E.P., A.N., J.-Å.N.; Methodology: E.P., A.N., J.-Å.N.; Investigation: E.P., J.-Å.N.; Data curation: E.P.; Formal analysis: E.P.; Visualization: E.P.; Validation: E.P., A.N.; Writing - original draft: E.P.; Writing - review & editing: all authors. Resources: A.N.; Supervision: A.N.; Project administration: A.N.; Funding acquisition: A.N., J.-Å.N., E.P.

Elin Persson (E.P.), Andreas Nord (A.N.), Ciarán Ó Cuív (C.Ó.C.), Maria Correia (M.C.), Joshua K. R. Tabh (J.K.R.T.), Elisa Thoral (E.T.), Josefin Svensson (J.S.), Jan-Åke Nilsson (J-Å.N.).

Additional published papers not included in this thesis

I. Correia, M., Thoral, E**., Persson, E.**, Chamkha, I., Elmér, E., & Nord, A. (2025). Postnatal development in the cold render bird mitochondria more susceptible to heat stress. *Proceedings of the Royal Society B: Biological Sciences*, 292, 20251027. doi: 10.1098/rspb.2025.1027

II. Nord, A., **Persson, E.**, Tabh, J. K. R. and Thoral, E. (2024). Shrinking body size may not provide meaningful thermoregulatory benefits in a warmer world. *Nature Ecology and Evolution*, 8(3), 387-389. doi: 10.1038/s41559-023-02307-2

III. Thoral, E., García Díaz, C. C., **Persson, E.**, Chamkha, I., Elmer, E., Ruuskanen, S. and Nord, A. (2024). The relationship between mitochondrial respiration, resting metabolic rate and blood cell count in great tits. *Biology Open*, 13(3), bio060302. doi: 10.1242/bio.060302

IV. Thoral, E., García Díaz, C. C., **Persson, E.**, Chamkha, I., Elmer, E., Ruuskanen, S. and Nord, A. (2024). Response to 'Commentary on Thoral et al. (2024) The relationship between mitochondrial respiration, resting metabolic rate and blood cell count in great tits'. *Biology Open*, 13(11), 061771. doi: 10.1242/bio.061771

Glossary

Air temperature – The temperature of air, measured using a thermometer shielded from solar radiation and other sources of heat exchange

Body temperature – Temperature of an animal's core

Cold tolerance limit - The lowest air temperature at which a bird can maintain metabolic heat production

Developmental plasticity – Permanent changes of the phenotype due to changes in the developmental environment

Dry heat loss – Heat loss from convection, conduction and radiation

Ectotherm – An animal that regulate body temperature through external sources and behaviour

Endotherm – An animal that regulate body temperature by generating and dissipating heat through internal processes in combination with external processes

Environmental temperature – Effective thermal environment experienced by an animal, integrating convective, conductive and radiative heat fluxes

Evaporative cooling efficiency/capacity – The ability to dissipate heat through evaporation of water. *Efficiency* is temperature dependent, whereas *capacity* is the maximal ability. Defined as the ratio between **Evaporative heat loss** – the amount of heat that can be dissipated through evaporation – and metabolic heat production (below)

Evaporative water loss – The amount of water evaporated from cutaneous and respiratory evaporation measured through respirometry

Heat tolerance limit - The highest air temperature a bird can tolerate before incurring pathologically high body temperature and loss of motor control

Hyperthermia – When core body temperature is above the normal body temperature range

Hypometabolism – Physiological state in which there is a reduction of metabolic rate

Hypothermia - When core body temperature is below the normal body temperature range

Metabolic heat production – The amount of heat produced by an animal. Typically measured as **Metabolic rate** – the rate of energy production – measured using respirometry

Normothermia - When core body temperature is within the normal body temperature range

Phenotypic flexibility – Reversible plastic modifications of the phenotype due to variation in the environment

Ptiloerection – Raising and fluffing of feathers by contraction of muscles

Summit metabolic rate – The highest metabolic rate achieved during cold exposure, typically measured through respirometry

Wet heat loss – Heat loss from cutaneous and respiratory evaporation

Background

Thermoregulatory pressures in a changing world

On relatively short timescales, weather can change dramatically, for example, between hours and days, but also within months to seasons. These fluctuations are predicted to become more pronounced with climate change (IPPC, 2021) leading to more frequent and severe heatwaves (Seneviratne et al., 2021). When a certain weather variable exceeds a threshold near its observed limits, it is defined as an extreme climatic event (Seneviratne et al., 2012; Ummenhofer & Meehl, 2017). These extreme weather events, such as heavy rainfall, drought, heatwaves and cold snaps, can vary in magnitude, frequency and duration (Seneviratne et al., 2012). If such events occur simultaneously (termed compound extremes; Seneviratne et al., 2021; Seneviratne et al., 2012), it is not difficult to imagine that the outcome of a heatwave will be more severe when it co-occurs with a drought. For example, heatwaves alone may not increase risks of wildfires, but co-occurrence with droughts may do so (Hao et al., 2022), with potential downstream consequences amplifying effects on wildlife.

Environmental temperature (see Glossary) affects performance in living organisms, both positively and negatively. Studies on birds, reptiles, and insects, demonstrate environmental temperature-dependent consequences on growth, maturation and survival (Cunningham et al., 2013; De Jong et al., 2023; Noble et al., 2018; Nord & Nilsson, 2011; Salaberria et al., 2013), as well as behaviour and reproduction (Archer et al., 2025; Cunningham et al., 2021; Edwards et al., 2015; Nilsson & Nord, 2018; Nord & Nilsson, 2019). To cope with persistent changes in environmental temperature, animals can either adapt (through evolutionary changes) or acclimate (through phenotypic plasticity). The plasticity to respond to changes in weather might differ between *ectotherms* (e.g., almost all invertebrates and reptiles) and *endotherms* (all birds and mammals, and some representatives from other taxa). Ectotherms, owing to their limited physiological ability to regulate *body temperature*, are predicted to be particularly sensitive to thermal fluctuations (Kingsolver et al., 2013). However, aquatic ectotherms generally show thermal plasticity surpassing that of terrestrial groups (Marder & Gavrieli-Levin, 1986; Noble et al., 2025), perhaps since they have fewer opportunities for behavioural thermoregulation. Endotherms, on the other hand, may tolerate thermal fluctuations better due to their ability to internally regulate body temperature.

For endotherms, the ability to control water and energy budgets by using physiological processes is important as high air or body temperatures can be lethal within hours or minutes, especially in small animals. There are indications that individual endotherms can handle short-term environmental temperature changes better when they have access to more variation in macrohabitats (e.g., a shaded branch compared to a sunlit branch), where for example environmental temperature can differ with several degrees between sites (reviewed by Cunningham et al., 2021). As average temperatures rise across the globe, an interesting question is whether adapting or acclimating to these changes comes at a cost for coping with cold exposure, meaning that an individual can be either more heat tolerant or more cold tolerant, but not both. Evidence for such a trade-off is evident at reproduction level, where ostriches (*Struthio camelus*) with high rates of egg laying in cold environments decreased rates of egg laying in warm environments, and vice versa (Schou et al., 2022). However, the physiological mechanisms underpinning this relationship have yet to be examined.

Keeping body temperature at an optimum range is likely instrumental to prevent somatic damage. Thus, high thermoregulatory precision and flexibility must be assumed essential for maintaining fitness in thermally variable environments. In a changing world, this increasing relevance of body temperature control raises questions about the ontogeny and evolution of thermoregulatory phenotypes and whether they can be programmed by prevailing temperature. The purpose of this thesis was to address these questions.

Body temperature regulation in endotherms

Body temperature is regulated through external processes (i.e., behavioural thermoregulation such as basking and shade-seeking) that is commonly used by both ectotherms and endotherms, or internal processes (i.e., endogenous heat production and dissipation [McKechnie, 2022]) that can only be used by endotherms.

Behavioural thermoregulation has two functions in animals living in warm environments: 1) to keep heat gain as low as possible; and 2) to increase heat loss (Sharpe et al., 2022). To lower heat exposure and minimize the risk of increased body temperature, foraging might shift from the warmest parts of the day to crepuscular periods when it is cooler (Andreasson et al., 2020a; Austin, 1976; Sharpe et al., 2022), or to shadier microhabitats (Austin, 1976).

Thermoregulation using endogenous heat production and dissipation

Endotherms regulate their body temperature using both internal and external processes. For example, through changes in insulation, metabolism (Box 1;

Martinez Del Rio et al., 2018; Scholander et al., 1950a; Yahav, 2015) and behaviour (Martinez Del Rio et al., 2018). Endotherms primarily gain heat through increases in metabolism, either by increasing cellular metabolism or activity levels (Box 1; Barcelo et al., 2017; McKechnie et al., 2021; reviewed by McKechnie, 2022). In addition, postural adjustment or other behavioural responses allow them to gain or lose heat from the environment, such as from sunlight, shade or wind (Pattinson et al., 2020; reviewed by McKechnie, 2022). For example, several species of shorebirds (the avian order of Charadriiformes) reduce heat gain by orienting their backs towards the sun with *ptiloerected* dorsal feathers. This behaviour decreases the amount of direct heat from sunlight reaching the skin (Grant, 1982). It also increases the air flow from wind that reaches the skin surface. In turn, this increases the amount of heat that can be lost by evaporation of water through the skin (i.e., cutaneous evaporation [Box 1]; Grant, 1982).

Heat loss occurs through two main pathways, that is, "*dry*" or "*wet*" *heat loss* (Box 1; Gates, 1980). Rates of heat dissipation can be decreased using counter-current heat exchangers (Midtgard, 1981), or increased by increasing circulation to thermal windows (i.e., non-insulated areas; Tattersall et al., 2009), or by changing insulatory properties. However, it is important to note that dry heat loss requires a thermal gradient between environmental temperature and body temperature. Since heat flows in the direction of this gradient, dry heat loss is only meaningful when environmental temperature is significantly lower than body temperature, and will even become negative when the environment is warmer than the body. After this, the only remaining way to lose heat is by evaporation of water through cutaneous and respiratory evaporation (Box 1), which is evident by significant increases in *evaporative water loss* during heat exposure (Calder & King, 1974; McKechnie and Wolf, 2010). Accordingly, the rate of evaporation, and so *evaporative heat loss*, increases when environmental temperature rises (Morrison et al., 2018), which is purported to put heat-exposed animals at risk of lethal dehydration (Albright et al. 2017). This suggest that we need to gain knowledge of thermoregulatory processes to understand animals' acclimation to increasingly variable environmental temperatures.

The relationship between heat production, heat loss and air temperature

The relationship between *metabolic rate* and *air temperature* in a resting and postabsorptive endothermic animal can be described using the Scholander-Irving model, which is an extension of Newton's law of cooling (Figure 1; Scholander et al., 1950a). The model shows that when changes in insulation are sufficient for body temperature maintenance, the metabolic rate and water expenditure is minimal and independent of air temperature. This range of air temperatures is called the "thermoneutral zone" (Figure 1). Outside of the thermoneutral zone, an animal must gain heat when air temperature drops, or lose heat when air temperature rises, if body temperature is to remain stable (Scholander et al., 1950a). At the lower end of the thermoneutral zone, the "lower critical temperature" indicates the air temperature below which an animal must start producing metabolic heat to stay warm (Figure 1; IUPS Thermal Commission, 2003). The "upper critical temperature", by analogy, indicates the air temperature above which heat loss is required to keep body temperature from rising, and can be defined by either an increase in metabolic rate or evaporation of water (Figure 1; IUPS Thermal Commission, 2003). Insulation, tissue composition (e.g., changes in the amount or aerobic activity of heat-generating tissues), and acclimation or adaptation to environmental temperature, can each affect the rate at which *metabolic heat production* and evaporation increase with decreasing or increasing air temperature outside of thermoneutrality.

The Scholander-Irving model is defined for postabsorptive animals at rest in darkness, which presents several difficulties for transferability to wild species. First, air temperature must be replaced with an integrated measure of the thermal environment, such as environmental temperature, to produce measurements relevant to natural conditions (McKechnie, 2022). Second, wakefulness as such increases metabolic heat production (Aschoff, 1981) and more heat is also produced through activity and food processing during daytime (Bech & Præsteng, 2004; Humphries & Careau, 2011). Therefore, it is possible that the shape and inflection points of the Scholander-Irving curve are different in natural settings, and when contrasting daytime and nighttime. Third, the Scholander-Irving model does not account for the fact that many wild animals live most of their lives outside of thermoneutrality, which has given rise to the misconception that such species or individuals are somehow at thermal disadvantage. Modern synthesis better accounts for all these subtleties by broadening the original framework proposed by Scholander et al. (1950a) to encompass prescriptive tolerance and survival zones, each defined by operative temperatures and the animals' capacity for evaporative heat loss and metabolic heat production (Mitchell et al., 2018).

