

Tomorrow is yesterday: early-life conditions shape ectotherm life histories

Reptile case studies in two hemispheres

Alexander Hansson

Department of Biological and Environmental Sciences
University of Gothenburg

&

School of Natural Sciences
University of Tasmania

2023



UNIVERSITY OF
GOTHENBURG



UNIVERSITY of
TASMANIA

This doctoral thesis in Natural Sciences, specializing in Biology, is authorised by the Faculty of Science to be publicly defended at 10:00 am on Friday the 20th of October, 2023 at the Department of Biological and Environmental Sciences, Medicinaregatan 7b, Gothenburg, Sweden.

The opponent is Professor Anders Forsman, Department of Biology and Environmental Science, Linnaeus University, Kalmar, Sweden.

Alexander Hansson

Dept. of Biological and Environmental Sciences | University of Gothenburg | Sweden
School of Natural Sciences | University of Tasmania | Australia

Email 1: alexander.hansson@bioenv.gu.se

Email 2: hansson.h.alexander@gmail.com

The papers and illustrations in this thesis are published with permission from:
The Company of Biologists (Paper I)

ISBN: 978-91-8069-423-0 (PRINT)

ISBN: 978-91-8069-424-7 (PDF)

Electronic version: <http://hdl.handle.net/2077/78394>

Printed by Stema Specialtryck AB

Cover art: Gilma Sobrino Rada, Gilmalu Design

In memory of my brother. You are missed.

*“The sight of a feather in a peacock’s tail,
whenever I gaze at it, makes me sick!”*

Charles Darwin

Abstract

Life history theory seeks to explain the overwhelming diversity of resource allocation strategies in nature by exploring how evolutionary forces optimise survival and reproduction within an organism's environment. Central to this theory is that resources are finite, and thus increased investment into one trait may reduce resources available for another trait. Understanding proximate drivers of resource allocation is therefore of great interest in evolutionary biology. In ectotherms, temperature is the most influential external factor and affects most physiological and behavioural functions. While temperature can influence traits at any life stage, changes during development are often irreversible and therefore most influential to fitness. However, predicting the direction of effects is challenging as these are often context-dependent and vary considerably among species and populations. This thesis aims to add to our understanding of proximate and long-term effects of early-life thermal conditions on traits associated with survival and reproduction.

This work is the outcome of a collaboration between the