Box 1. Body temperature control

Insulation: Heat loss can be reduced through insulation, such as fat, hair and feathers, and by modifcation of insulatory properties (Scholander et al., 1950a). For example, both feather structure and plumage density, as well as ptiloerection (i.e., “fluffing” of feathers) lower heat loss rate by trapping warm air produced by the body within the plumage (Nord et al., 2023; Osváth et al., 2018; Pap et al., 2020; Scholander et al., 1950b). Ptiloerection could also increase heat loss by allowing more air to flow over skin surfaces (Grant, 1982).

Metabolic heat production: Heat is generated through biochemical reactions: through shivering (i.e., contractions of muscles), by mitochondria, and as a byproduct of food processing and activity (Bech & Præsteng, 2004; Humphries & Careau, 2011; reviewed by McKechnie, 2022). While shivering is the main method of heat production in cold environments in birds, heat is also produced by non-shivering thermogenesis. In mammals, brown adipose tissue is a mitochondria-rich, exclusively thermogenic, tissue where heat is produced via mitochondrial uncoupling mediated by uncoupling protein 1 (UCP1, or ‘thermogenin’; Jastroch et al., 2010; Jastroch et al., 2018). Non-shivering in birds is dubious, but if it occurs it likely follows a different physiological pathway, such as futile pumping of Ca_2^+ ions in the sarcoplasmic reticulum under control by sarcolipin (Dumonteil et al., 1993, 1995; Nowack et al., 2017).

Dry heat transfer: Heat exchange occurs through **radiation** when infrared radiation is emitted from the body. It occurs in any animate or inanimate object warmer than absolute zero (i.e., -273.15°C, or 0 K) without requiring direct contact (Clarke, 2017). When the body is warmer than the surroundings, radiative heat flux is usually negative. **Conduction** is transferring of heat energy between a body and an adjacent surface in direct contact. Heat moves over a thermal gradient from the warmer object to the cooler object, resulting in heat loss or gain depending on the direction of the gradient (Clarke, 2017). **Convection** is transfer of heat by the movement of a fluid over a surface. Heat loss via convection occurs when warm air (or water, etc.) surrounding the body is moved away and replaced by cooler air from the exterior environment (Clarke, 2017).

Wet heat loss: The rate of **cutaneous evaporation** (evaporation through the skin surface) depends on characteristics of the animal’s integument. For example, many mammals regulate water loss via sweat glands, which birds do not posses. In addition, bird feathers restrict water loss through evaporation (Clarke, 2017). Yet, cutaneous respiration is typically the single largest contributor to evaporative heat loss in birds (Angilletta et al., 2010; Boyles et al., 2011; Ro & Williams, 2010). In columbids, cutaneous evaporation can be regulated and has evolved as the main method for heat loss, and is facilitated by ptiloerection (Marder & Gavrieli-Levin, 1986; 1987). It remains unclear if other bird taxa have similar adaptations. **Respiratory evaporation** can occur either through panting or gular fluttering. During panting – a ubiquitous process in birds – respiratory frequency increases as tidal volume decreases to allow for a larger air flow. This requires muscular work through engagement of the thoracic musculature and comes at the cost of an increase in metabolic heat production (Dawson, 1982). During gular fluttering, which is more phylogenetically constricted than panting, evaporation through vibrations of the gular membranes increases heat loss (Angilletta et al., 2010; Dawson, 1982). Both panting and gular fluttering results in heat dissipation through increased air flow over the moist surfaces in the buccal cavity and respiratory tract (McKechnie, 2022).

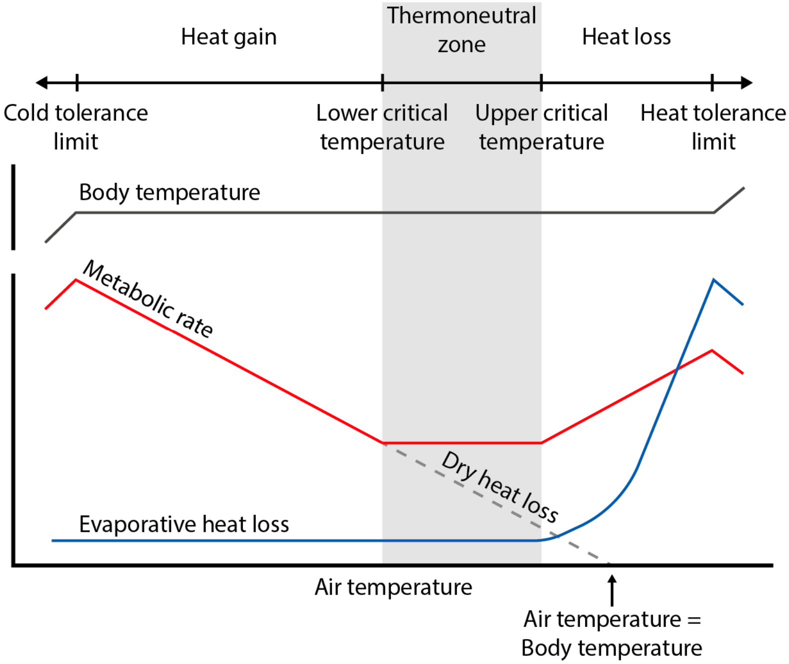

Figure 1. Metabolic rate, evaporative heat loss, dry heat loss and body temperature in relation to air temperature as originally proposed by Scholander et al. (1950a)**.** Within the thermoneutral zone (grey shades area), where insulation is sufficient to keep body temperature at a stable level, metabolic rate is minimal and independent of air temperature. When air temperature increases above the upper critical temperature, increases in evaporative heat loss and/or metabolic rate occur to drive heat dissipation, keeping body temperature stable. Below the lower critical temperature, metabolic rate increases linearly with decreasing air temperature, reflecting facultative thermogenesis. *Cold-* and *heat tolerance limits* (see main text) represent the lowest and highest, respectively, air temperatures tolerated before thermoregulatory failiure.

Behavioural thermoregulation and missed opportunity costs

Increased energy and water costs of physiological thermoregulation during heat exposure are often balanced by an increased use of behavioural thermoregulation (Cunningham et al., 2021). Such an increase can directly limit time spent foraging (Cunningham et al., 2013; du Plessis et al., 2012) and may ultimately lead to reductions in body mass (van de Ven et al, 2019). Such adjustments often carry costs of their own. Shifting activity, such as foraging, away from the warmest part of the day to favour thermoregulation could result in missed opportunities for other essential activities, such as offspring provisioning or territory defence (reviewed by Cunningham et al., 2021).

Birds not only face a greater risk of overheating – hence incurring somatic damage – while caring for their nestlings (Nilsson and Nord, 2018), but missed opportunity costs may accumulate and result in severe effects on, for example, reproduction and survival (Cunningham et al., 2021; Andreasson et al., 2020a; Nord & Nilsson, 2019). This is seen for example in southern yellow-billed hornbills (*Tockus leucomelas*). Males of this species had lower foraging efficiency during high environmental temperatures because they increased the time spent thermoregulating (van de Ven et al., 2019). The resultant lower provisioning rates decreased nestling body mass, causing the probability of successful fledging to drop below 50% during hot days (van de Ven et al., 2020). In extreme cases, high environmental temperatures during the reproductive season can even result in complete abandonment of the breeding attempt (Sharpe et al., 2019; Pattinson et al., 2022).

The ontogeny of thermoregulation in birds

Coping with extreme environmental temperatures is different for juveniles than for adults. Embryos and altricial juveniles (i.e., species where chicks hatch undeveloped and naked), are poikilothermic (i.e., their body temperature varies with ambient temperature) until thermoregulatory capacity has fully developed (Geiser et al., 2019; Pereyra & Morton, 2001). Precocial species (i.e., species where newly hatched chicks are feathered and forage independently from hatching onwards), on the other hand, have an almost fully developed thermoregulatory system at hatching which will be fully developed within the first couple of weeks post-hatch (Nord & Nilsson, 2021; Price & Dzialowski, 2018; reviewed by Yahav, 2015). Before sufficient insulation, thermogenic mass, or both, has been obtained, juveniles depend on their parents to gain or lose heat.

Altricial bird species develop thermogenic capacity approximately one-third to halfway to adult size (reviewed by Yahav, 2015), but are not functionally homeothermic. Hence, even if the physiological systems for heat production are functional at a comparatively young age and thermoregulatory mechanisms have started to work (Hohtola & Visser, 1998; Visser, 1998), altricial birds are not able to maintain a stable body temperature independent of environmental temperature until much later (Andreasson et al., 2016). For example, in starlings (*Sturnus vulgaris*), muscles have matured enough for an increase in metabolic heat production at day 4 after hatching (reviewed by Hohtola & Visser, 1998; Ricklefs & Webb, 1985). In line with this, the first endothermic responses in blue tits (*Cyanistes caeruleus*) have been suggested to occur at a body mass of around 6.3 g (reviewed by Visser, 1998), which roughly translates to day 6 after hatching [Figures 5C, 14C; **Paper V**]). However, the thermogenic capacity at this age is still not sufficiently developed to allow homeothermy at even comparatively mild air temperatures (Andreasson et al., 2016; Engert et al., 2025; **Paper V**).

In comparison with altricial birds, thermoregulatory competence in precocial birds develops during late incubation and during the first 10 days after hatch (reviewed by Yahav, 2015). The metabolic rate of embryos increases and stabilizes close to hatching when the hatching mass is reached (Prinzinger et al., 1995). Yet, the thermoregulatory capacity at this stage is still not enough to keep body temperature stable (Nord & Nilsson, 2021). Thus, precocial juveniles alternate between independent foraging and brooding by the attending female until thermal independence occurs (e.g., Jørgensen & Blix, 1985; Pedersen & Steen, 1979). However, precocial species have more opportunities to use behavioural thermoregulation compared to altricial species that are confined to a nest (but see Woodruff et al., 2025). This may render altricial species more vulnerable to heat exposure in the nest compared to precocial birds, whereas precocial birds may be more sensitive to low early-life temperature as they cannot exploit the sheltered confines of a nest and huddle for warmth.

Permanent and reversible responses to developmental temperatures

Changes in environmental temperatures during development can affect both juvenile morphology and physiology. It has been suggested that these effects act on homeostasis and physiological pathways, such as, thermogenesis (Bize et al., 2010; Piestun et al., 2008). Such changes may reflect *developmental plasticity*, that is, permanent changes of the phenotype due to changes in the developmental environment (Figure 2A; Piersma & Drent, 2003), or *phenotypic flexibility*, that is, reversible modifications of the phenotype due to variation in the environment (Figure 2B; Piersma & Drent, 2003). Thus, variation in developmental temperature may therefore impact how animals handle high or low environmental temperatures as adults (reviewed by Nord & Giroud, 2020). For instance, pulses of higher incubation temperature during embryonic development leads to improved postnatal heat tolerance in the chicken (e.g., Piestun et al., 2011). Moreover, studies have shown that there is greater control of body temperature and higher survival in chickens that were heat- or cold-manipulated during embryonic or perinatal development, and then exposed to heat- or cold-stress, respectively, several weeks after hatching (Arjona et al., 1988; Shinder et al., 2002; Yahav & Hurwitz, 1996).

Both developmental plasticity and phenotypic flexibility can be either ameliorating or constraining depending on the degree of overlap between juvenile and parental environments, and the time course over which these effects remain (Figure 2A-B; Nord & Giroud, 2020). If environmental developmental temperature causes permanent changes that prime temperature acclimation, birds developing under such conditions would be better equipped to handle prevailing environmental temperatures as adults. Hence, high environmental temperatures would prime heat acclimation, and birds developing under such conditions would handle high environmental temperatures better by having, for example, lower metabolic heat production and higher *evaporative cooling capacity* (Figure 2A). Similarly, if acclimation to cold temperatures is primed by cold environmental temperatures, birds developing under cold conditions would be better at handling cold environmental temperatures, for example, by increasing their metabolic heat production (Figure 2A). This is usually referred to as the 'environmental matching' hypothesis (Monaghan, 2008; Nord & Giroud, 2020).

If environmental developmental temperature outside of optimal ranges causes permanent changes that constrain temperature acclimation, birds developing under stressfully high or low environmental temperatures would be less heat- or cold tolerant, respectively. This could for example be reflected by higher metabolic heat production and a decreased capacity for evaporative cooling during a heat-challenge (Figure 2A). By analogy, birds developing under cold conditions would have lower metabolic heat production and higher evaporative cooling capacity during cold temperature conditions (Figure 2A). This is usually referred to as the 'silver spoon' hypothesis (Monaghan, 2008; Nord & Giroud, 2020). Regardless of whether these effects are ameliorating or constraining, it is predicted that they will remain in adulthood if they reflect developmental plasticity.

If effects of developmental temperature on thermoregulatory traits reflect phenotypic flexibility, the effects caused by changes in environmental temperature during juvenile development are predicted to revert to pre-acclimation levels once the thermal stressor disappears. Hence, adults would have no remaining thermoregulatory benefits from their juvenile environment. For example, while heat-exposed juveniles decrease metabolic heat production and increase evaporative cooling capacity in warm conditions and, by analogy, increase metabolic heat production and decrease evaporative cooling capacity in response to cold exposure, the adult thermoregulatory phenotype reflect the current thermal environment (Figure 2B).

In all, morphological and physiological responses to changes in environmental temperatures may be interpreted as thermal adaptations to increase fitness when juvenile and adult environmental conditions overlap (cf. Nichelmann, 2004), but decrease fitness when they do not. Most studies have investigated these effects during embryogenesis, leaving a critical knowledge gap with regards to the consequences of variation in postnatal developmental temperatures. Therefore, in **Papers I, II** and **V**, I tested whether effects of postnatal development in heatwave- or cold snap-like temperatures affected thermoregulatory traits in juveniles and whether any such effects remained in later life stages, allowing me to draw conclusions regarding to roles of developmental plasticity and phenotypic flexibility in thermal adaptation.

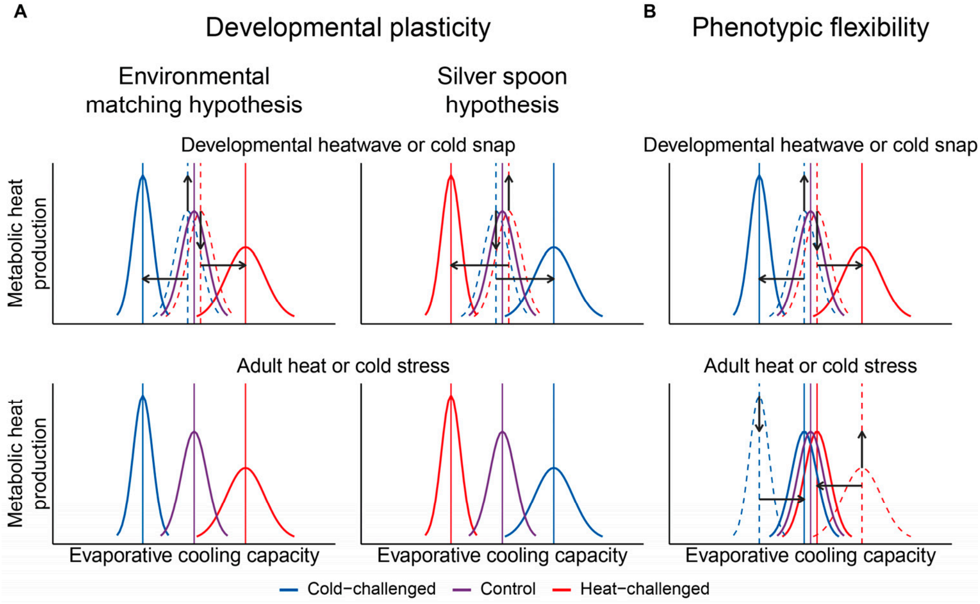

Figure 2. Hypothetical scenarios of physiological changes reflecting developmental plasticity and phenotypic flexibility in response to developemental heatwaves or cold snaps. Thermophysiological changes are represented by metabolic heat production and evaporative cooling capacity. (A) The developmental plasticity scenario is illustrated for heat and cold exposure under two hypotheses: the ‘environmental matching’ hypothesis and the ‘silver spoon’ hypothesis. A heatwave under the environmental matching hypothesis results in a decreased metabolic heat production and increased evaporative cooling capacity (i.e., increased heat tolerance), whereas under a cold snap it leads to increased metabolic heat production and decreased evaporative cooling capacity (i.e., increased cold tolerance). Under the silver spoon hypothesis, a heatwave leads to decreased heat tolerance, higher metabolic heat production and lower evaporative cooling capacity, and a cold snap leads to decreased cold tolerance, lower metabolic heat production and higher evaporative cooling capacity at both ages. When changes reflect developmental plasticity effects are non-reversible and effects gained as juveniles remain as adults (A). (B) When changes reflect phenotypic flexibility, juveniles decrease metabolic rate and increase evaporative cooling capacity during a heatwave, and increase metabolic heat production and decrease evaporative cooling capacity during a cold snap. However, effects are reversible such that there are no remaining effects on temperature tolerance in adults (B). Arrows: predicted directions. Dashed lines: starting points of traits. Adapted from Figure 1 in **Paper I**.

A trade-off between thermoregulation and growth

When environmental temperature rises towards and above body temperature, increases in evaporative heat loss must occur to defend *normothermia* (Talbot et al., 2017; Williams & Tieleman, 2005). This in turn, intensifies dehydration risk (Albright et al., 2017) and sometimes raises energy expenditure (Smith et al., 2017; Whitfield et al., 2015; Wolf & Walsberg, 1996), especially when there is no possibility to escape increasing environmental temperature (e.g., for some juveniles; see above). Under these circumstances, more resources are allocated for thermoregulation and less likely remain for other purposes such as growth and maturation. This trade-off between thermoregulation and growth may explain why several studies report negative impacts of high environmental temperatures on key juvenile condition traits such as body mass (Andrew et al., 2017; Burness et al., 2013; Cunningham et al., 2013; Rodriguez & Barba, 2016b; van de Ven et al., 2020) and growth rate (Andreasson et al., 2018; Deaton et al., 1978). Yet in some cases, high developmental temperature has been found to increase nestling growth rate and body mass gain (Dawson et al., 2005; McCarty & Winkler, 1999).

The discrepancies in effects (both positive and negative) of variation in environmental developmental temperatures could depend on the prevailing thermal environment in the study area, with positive effects in cooler environments and negative in warmer environments (Andreasson et al., 2018; Dawson et al., 2005; Rodriguez & Barba, 2016a, 2016b; reviewed by Andreason et al., 2020). For example, an increase in nest temperature in cooler environments could reduce the need of thermoregulation and optimize growth, while increases in nest temperature in warmer environments would enhance the need of thermoregulation and require resources that would otherwise have been invested in growth (cf. Tabh & Nord, 2023). The wide range of responses to postnatal developmental temperature conditions indicates that we need a deeper understanding of morphological and physiological responses in a broad range of circumstances. For example, few studies have investigated if any effects of developmental temperature on thermoregulation remain into adulthood, and whether chicks can compensate for any somatic costs incurred by early heat exposure in later life stages. Thus, in **Paper V**, I studied the effects of increased early-life environmental temperature on thermoregulatory traits and body size to investigate whether increased investment in thermoregulation demands resources that could otherwise have been invested in growth.

The thermoregulatory role of shrinking body size in warm temperatures

Concurrent with increasing global temperature, amassing evidence shows that birds, as well as mammals, are shrinking and shapeshifting (Ryding et al., 2021; Searing et al., 2023; Sheridan & Bickford, 2011; Weeks et al., 2020). When body size decreases and body shape elongates, the surface area to volume ratio increases. Such changes in body size and shape leads to a larger area available for heat loss from wet or dry pathways (Box 1) and should therefore aid heat dissipation when environmental temperature is high, and vice versa in the cold.

The benefits of increasing surface area to volume ratio follows from predictions of Bergmann’s Rule (Bergmann, 1847) – that body size decreases with increasing environmental temperature – and Allen’s Rule (Allen, 1877) – that appendage length increases with increasing environmental temperature – (ecogeographical rules). Hence, the negative correlation between increasing environmental temperature and body size has been suggested to reflect an adaptive response to gain thermoregulatory benefits by increasing surface-area-to-volume ratios and, therefore, rates of passive heat loss (Baldwin et al., 2023; Ryding et al., 2021; Youngflesh et al., 2022).

Despite decreasing body size and elongating shape, it is questionable whether such changes have relevant effects on thermoregulatory costs in endotherms, where physiological mechanisms for heat production as well as retention and dissipation of heat (e.g., thermal windows and counter-current heat exchangers) have evolved to keep body temperature stable. Consequently, it has been argued that a lower surface area to volume ratio would be of little importance in cold environments (Scholander, 1955; supported by Steudel et al., 1994). In high environmental temperatures, similar doubts have been raised based on predictions from physiological allometries, where reported decreases in body size are assumed to contribute only negligible changes in total heat loss, far smaller than would be expected from a standard thermoregulatory response to increased temperature (Nord et al., 2024). The small changes in surface area to volume ratio together with a limited effect on heat loss suggests that thermoregulatory benefits due to changing body size are restricted. However, there is a lack of studies where the relationship between shrinking body size and thermoregulation has been tested empirically. Hence, in **Paper III** I tested whether differences in body size and appendage length affect the capacity to thermoregulate in warm and cold air temperatures. Then, in **Paper IV**, I exploited the process of domestication to study if phenotypes that fall considerably outside of the typical population range influence thermoregulatory competence.

Aims of the thesis

The overarching goals of my thesis was to improve the understanding of effects of extreme weather events and prevailing temperature on the ontogeny of thermoregulatory physiology and development in birds, and to understand the effects of body size on thermoregulation. Accordingly, I explored: 1) whether the thermal environment during development influences variation in thermoregulatory traits at later life stages; 2) if decreasing body size in response to variation in developmental temperature has meaningful thermoregulatory value; and 3) if developmental heat exposure causes a trade-off between growth and thermoregulatory demand.

First, I investigated whether growing up during a heatwave or cold-snap caused any short- or long-term physiological and morphological consequences in controlled laboratory studies (**Papers I** and **II**). Specifically, I tested whether an early postnatal heatwave or cold-snap impacted thermal, metabolic and hygric physiology in Japanese quail during submaximal thermal exposure, similar to effects that have been reported based on manipulation of prenatal temperature (**Paper I**). In addition, I investigated if cold or warm postnatal developmental temperatures affect *heat*- and *cold tolerance limits* in Japanese quail, and whether there is a trade-off between thermoregulatory traits mediating heat- and cold tolerance, respectively (**Paper II**). Additionally, I tested whether any effects of developmental temperature were permanent or reversible, reflecting developmental plasticity and phenotypic flexibility, respectively.

Second, I studied the correlation between body size and thermoregulatory capacity in Japanese quail (**Papers III** and **IV**). Evidence indicates that animals are shrinking and shapeshifting in conjunction with increasing global temperature, but whether these changes confer thermoregulatory benefits remains unclear. In **Paper III**, I tested if body size and appendage lengths directly influenced thermoregulatory costs in warm or cold temperatures, combining empirical measurement and statistical forecasting. In **Paper IV**, I harnessed the outcomes of agricultural selection to study how morphology affected evaporating cooling capacity and heat tolerance limits when body size differences are extreme, by comparing three different breeds of Japanese quail.

Finally, in **Paper V**, I tested critical theory developed in laboratory work in a wild study system by investigating short- and medium-term morphological and physiological effects of the post-hatch thermal environment and the possible trade-off between somatic growth and thermoregulation in a nestbox-nesting population of blue tits. Here, I wanted to study thermoregulation and the intersection between development, plasticity, and body size, asking whether there are developmental costs associated with early-life heat exposure that were reflected in a trade-off between thermoregulation and growth.

Figure 3. Sunset over the north-eastern part of the blue tit study area in late May. Photo: author.

General methods

To answer the questions addressed in this thesis, I used both controlled laboratory experiments and an experiment in the wild, each controlling postnatal developmental temperature and measuring body size and thermophysiological traits in two study species.

Study species

Japanese quail

The Japanese quail (*Coturnix japonica*) is distributed across eastern Asia where it occurs in a wide range of habitats, preferably with dense vegetation such as grassy fields, shrubs, and agricultural lands (del Hoyo et al., 1994). Wild Japanese quail is a relatively small (Baer et al., 2015), primarily ground-living species. It is a precocial bird with fast growth, attaining adult size (90-100 g) and reaching reproductive maturity within 6-8 weeks (Baer et al., 2015). Females produce up to 3 clutches of 14 eggs each in a year, with each egg weighing about 7 g (Lukanov & Pavlova, 2020). Japanese quail are difficult to study in the wild due to their low population density and secretive behaviours. Fortunately, or unfortunately, Japanese quail have a long history of association with humans, both as a model species in research and as a domesticated bird used in the food industry (Baer et al., 2015). In general, since the Japanese quail is a precocial species, it is easy to rear and maintain chicks in captive environments without parental care. In optimal housing conditions, the birds reach adult size and reproductive maturity within 6-8 weeks. Some breeds used for meat production can reach up to 600 g (Baer et al., 2015), and females of breeds bred for egg production can lay more than 250 eggs per year, each weighing 12-14g (Lukanov & Pavlova, 2020). Owing to their remarkably short time from hatching to adulthood for a vertebrate species, long-term studies can be performed over relatively short time spans. In this thesis, three different breeds of quail were used: 1) a semi-domesticated, wildtype, small breed (126.3 ± 11.1 g; Figure 4C-D; **Paper IV**); 2) a medium-sized domesticated breed (247.7 ± 8.5 g; Figure 4B,E; **Papers I, II, III** and **IV**); and 3) a large-sized domesticated breed (383.7 ± 11.4 g; Figure 4A,D; **Paper IV**). All breeds were purchased as eggs from breeders located around Skåne (Sweden) and Germany and then incubated, hatched and reared at Lund University.

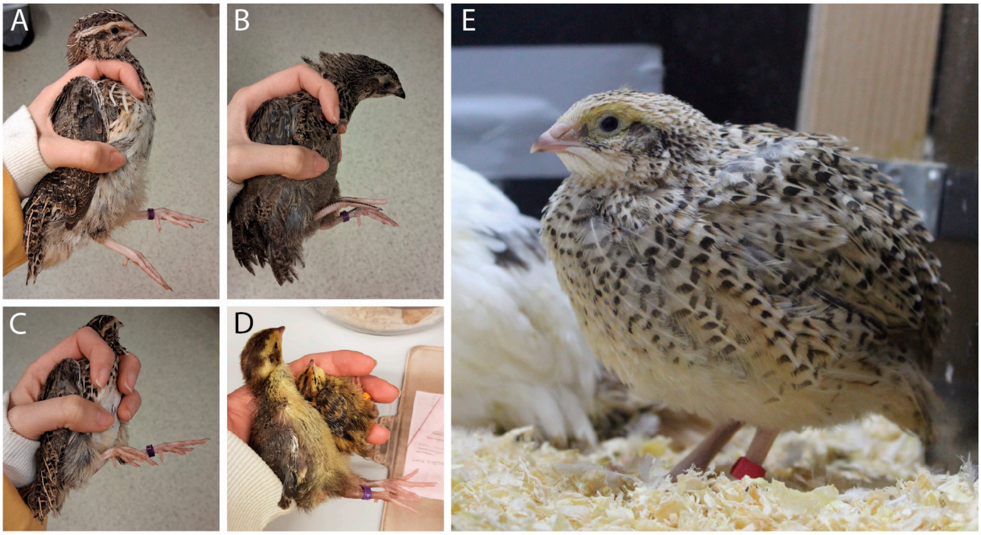

Figure 4. Japanese quail of different breeds and ages used in experiments. (A) Four-week-old large quail. (B) Four-week-old medium quail. (C) Four-week-old small quail. (D) One-week-old large and small quail. (E) Three-week-old medium quail. Photos A-D: author. Photo E: Maria Correia

Eurasian blue tit

The Eurasian blue tit (Figure 5A-D) is a small (7.5-14.7 g) and well-studied altricial bird species found throughout Europe and western Asia where it inhabits both deciduous and mixed forests (del Hoyo et al., 2007). In Scandinavia, blue tits are partial migrants, with mostly females and juveniles performing the migration (Smith & Nilsson, 1987; Nilsson et al., 2006). It is a cavity-nesting passerine which readily accepts nestboxes in addition to natural tree cavities (del Hoyo et al., 2007). A clutch of 10-14 eggs is incubated by the female alone for 12-13 days (Nilsson, 2000). During the first 6-7 days after hatching, nestlings are intermittently brooded by the female, while both parents feed the nestlings from hatch until fledging (Perrins, 1979). Post-fledging parental care extends for some weeks, before fledglings become fully independent (Perrins, 1979).

I studied blue tits in a nestbox population located approximately 20 km east of Lund situated near Övedskloster (55°70′N, 13°61′E) and around Lake Krankesjön (55°42′N, 13°28′E) in southernmost Sweden (Figures 3, 9), where the breeding season extends between April and June. The study site around Lake Krankesjön is a military exercise field and consist of grasslands (which was grazed by cattle during the study period) with interspersed deciduous woodlots (of mostly beech [*Fagus sylvatica*], oak [*Quercus robur*], birch [*Betula* spp.] and alder [*Alnus glutinosa*]) and continuously forested areas around the lakeshore. The area near Övedskloster is continuously forested, mostly consisting of beech and oak.

The nestboxes, which are placed 1.5-1.7 m above ground on trees, are mainly used by blue tits and marsh tits (*Poecile palustris*) but occasionally also by great tits (*Parus major*) and pied flycatchers (*Ficedula hypoleuca*). Data on the breeding biology of these birds have been collected in a standardised manner since 1983. Since blue tits readily breed in nestboxes, manipulation of developmental temperature can be undertaken with relative ease by increasing the nestbox temperature, making it feasible to test theory under more natural conditions.

Figure 5. Blue tits of different ages. (A) Adult blue tit caught for long-term monitoring of field site. (B) One-day-old blue tit nestlings, (C) 6-day-old blue tit nestling, and (D) 14-day-old blue tit nestlings. The blue tit is an altricial species, at 6 days of age feathers have started to emerge and at 14 days of age nestlings are fully feathered with the juvenile plumage. The chicks undergo a post-fledging moult into their first adult plumage during the summer. Photos: author.

Experimental heat- and cold challenges

Japanese quail eggs were incubated at 37.5°C and 50% humidity for 17-22 days. At hatching, the chicks were transferred into open pens (**Paper I, II** and **IV**) or to stacked cages (**Paper IV**) where they were reared in one of three temperature conditions: cold (10°C), mild (20°C) or warm (30°C). Birds in cold conditions were housed in a cooling room, whereas birds in warm conditions were housed in a room equipped with electric heaters (Figure 6A). In **Paper I**, birds were housed in the different temperature conditions until 3 weeks of age. When birds reached 3-weeks-old, I transferred all birds to new pens in mild conditions. In **Paper II**, birds were housed in either warm or cold conditions until 9 weeks of age, after which half of each treatment group were transferred to mild conditions (20°C), and the other half remained in their original treatment conditions. In **Paper III**, I used data collected from the birds used in **Papers I** and **II**. In **Paper IV**, all birds were housed in mild temperature throughout the experiment.

Figure 6. Manipulation of environmental temperature. (A) Example of set up with stacked cages for heat-challenge experiments in Japanese quail. (B) Placement of handwarmers in blue tit nestboxes, used to manipulate developmental temperature after hatching. Temperature-measuring devices (iButtons: 0.0625°C resolution; accuracy ± 0.5°C) were placed by the nest cup and at the ceiling. Photos: author.

Blue tits nestlings were experimentally heated from the day after hatching until 6-day-old using chemical handwarmers placed around the nest cup (**Paper V**; Figure 6B). The handwarmers were changed once daily. Heated nestboxes were 8.2°C warmer than control nestboxes during daytime (30.3 ± 0.6°C vs. 22.1 ± 0.5 °C) and 4.6°C warmer during the full 24 h (25.2 ± 0.6°C vs. 20.6 ± 0.6°C). To control for the effect of novel objects in the nestbox, I manipulated control nestboxes using non-heating, exhausted handwarmers.

Measurements of thermoregulatory traits

Throughout this thesis, thermoregulatory traits were measured using different approaches. Metabolic heat production, evaporative water loss, and *evaporative cooling efficiency* were measured at submaximal air temperatures. At extreme air temperatures, *summit metabolic rate*, metabolic heat production, evaporative water loss, evaporative cooling capacity, and heat- and cold tolerance limits were measured. Body temperature was measured at both submaximal and extreme air temperatures.

Whole animal metabolism can be approximated from measurements of gas exchange using flow-through respirometry (i.e., the instantaneous metabolic rate) at a given air temperature and time. I pushed air through an airtight respirometry chamber (Figure 7) and measured changes in gas concentrations (of oxygen, carbon dioxide and water) between ingoing and outgoing air to subsequently calculate metabolic heat production and evaporative water loss in the birds (Box 2; Lighton, 2019). Since disturbances (such as variation in ingoing gas concentrations and instrument drift) may occur, I measured baseline values in ingoing air at least twice, as a minimum in the beginning and end of an experiment.

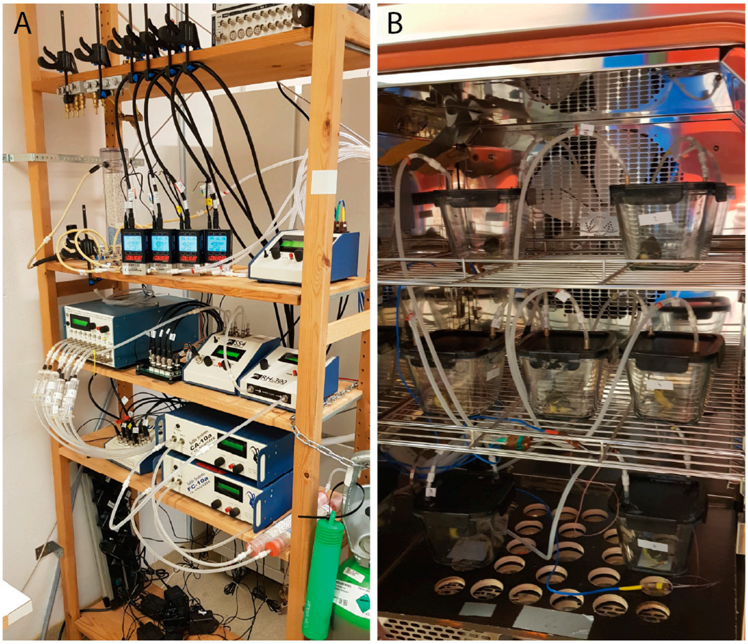

Figure 7. Set up during respirometry measurements. (A) Instruments measuring oxygen, carbon dioxide and water vapour concentrations during respirometry measurements. (B) Seven 14-day-old blue tit nestlings placed in respirometry chambers ready to be measured during the night (**Paper V**). Dried air was pushed through the sealed glass respirometry chambers, in which the bird was placed. Photos: author.

Box 2. Calculations of metabolic traits based on changes in gas concentrations

Metabolic rate: Metabolic rate, which is equal to metabolic heat production, can be measured using either wet or dry air, by scrubbing it from water vapour. Before measurements of oxygen, carbon dioxide can be removed from the airflow to avoid diluting oxygen concentrations and compensations of that. Hence, oxygen consumption (ml/min) was calculated following eq. 11.1 in Lighton (2019):

$$VO_2 = FR_e(F_iO_2 - F''_eO_2) / (1 - F_iO_2)$$

where F_iO_2 is the fraction of oxygen in the incoming airflow, F''_eO_2 is the fraction of oxygen in the outgoing airflow scrubbed of water and carbon dioxide, and FR_e is flow rate in ml/min. Oxygen consumption was converted to metabolic heat production (W), assuming that 1 ml of oxygen = 20 J (Kleiber, 1961). Precise measurements of gas concentrations can be performed when the air stream is dried. Hence, I used Dalton’s law of partial pressures to mathematically ‘dry’ carbon dioxide data before the other calculations was performed using eq. 8.7 in Lighton (2019):

$$CO_2' = CO_2 \times BP / (BP - WVP)$$

where BP = gas pressure in kPa and WVP = water vapor pressure (in kPa). Then, carbon dioxide concentrations were calculated following eq. 11.6 in Lighton (2019):

$$VCO_2 = [FR_e(F'_eCO_2 - F_iCO_2) - F_eCO_2(VO_2)] / (1 - F_eCO_2)$$

where F_iCO_2 is the fraction of carbon dioxide in the incoming airflow, F_eCO_2 is the fraction of carbon dioxide in the outgoing airflow, F'_eCO_2 is the fraction of carbon dioxide in scrubbed outgoing airflow, VO_2 is oxygen concentration, and FR_e is flow rate in ml/min.

Finally, in **Paper IV** the incurrent air was not scrubbed of water vapour. Hence, the airstream was mathematically dried using eq. 8.6 in Lighton (2019).

Evaporative water loss: Evaporative water loss (mg/min) was calculated according to eq. 11.9 in Lighton (2019):

$$VH_2O = FR_e(F_eH_2O - F_iH_2O) / (1 - F_iH_2O)$$

where F_iH_2O and F_eH_2O are the fraction of water vapour in the incoming and outgoing airflows, respectively, and FR_e is flowrate in ml/min. Evaporative water loss was converted to evaporative heat loss (W), assuming that 2406 J is required to evaporate 1 ml of water (Wallace & Hobbs, 2006).

Evaporative cooling efficiency/capacity: The ability to dissipate heat through evaporation of water was calculated as the ratio between evaporative heat loss and metabolic heat production (Lasiewski et al., 1966).

Measurements of metabolic rate and evaporative water loss during submaximal air temperatures

To test how thermoregulation during submaximal temperatures was affected by developmental temperature and body size, I measured the average metabolic heat production when the animal displays minimal activity at different submaximal air temperatures (similar to resting metabolic rate that is measured in thermoneutrality; IUPS Thermal Commission, 2003). In **Papers I** and **III**, air temperatures ranged from cool (10°C) to warm (40°C). In **Paper IV**, air temperatures ranged from 2.5°C to 37.5°C. In **Paper V**, air temperatures ranged 20°C to 40°C. Birds were measured individually in respirometry chambers, with 4 (**Papers I, III and IV**) or 7 (**Paper V**) chambers simultaneously placed inside a climate test chamber (Weiss Umwelttechnik C180/-40, Reiskirchen, Germany) during experiments. Since I measured the evaporation of water during measurements, all sources for extra water (e.g. from faeces) were accounted for. A grid platform was placed over a reservoir of mineral oil in the metabolic chambers to prevent disturbances from evaporation during measurements (Lasiewski et al., 1966; **Papers I, III** and **IV**). This approach was not feasible in **Paper V** since a platform could not be fitted securely in the respirometry chambers used for the experiment. Hence, I counted the number of faecal sacs produced during measurement and used this as a covariate in analyses.

Measurements were performed either during daytime (**Papers I** and **III**) or during nighttime (**Papers IV** and **V**). To not disrupt the diurnal cycle, the lights in the climate test chamber were on during daytime measurements, whereas lights were off during metabolic measurements performed at nighttime. Measurements started with an acclimation period (range in **Papers I**, **III** and **V**: 10-60 min; in **Paper IV**: 3 h) and a baseline of incoming gas concentrations which was followed by sequential data collection of gas concentrations for each bird, after which, air temperature was either decreased or increased, and gas concentrations were measured again (Figure 8A). Air temperature inside of the respirometry chambers was measured using copper-constantan (Type T) thermocouples.

Measurements of cold tolerance during sliding cold exposure

I measured the effects on developmental temperature on the cold tolerance limit and summit metabolic rate in **Paper II**. The latter was defined as the highest metabolic rate that can be achieved during cold exposure (IUPS Thermal Commission, 2003), and the cold tolerance limit was the air temperature at this point. During the experiment, air temperature in the climate chamber decreased by 20°C/h until birds reached their cold tolerance limits. I used a dry gas mixture of helium and oxygen (79 and 21% respectively; helox) to ventilate the respirometry chambers. Because the conductivity of helium is approximately four times higher than that of nitrogen, helox gas induces a considerably faster rate of heat loss compared to atmospheric air. Consequently, summit metabolic rate can be reached at much milder air temperatures, reducing the duration of the experiment and minimizing risk of cold injury (Rosenmann & Morrison, 1974). A bird was placed in a respirometry chamber and measurements were conducted on one bird at a time. An experiment started with an acclimation period (15 min) after which the sliding cold exposure commenced (Figure 8B). The measurement ended when a bird no longer increased its metabolic heat production despite reduction in air temperature (Figure 8B).

Measurements of heat tolerance during increments of increasing air temperature

Heat tolerance was measured both to study the effects of developmental temperature (**Paper II**) and of body size (**Paper IV**). I defined the heat tolerance limit as the highest air temperature which a bird can tolerate before either incurring harmful *hyperthermia* or losing motor control (were evaporative water loss did not increase further in response to increasing air temperatures). Evaporative cooling capacity was derived from evaporative water loss at this temperature. As described above, a reservoir of mineral oil was used to prevent evaporation from faeces from influencing measurements of evaporative water loss. Birds were individually placed in a respirometry chamber. A measurement started with an acclimation period (range: 30-60 min) in thermoneutrality, after which the air temperature was acutely raised to a point beyond which the bird started to increase its evaporation. Once gas concentrations were stable, chamber temperature was increased in 2°C increments (Figure 8C; Noakes et al., 2016; Talbot et al., 2018) until birds reached their heat tolerance limits. The measurement ended when a bird could not compensate the air temperature increase by increasing evaporative water loss, resulting in stress, loss of coordination, or severely hyperthermic (> 45°C; Figure 8C; Talbot et al., 2018; Whitfield et al., 2015).

Measurements of core body temperature

Body temperature was measured in different ways depending on the species. In Japanese quail (**Papers I, II, III** and **IV**), body temperature was recorded using a temperature-sensitive passive integrated transponder tag (LifeChip BioTherm, Destron Fearing, South St Paul, MN, USA) implanted into the intraperitoneal cavity. The skin at the distal end of the sternum was sterilized using 70% ethanol and topically anaesthetized with 5% lidocaine and prilocaine ointment. Thirty to 45 min later, the skin was sterilized again before intraperitoneal implantation of a sterile tag with a 12-guage syringe beneath the distal tip of the sternum. The incision was closed using cyanoacrylate glue, after which the closed incision was covered with antiseptic ointment (1% hydrogen peroxide). The implantation of the tag allowed for contact-free core body temperature measurements by using custom made antennas placed adjacent to the birds. Body temperature was measured throughout the experiment without interrupting measurements or causing further disturbance.

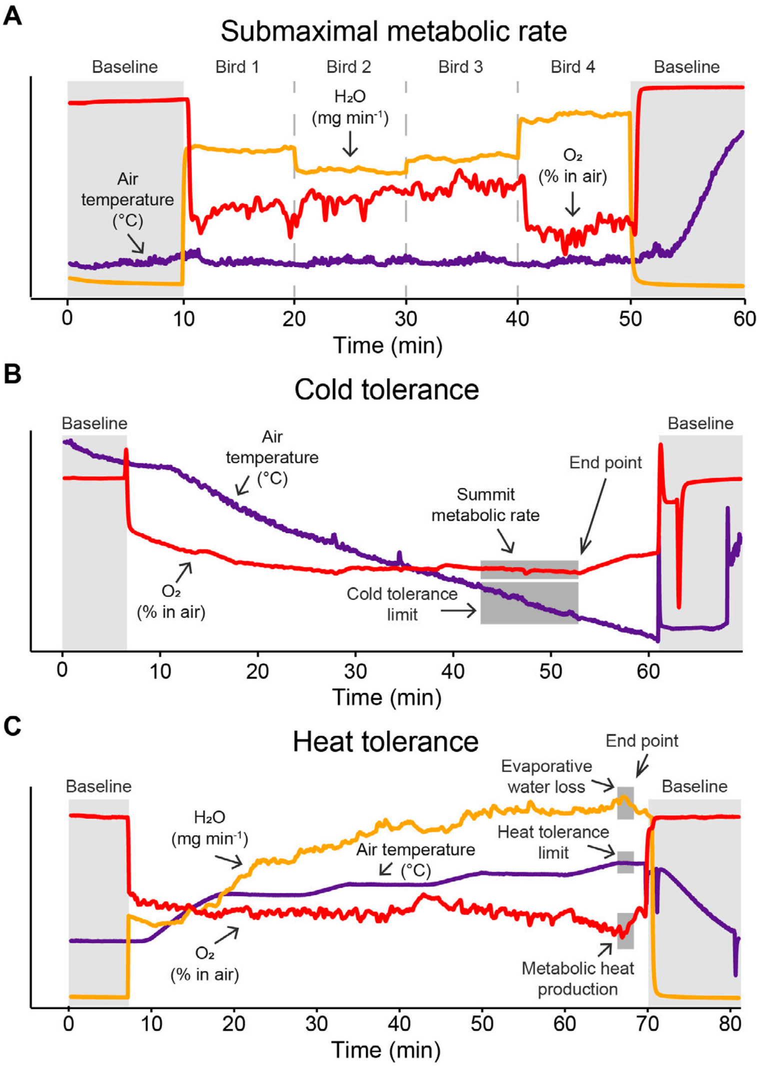

Figure 8. Raw data examples from the three different methods of metabolic measurements used in this thesis. (A) Metabolic rate measurements were used in **Papers I**, **III**, **IV** and **V**. The most stable 2 min of oxygen (O_2) consumption for each bird and air temperature was used for subsequent analyses. Panel A shows measurement at one air temperature for four birds measured for 10 min each in sequence, starting and ending with a baseline. (B) Cold tolerance measurements were used in **Paper I**I. The mean of 10 min before the endpoint was used for calculations of cold tolerance limit and summit metabolic rate. An experiment started and ended with a baseline. One bird was measured at a time. (C) Heat tolerance measurements were used in **Paper II**. The mean of the most stable 2 min at the highest air temperature reached was used for calculations of heat tolerance limit, metabolic heat production and evaporative water loss. The experiment started and ended with a baseline. One bird was measured at a time. Adapted from Figure S1 in **Paper II**.

In blue tits (**Paper V**), body temperature was measured using a Testo 925 thermometer, by inserting a 0.9 mm chromel-alumel (type K) thermocouple 12 mm (10 mm in 6-day old nestlings) through the cloaca. Further insertion does not change body temperature readings (Andreasson et al., 2018). Body temperature measurements were taken directly at capture to minimize effects of handling induced stress which may occur shortly after disturbance and influence body temperature (Andreasson et al., 2020b; Lewden et al., 2017; Cabanac & Guillemette, 2001; Nord & Folkow, 2019; reviewed by McCafferty et al., 2015).

Figure 9. Blue tit nestlings are returned to the nestbox after morphology and body temperature measurements. Photo: Kasper Hård.

Contributions to the field

Phenotypic flexibility drives thermoregulatory responses to postnatal development temperature

Since evaporative cooling efficiency or capacity is important for tolerating heat exposure (McKechnie et al., 2016; McKechnie & Wolf, 2019), I expected that heat acclimated birds should be better able to handle high environmental temperatures. The results in **Paper I** showed that Japanese quail that were raised in warm postnatal temperature conditions during the first 3 weeks after hatching were better able to handle warm conditions as juveniles (3 weeks old) compared to quail raised in mild conditions: warm-reared quail had a lower metabolic heat production than mild-reared quail and therefore, produced less heat (Figure 10A). Recent work shows that birds may use metabolic suppression (i.e., *hypometabolism*) in response to elevated environmental temperatures (Voges et al., 2024), which reduces the need to dissipate heat. I found no difference in evaporative water loss between treatment groups, but as a result of the lowered metabolic heat production in warm-reared juveniles, their evaporative cooling efficiency improved (Figure 10B). This corroborates a study on heat acclimated adult zebra finches (*Taeniopygia guttata*; Wojciechowski et al., 2021), but contrasts recent work where a heat challenge in zebra finches had no effect on metabolic heat production or evaporative water loss (Ton et al., 2021). After 5 weeks in mild conditions (i.e., at 8 weeks of age), metabolic heat production and evaporative cooling efficiency no longer differed between warm-reared birds and mild-reared birds (Figures 10A-B), suggesting effects are flexible, reflecting phenotypic flexibility.

There was no evidence for improved ability to handle cold temperatures in cold-reared quail compared to mild-reared quail at any age (3 and 8 weeks; Figure 10C-D): metabolic heat production, evaporative cooling efficiency and body temperature were all unaffected by the experiment. The lack of effects on metabolic heat production in cold-reared quail contrasts with the increased metabolic heat production typically observed during seasonal acclimatisation to low environmental temperatures in nature (reviewed by Swanson & Vézina, 2015). It is possible that the cold developmental temperature was not low enough to affect metabolic heat production recorded at submaximal cold exposure. In line with this, the metabolic response to winter conditions has been shown to be higher in colder winters months than in milder winters months (Petit et al., 2013). However, since studies have found that basal and summit metabolic rate are not always correlated (Petit et al., 2013; Swanson et al., 2012), cold conditions could still have affected cold tolerance traits even if such effects could not be demonstrated by measuring cold juveniles in submaximal air temperatures.

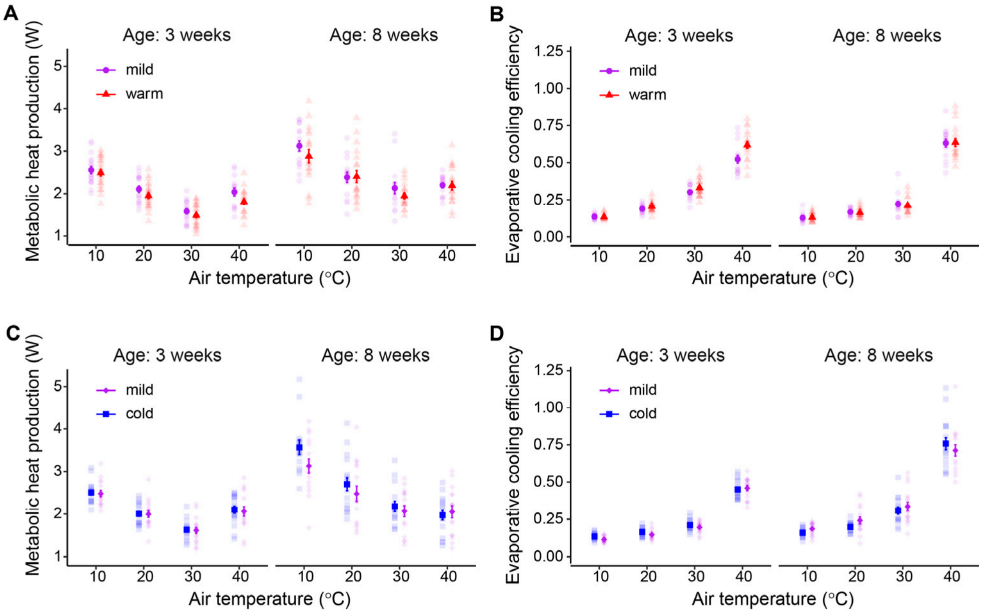

Figure 10. Effects of variation in postnatal developmental temperatures on metabolic heat production and evaporative cooling efficiency in Japanese quail. Birds were reared under warm (30°C), cold (10°C) or mild (20°C; control) conditions until 3 weeks of age, after which they were transferred to mild conditions until 8 weeks of age. (A) Metabolic heat production and (B) evaporative cooling efficiency of warm-reared and mild-reared Japanese quail in different air temperatures. (C) Metabolic heat production and (D) evaporative cooling efficiency of cold-reared and mild-reared Japanese quail in different air temperatures. Semi-transparent points: raw data. Data were collected in two separate studies (see **Paper I**). Adapted from Figure 3 in **Paper I**.

The findings from **Paper I** were expanded on in **Paper II**. Here, I shifted to investigating effects on maximal heat- and cold tolerance. Maximal temperature tolerance limits are likely to be well beyond environmental temperatures a bird would be expected to meet in nature, but individuals that are able to tolerate extreme environmental temperatures might also be better able to endure submaximal thermal stress while accumulating somatic costs at a lower rate (cf. Orsted et al., 2022). In addition, I investigated if acclimation to extreme environmental temperatures causes trade-offs between heat- and cold tolerance, as seen in ostriches (Schou et al., 2022), since if birds acclimate to a prevailing thermal condition it might come at a cost of tolerating fluctuating environmental temperatures.

The results showed that warm postnatal developmental temperature improved heat tolerance: quail that were raised in warm conditions were able to evaporate more water and showed improved heat tolerance limits compared with quail raised in cold conditions (Figure 11A-B). By analogy, but unlike in **Paper I**, cold developmental temperature improved cold tolerance, such that cold-reared quail improved thermogenic capacity reflected by a higher summit metabolic rate, which improved cold tolerance limits compared with warm-reared birds (Figure 11C-D). Increased temperature tolerance and higher thermoregulatory competence may enable birds to sustain their foraging activity, or exploit thermally challenging microhabitats, thereby minimizing the missed opportunity costs associated with temperature fluctuations.

Despite expected differences in heat- and cold responses among treatment groups, I found no evidence for a trade-off between heat- and cold tolerance at the level of individual thermoregulation, indicating that heat tolerance is not influenced by enhanced cold tolerance and that cold-adaptation might not enhance the risk of detrimental hyperthermia. This may be because thermogenesis and thermolysis operate through largely distinct physiological pathways. It is possible, however, that the relationship between them may be different depending on which pathway that is used for evaporation. Evaporative respiration occurs either through panting – which is energetically demanding and thus also increase metabolic heat production (McKechnie et al., 2021; McKechnie et al., 2016; Smit et al., 2018) – or through gular fluttering that requires little energy (O'Connor et al., 2017; Talbot et al., 2018; Talbot et al., 2017). Therefore, a trade-off might emerge in species that are phylogenetically constrained to panting (such as passerines; e.g., McKechnie et al., 2021; McKechnie et al., 2016; Smit et al., 2018), but not in species using gular fluttering such as the Japanese quail.

By investigating whether effects on thermoregulation reflected developmental plasticity or phenotypic flexibility by transferring the birds to mild, common-garden, conditions, I could conclude that the effects were largely reversed after a period of 3 weeks. The reversal of traits is in line with previous studies also demonstrating reversal of the phenotypic responses to postnatal developmental temperatures (**Paper I**; Liew et al., 2003). There was a difference in the timeline for reversal between traits, however. This might impact the capacity to handle unstable environmental temperatures, at least if reversal times are mismatched with the speed of which environmental temperature changes.

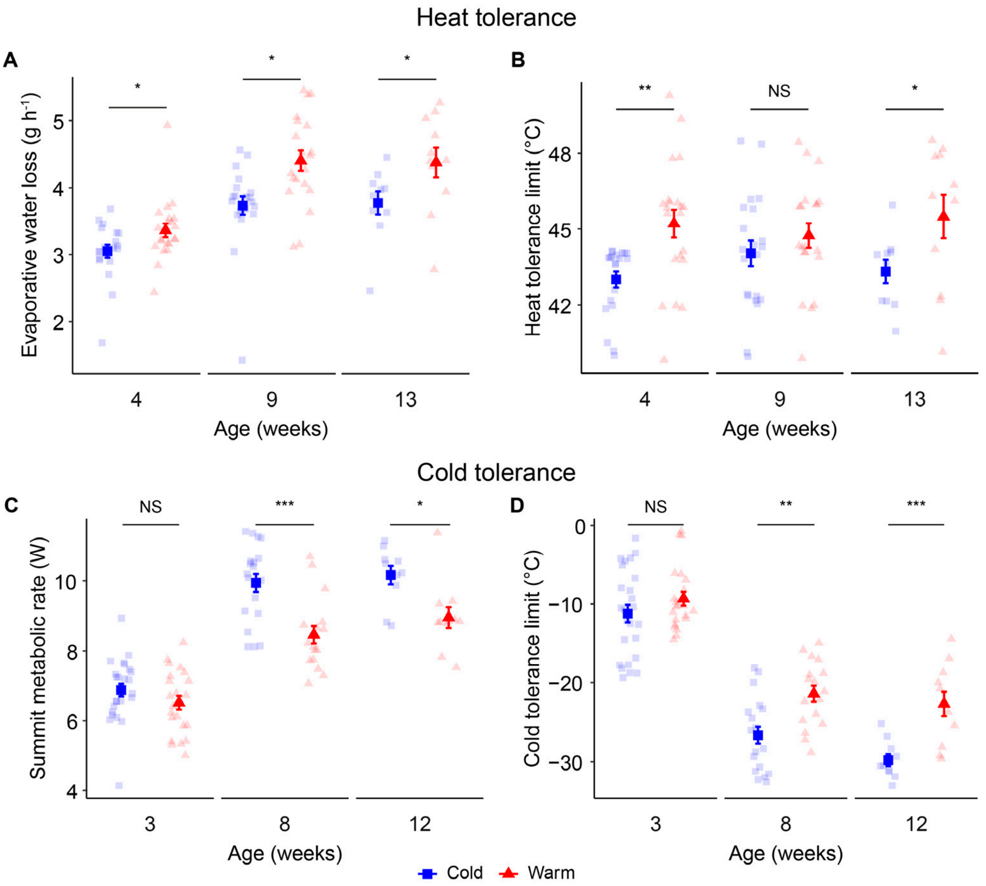

Figure 11. Increased heat- and cold tolerance in temperature-acclimated Japanese quail. Panels show (A) evaporative water loss and (B) heat tolerance limit from heat tolerance measurements, and (C) summit metabolic rate and (D) cold tolerance limit from cold tolerance measurements. Quail were reared in warm (30°C) or cold (10°C) conditions until 13 weeks of age. At 9 weeks of age, half of each treatment group were transferred to mild conditions (20°C) for investigating if effects are lasting. Semi-transparent points: raw data. Asterisks represent levels of significance (NS: $p > 0.05$; *: $0.05 \geq p > 0.01$; **: $0.01 \geq p > 0.001$; ***: $p \leq 0.001$). Adapted from Figures 2 and 3 in **Paper II**.

The results from **Paper II** indicate that there is space to acclimate thermoregulatory traits and temperature tolerance in the expected direction. However, my study showed that there was a much larger span for acclimation to colder environmental temperatures (around 7°C difference in cold tolerance limit; Figure 11D) than there was for acclimation to warmer environmental temperatures (around 2°C difference in heat tolerance limit; Figure 11B) at the organismal level. This is consistent with our previous research showing that, at the subcellular level, acclimation to cold environmental conditions improves the thermal sensitivity of mitochondria (i.e., how mitochondria respond to temperature), whereas acclimation to warm temperatures provides no advantage during a heat-challenge (Correia et al., 2025). The small span for acclimation to high environmental temperature seen at both organismal and subcellular levels raises concerns shared with those for ectotherms: a low capacity to acclimate heat tolerance limits constrains the potential for evolutionary rescue from climate warming (Jørgensen et al., 2022; Morgan et al., 2020).

Taken together, the results from **Papers I** and **II** demonstrate that birds raised in warm postnatal developmental temperatures were better able to cope with both moderate (submaximal) air temperatures and extreme (maximal) warm air temperatures. Effects of cold postnatal development temperature, on the other hand, contrasts between **Paper I** and **Paper II**, such that there were no effects at moderate air temperatures, but apparent effects at extreme cold air temperature even though rearing temperatures were the same. This suggests that to capture the full dynamics of postnatal developmental temperature-effects measurements should be taken over air temperatures ranging from submaximal to the thermal limits. Furthermore, thermoregulatory traits in both **Papers I** and **II** were shown to be reversible. This indicates that, while effects of thermal challenges in the prenatal environment may have lasting effects on an individual's thermoregulatory competence (via developmental plasticity; e.g., Arjona et al., 1988), effects caused by postnatal development temperature challenges reflect phenotypic flexibility.

A small body does not facilitate thermoregulation

The results in **Paper III** showed that the assumption that an increased ratio between surface area to volume facilitates thermoregulation depends on context. In cold temperatures, effects of body size, tarsus and bill length on thermoregulation are found only in juveniles and they are surprisingly limited. In response to cold temperatures, following predictions of Bergmann's and Allen's rules (Bergmann, 1847; Allen, 1877), juvenile quail that were smaller with longer legs (i.e., tarsi) had higher metabolic slopes (i.e., the rate of increase in metabolism) compared with larger quail with shorter legs when exposed to mild cold. However, the effect sizes were small, with body masses that were very small (2 standard deviations below the mean) and tarsus lengths that were very long (2 standard deviations above the mean) predicted to increase metabolism above average by 6.5% and 2.8%, respectively. In adults, the predictions were not supported by our findings.

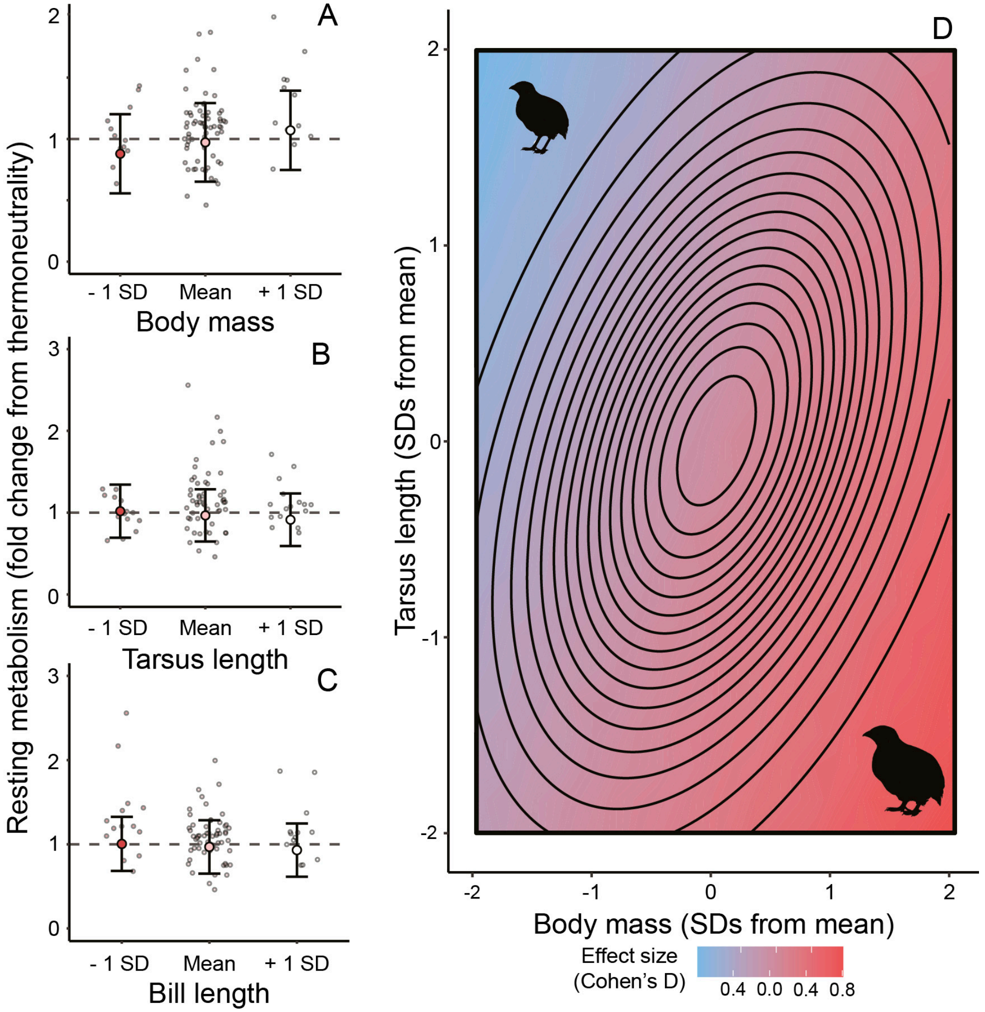

Figure 12. Effects of morphology and experienced temperature on metabolic responses to heat in Japanese quail. Panels show effects of (A) body mass, (B) tarsus length and (C) bill length in adult birds' resting metabolism (as fold change from 30 to 40°C) Large points: predicted variables. Error bars: ±1 standard deviation (SD). Small points: raw data. Panel D shows the combined effects of body mass and tarsus length on metabolic slopes in heat relative to the mean. Effects: mean Cohen's D values, >0.8 large effect size, >0.5 medium effect size and >0.2 small effect size. The multivariate normal distribution of phenotypes in quail is shown by the circles, where the centre is the peak of the distribution and outer circles represent rare phenotypes. Adapted from Figure 2 in **Paper III**.

Warm-reared quail exhibited reduced body size and longer appendages, similar to what have been found in nature. Body size, tarsus and bill length independently affected costs of thermoregulation as juveniles and adults. However, the effects were small, suggesting there is limited benefits on thermoregulation of shrinking and shape shifting. In juveniles, metabolic responses to heat exposure increased in quail with larger body mass and short legs and bills in warm environmental temperatures compared to small quail with long legs and bills. In addition, patterns in evaporative cooling efficiency implies that the increased metabolism in larger birds was linked to a constrained capacity to counteract endogenous heat production via evaporative pathways. The increased metabolic response could reflect a lower capacity to lose heat from combined wet and dry heat loss. As a result, large birds might have to rely on increased panting, which increases metabolic heat production. Also in adults, metabolic responses to heat exposure increased with increased body mass (Figure 12A). However, larger appendage lengths (which were common among larger individuals) led to slight reductions in the energetic costs of high temperatures (Figures 12B-C), thus partially counter-acting the metabolic consequences of a large body size in the heat. Yet, phenotypes expected to suffer moderate to large thermoregulatory costs required substantial deviations from allometric expectations (i.e., having a large body with short limbs) that were uncommon in our population, while those expected to obtain moderate or large benefits (i.e., having a small body size with long limbs) were absent (Figure 12E).

Paper III predicted that only birds with substantial (unnatural) deviations from allometry benefit from mass reductions. These results were expanded on in **Paper IV**, by testing the hypothesis that only body sizes outside of the natural range influence thermoregulation. Therefore, I exploited agricultural selection to compare thermoregulatory traits in Japanese quail breeds that varied more in body mass than what can be observed in any natural population: small birds weighed only half of the medium birds, and three times less than the large birds. Medium birds, in turn, had a 0.3-fold body mass of that than large birds. The results showed that small quail had improved heat tolerance compared to both medium and large quail (Figure 13A). Specifically, while metabolic heat production and evaporative water loss increased as expected with increasing body size (Figure 13B), small quail had higher evaporative cooling capacity and higher evaporative scope (Figure 13C). Despite this, thermoneutral zones were similar between the different breeds. This insight, in combination with differences in heat tolerance limits, indicates that usage of thermoneutral zone boundaries to understand constrains of hot temperature on birds is not without problems. That is, using thermoneutral zones to estimate heat constraints could result in over- or underestimation of tolerance limits. Even though small birds had higher evaporative cooling capacity and higher evaporative scope, allowing them to tolerate higher air temperatures, a reduction in body size could have other consequences (McKechnie et al., 2021). For example, smaller birds dehydrate faster than larger birds and could therefore, somewhat counterintuitively, be more vulnerable to hyperthermia (McKechnie et al., 2021) despite having higher heat tolerance limits.

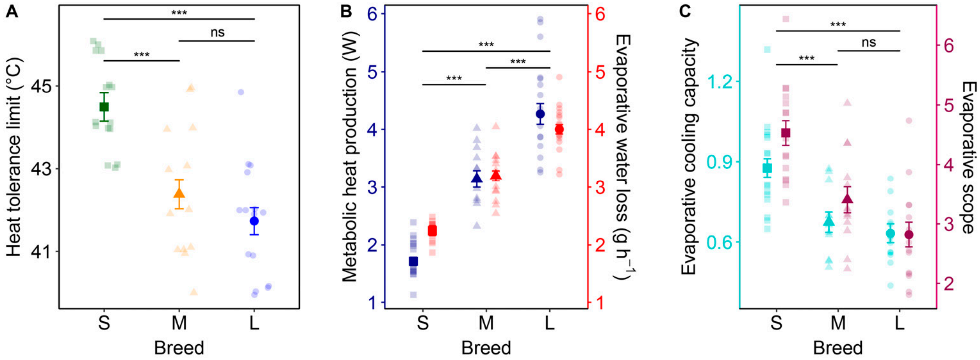

Figure 13. Heat tolerance traits in Japanese quail from three different breeds. Panels show (A) heat tolerance limit, (B) metabolic heat production and evaporative water loss, and (C) evaporative scope and evaporative cooling capacity, averaged over quail of 3 and 10 weeks of age. Semi-transparent points: raw data mean of age-specific measurement. Dashed line: representation of an evaporative cooling capacity of 1. Asterisks represent levels of significance (ns: $p > 0.05$; *: $0.05 \geq p > 0.01$; **: $0.01 \geq p > 0.001$; ***: $p \leq 0.001$). Adapted from Figure 2 in **Paper IV**.

Overall, the findings in **Papers III** and **IV** suggest that shrinking body size has negligible effects on thermoregulatory competence unless size differences are extreme. Hence, shifting thermoregulatory demands under a warming climate probably exerts, at most, limited selective pressure on morphology. Moreover, it is possible that large birds have competitive advantages that provide priority access to limited resources (e.g., water and food), which would improve heat tolerance, and/or to microhabitats that are cooler than prevailing environmental temperature. This could explain why positive selection on body size appears to remain even though global temperatures keep increasing (Siepielski et al., 2019).

Increased thermoregulatory demands limit growth

The results of **Paper V** show evidence for a trade-off between thermoregulation and growth in blue tit nestlings. Specifically, I found that experimentally increased postnatal developmental temperatures resulted in increased body temperature in 6-day-old nestlings (Figure 14A). In line with results from **Paper I**, the nestlings decreased their metabolic heat production as a response to heating compared to control nestlings (Figure 14E), probably to minimize heat load. Mechanistically, reduced metabolic heat production in heated nestlings could reflect both hypometabolism and a reduced efficiency of the metabolic machinery (Hohtola & Visser, 1998) either as an adaptive response to heat exposure or as a consequence of a lower demand for heat production. Yet, the compensation was imperfect because heated nestlings had lower body mass compared with control nestlings (Figure 14C). The trade-off between thermoregulatory demand and growth was further supported by a negative relationship between body temperature and body mass: heated nestlings weighed 0.26 g less for each 1°C increase in body temperature. Interestingly, the decreased growth in heated nestlings is in line with the observations of shrinking body sizes in warmer environmental temperatures (discussed above), and points to a possible developmental component of extant size declines in birds (Tabh & Nord, 2023; Weeks et al., 2022).

After 8 days without a heat challenge, near fledging, no effects of the warm developmental temperature on body mass or thermoregulatory traits remained (Figures 14B,D,F). Nor was there any relationship between body mass and body temperature. In other words, nestlings had compensated for the lower body mass which suggests that they can catch up after a bad start. However, there might be costs connected to this compensation that can be paid over both short- and long timescales (Metcalfe & Monaghan, 2001). These costs can be both physiological and ecological, and include predation risk, fat deposition rate and reduced lifespan (Metcalfe & Monaghan, 2001). For example, zebra finches that compensate for small body size (from suboptimal rearing environment) with faster growth were found to have reduced lifespan (Metcalfe & Monaghan, 2001). On the other hand, compensatory growth should also be associated with some benefits, such as increased reproductive success (Metcalfe & Monaghan, 2001) or survival.

The results from **Paper V** are consistent with the findings in **Papers I** and **II**, suggesting that postnatal developmental temperatures reflect phenotypic flexibility and not developmental plasticity. Yet, in **Paper V** I found negative effects of developmental heat exposure on body mass growth, which was not evident in **Papers I** and **II**. This discrepancy suggests that studies in the wild reveal potential trade-offs between thermoregulation and growth that captive studies miss.

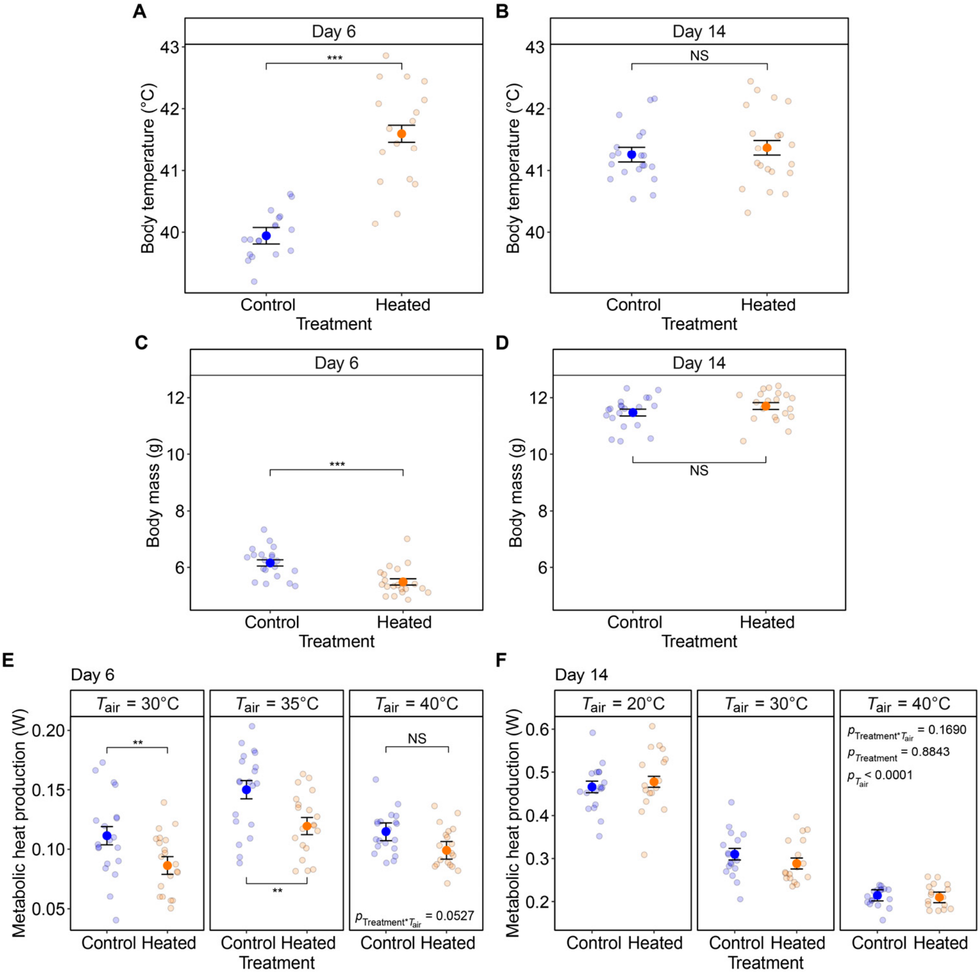

Figure 14. Effects of developmental temperature on morphological and thermophysiological traits in blue tits. Nestlings were heat challenged during the first 6 days after hatching, after which the heat stressor was removed. Panels show body temperature in (A) 6-day-old and (B) 14-day-old nestlings, body mass in (C) 6-day-old and (C) 14-day-old-nestlings, and metabolic heat production in different air temperatures (T_{air}) in (E) 6-day-old and (F) 14-day-old nestlings. Semi-transparent points: raw data. Asterisks represent levels of significance (NS: $p > 0.05$; *: $0.05 \geq p > 0.01$; **: $0.01 \geq p > 0.001$; ***: $p \leq 0.001$). Adapted from Figures 2 and 3 in **Paper V**.

Conclusions and future directions

An animal's performance (i.e., the ability to function and survive) is related to its body temperature through a non-linear relationship (Angilletta et al., 2010; Boyles et al., 2011; Cunningham et al., 2021). Performance is optimized over a range of body temperatures that are species-specific. While the body temperature of ectotherms vary widely with the thermal environment, endotherms usually have a narrower range of stable body temperatures. In both cases, performance declines with hyper- or *hypothermia* (i.e., when core body temperature is above or below the range for normal body temperature of a species [IUPS Thermal Commission, 2003]; Angilletta et al., 2010; Boyles et al., 2011; Cunningham et al., 2021), which in turn can be more likely at high or low environmental temperatures. Thus, the ability to control thermoregulation with high precision and flexibility is important in thermally variable environments. In this thesis, I studied what determines the success with which birds achieve such control.

I have shown that changes in postnatal developmental temperature, in laboratory conditions and in the wild, have short-term effects on both physiology and morphology in birds. In both sets of environmental conditions, rearing temperature had priming effects on thermoregulatory traits (**Papers I**, **II** and **V**), but high developmental temperature in wild birds were associated with costs suggestive of a trade-off between thermoregulation and growth (**Paper V**). Nevertheless, the effects of developmental temperature on physiology and morphology of developmental temperature, seen in **Papers I, II** and **V**, remained only for as long as the birds experienced an environmental temperature-challenge. This suggests that postnatal developmental temperature does not cause permanent programming reflecting developmental plasticity, but that the effects are reversible and reflect phenotypic flexibility. Studies on ectotherms suggests that phenotypic flexibility is costly and may be lost in stable environments (Morgan et al., 2022). The results in **Papers I, II** and **V** indicates that costs of phenotypic flexibility in endotherms might be less pronounced than have been observed in some ectotherms (Morgan et al., 2022). While developmental plasticity is likely to be beneficial in stable environments where juvenile and adult thermal conditions are matched, phenotypic flexibility is likely to evolve when environmental conditions fluctuate within and between life stages, or when animals are highly mobile. In birds and other endotherms, phenotypic flexibility could therefore increase the matching of phenotypes and the surrounding environment.

I expected that effects on thermoregulatory traits would be lasting. While this was not the case, it is still possible that there are lasting effects on other traits. For example, some studies have reported lasting effects of developmental temperature on survival and recruitment rate (Andreasson et al., 2018; Greño et al., 2007; Hepp & Kennamer, 2012; Nord & Nilsson, 2016; Woodruff et al., 2025). Even though thermoregulatory traits might be flexible (as seen in **Papers I, II** and **V**), future research should investigate other traits that are likely to be affected by postnatal developmental temperatures, asking if these are subject to long-lasting consequences that remain to later life stages. Since most birds have developed a functional, responsive, thermoregulatory system from an early age (e.g., Andreasson et al., 2016; Engert et al., 2025; **Paper V**), it is possible that the manipulations employed in this thesis were timed after the window for developmental plasticity had closed. In line with this, a range of studies performed in poultry production contexts shows that embryonic thermal manipulation typically results in increased ability to handle matched thermal environment in adulthood (e.g., Piestun et al., 2011). One example of longer-lasting effects of developmental temperature is appendage length. However, **Paper III** and **Paper IV** showed that body size and shape differences must surpass allometric expectations for natural populations to have meaningful impacts on thermoregulation.

Several outstanding questions about the effects of developmental temperature on the ontogeny of growth and thermoregulation remain. In brief, future studies should focus on: (i) broader ecological relevance (e.g., laboratory vs wild conditions); (ii) mechanisms underlying thermal acclimation (e.g., endocrine pathways connected to thermoregulation; Box 3); and (iii) intra- and intergenerational effects of developmental temperature conditions on thermoregulatory traits, such as heat- and cold tolerance.

First, my studies highlight the importance of investigating thermophysiological consequences of developmental temperature by measuring multiple traits under different conditions, as these effects may vary depending on the trait and condition (e.g., laboratory vs. wild) studied. It is important that future studies include wild species both under controlled laboratory settings and in nature to gain knowledge about the full picture of effects of environmental temperature stress in ecologically relevant settings. **Paper V** highlights why this matters.

Second, the effects of developmental thermal acclimation on the mechanisms behind endocrine regulation of thermoregulation and water balance are poorly understood. Since thermoregulation demands increased energetic expenditure in cold environments and increased water use in warm environments (reviewed by McKechnie, 2022), examining the mechanism of water and energy intake is important for a deeper understanding of thermoregulatory processes. Molecular and endocrine mechanisms underlaying thermoregulation may facilitate or constrain thermal acclimation through well-known pathways, including thyroid hormones acting on thermogenesis, corticosterone acting on homeostasis, and molecular mechanisms that protect cells from heat stress (e.g., heat shock proteins; Dubrez et al., 2020). A higher water usage during high environmental temperatures could be addressed by investigating lesser-known pathways, such as the antidiuretic hormone arginine vasotocin (the avian analogue of the mammalian arginine vasopressin). The potential thermoregulatory role of arginine vasotocin is demonstrated in some studies. For example, circulating arginine vasotocin increased during dehydration in Japanese quail and domestic fowl (Chaturvedi et al., 2000; Stallone and Braun, 1986), which could affect fluid retention (Takahashi et al., 1995; Box 3).

Third, little is known about the inheritance of phenotypes acquired through thermal acclimation, or of thermoregulatory traits in general. The parental environment may cause epigenetic changes (i.e., changes in gene expression without changes in genetic code) or give rise to maternal effects (Bleu et al., 2017; Ruuskanen, 2015; Uller, 2008). If this pertains also to thermally acclimated parental phenotypes, the parents' thermal environment could affect how the next generation thermoregulates (e.g., Donelson et al., 2012; reviewed by Donelson et al., 2018; Zizzari & Ellers, 2014). These questions have been studied in ectotherms and plants (Deng et al., 2021; Groot et al., 2016; Latzel et al., 2014). For example, fruit flies (*Drosphila melanogaster*) that were reared in variable environmental temperatures increased heat tolerance compared to flies reared at constant environmental temperatures (Cavieres et al., 2019). These effects extended to the next generation: fruit fly offspring from flies reared in variable environmental temperatures showed improved thermal performance curves of locomotor performance in constant environmental temperatures compared to offspring from flies reared under constant environmental temperatures (Cavieres et al., 2019). Little is known about non-genetic inheritance in birds and other endotherms. However, zebra finch nestlings from parents incubated in cold environmental temperatures had a lower body mass and a smaller bill than nestlings from control-incubated parents (Hope & Angelier, 2024), suggesting similar mechanisms may exist in more complex animals. Although inheritance could be ameliorating if parental and juvenile environmental conditions overlap, (following the 'environmental matching' hypothesis), inherited effects could also be constraining (following the 'silver spoon' hypothesis), if inheritance causes a mismatch between the parental and offspring environments. Hence, future studies should elucidate intergenerational effects.

In conclusion, my thesis shows that while postnatal developmental temperatures seem to prime thermoregulatory performance, it reflects phenotypic flexibility and does not carry long-term consequences on thermoregulation. However, if any such acclimation to the thermal environment reverse at a different timescale than the thermal environment, or if effects are inherited, birds that developed under extreme weather events could still be mismatched to their prevailing thermal environment. Additionally, changing morphologies as a means of lowering thermoregulatory costs in warming climates have limited benefits, especially when the potential to buffer effects of environmental temperature is high (e.g., through thermal acclimation via phenotypic flexibility). The research priorities going forward should focus on mechanisms underlying these changes, for example by measuring hormones and molecular responses during temperature challenges. In addition, future work should investigate whether parental thermal environments can affect offspring phenotypes through genetic and non-genetic effects, for example, by breeding thermally acclimated birds and test heat tolerance amongst their offspring. By doing this, the research field will gain much needed knowledge about how wildlife will respond to the prevailing and future environment.

Box 3. Physiological pathways of the endocrine control of thermoregulation

Thermogenesis: The hypothalamus–pituitary–thyroid axis has been shown to be sensitive to heat stimulation during development. This axis regulates thyroid hormones connected to thermogenesis (Ruuskanen et al., 2021). Cold exposure increases levels of the thyroid hormone triiodothyronine which binds to receptors and impacts gene expression to change metabolic rates (Ruuskanen et al., 2021). For example, broilers that were heat-challenged as embryos had lower concentrations of the thyroid hormone triiodothyronine during a heat challenge in adolescence (Piestun et al., 2008).

Homeostasis: The hypothalamus–pituitary–adrenal axis regulates the major stress hormone corticosterone (glucocorticoid hormone) that is important for sustaining homeostasis (Ruuskanen et al., 2021). Corticosterone has been shown to increase in response to both heat- (Piestun et al., 2008) and cold- (Bize et al., 2010) challenges. Therefore, responses and adaptions of shifts in environmental temperature in an individual have been suggested to be linked to corticosterone (Ruuskanen et al., 2021). A possible explanation is that corticosterone facilitates the mobilisation of endogenous energy reserves and/or activates foraging behaviour to sustain elevated metabolic expenditure under cold conditions (de Bruijn & Romero, 2011; Jimeno et al., 2018).

Water balance: Since evaporative heat loss requires water (Nord & Williams, 2015; Tieleman & Williams, 1999), hormones controlling water balance likely play a role in thermoregulation. The hormone arginine vasotocin, which is a functional analogue to the main mammalian antidiuretic hormone arginine vasopressin, has been shown to be involved in avian water balance (Goldstein, 2006), with an increase in circulating levels during dehydration (Robinzon et al., 1990). Moreover, exogenous administration of arginine vasotocin results in fluid retention in the avian kidney (Takahashi et al., 1995). Additionally, exogenous arginine vasotocin reduced shivering, lowered body temperature and decreased plasma levels of triiodothyronine (Hassinen et al., 1994; Hassinen et al., 1999; John & George, 1992), indicating a role in lowering heat gain.

Acknowledgements

When I write this it is a beautiful spring day and almost time to hand in. Although you all have been a part of this journey and that means the most to me, I am not good at doing thank you. When I reflect at these more than 4 years, I recall good, and maybe not as good, memories. But at the same time, I also see how much I have grown as a person and as a scientist, at that is because of you (both mentioned here and not). Thank you!

Andreas, you allowed me to be me, to be angry, frustrated, sad, or happy. You saw me for who I am and never judged (maybe a bit), even during my not so smart moments. Thank you for believing in me when I did not, for always being there, for your support through every small to large step on this path. I am (still) amazed of your knowledge, of how you manage to do everything you do and have time for others. Sometimes I think you are not human. It has been a wonderful journey, and I will always be grateful.

Lars, thank you for always supporting me and making sure that I was not overwhelmed with projects and tasks to do. And most importantly that I would make it all the way. You have been a great co-supervisor. **Lettice**, I take it as something positive that I have not needed you more than I have as a mentor. You have inspired me to see that if you want something, you can make it happen. **Susanne**, I will always appreciate that you made sure that everything was okey and that you would help me if needed. Thank you for all input during meetings, in offices and hallways.

Josh, I am grateful to have shared these past 4 years with you. Thank you for the discussions, fika, dancing and everything else. Including comments for improving this text. **Elisa**, you have inspired me so much. I am so thankful that our paths crossed. You make every day brighter. **Maria**, you are an amazing person. What would I have done if you did not join our group for a, not so short, time. **Malin**, thank you for being there and listening when no one else understood. And to the rest of the past and present lab group, **Livia**, **Samantha**, **Katherine**, **Chloé**, et al., hanging out with you never gets boring.

Jocke, thank you for all the inspiration since early bachelor's courses. For all help with fieldwork. For showing that caring for other people are as important, if not more, than anything else. **Fredrik**, thank you for being around when needed, for discussions, field work, support and help. **Hanna W.**, thank you for telling the truth and what I needed to hear, and for showing interest in my work. **Johan N.**, thank you for all encouragement, it has meant a lot. To the rest of the Ecological and Evolutionary Physiology research group, **Caroline**, **Arne**, **Zsófia**, **Ernö**, **Amparo**, and all other past and present temporary and permanent members, I have learnt so much.

Susana, teaching with you was never boring (although I will not miss the bike). You have given so much joy. **Elsie**, thank you for the valuable feedback on this work. For helping with all my stupid questions, and for bringing joy on daily basis. **Rae**, when we started our master's, I never thought we would end up here almost at the same time. Sharing discussions, courses, coffee breaks, lab meetings, field work, etc. has been wonderful. Many thanks to the current and past PhD students, **Violeta**, **Robin**, **Pablo**, **Jesper**, **Frida**, **Simon**, **Erica**, **Emma K.**, **Sofie**, **David**, **Agnes**, **Anna**, **Linus H.**, **Ann-Kathrin**, **Johan K. J.**, **Kalle**, **Kristaps**, **Iain**, **Katie**, **Jaume**, **Qinyang**, **Twinkle**, **Ximena**, **Sara**, **Agnieszka**, **Hanna T.**, **Emma E.**, **Nima**, **Blahoslav**, **Ayan**, **Shubham**, **Anca**, **Nikol**, et al., this journey would not have been the same without you. I am happy to have met you.

Linus M., thank you for all the support you have given me, for believing that this would come true.

And to my family, you are the best! Your support through every scary moment that led to something good is wonderful. **Mamma**, jag vet att jag är totala motsatsen till vad du är, ändå har du stöttat varje beslut jag gjort. Tack för all vägledning under tiden. **Pappa**, tack för att du alltid visat intresse för det jag har gjort, och för att du alltid försökt att hjälpa när hjälp har behövts. **Amanda**, tack för att du fick mig att tänka på annat än jobb när det behövdes, för att du var frustrerad tillsammans med mig.

Kasper, tack för alla diskussioner all hjälp med konstiga frågor och att alltid försöka övertyga mig om att jag vet mer än vad du gör. Ditt orubbliga stöd och din förståelse under långa dagar som förvandlades till månader, i labbet och ute i fält. Du har fått långa och tråkiga dagar att kännas värda genom att alltid finnas vid min sida. Jag hade aldrig klarat det utan dig. Och jag kommer inte alls bara sitta där och vara värdelös ;)

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Temperature-dependent ontogeny of bird thermoregulation and growth

I. **Persson, E.,** Cuív, C. Ó., & Nord, A. (2024). Thermoregulatory effects of growing up during a heatwave or a cold snap in Japanese quail. *Journal of Experimental Biology*, 227(2), jeb246876. doi: 10.1242/jeb.246876

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III. Tabh, J. K. R., **Persson, E.,** Correia, M., Cuív, C. Ó., Thoral, E., & Nord, A. (2025). Limited evidence that body size shrinking and shape-shifting alleviate thermoregulatory pressures in a warmer world. *Communications Biology*, 8(1), 707. doi: 10.1038/s42003-025-08131-7

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V. **Persson, E.,** Nilsson, J-Å., & Nord, A., Experimental evidence for a tradeoff between growth and thermoregulation in blue tit nestlings. *Submitted*.

Printed by Media-Tryck, Lund 2026 NORDIC SWAN ECOLABEL 3041 0903

LUND UNIVERSITY

Department of Biology
Faculty of Science

ISBN 978-91-90202-02-9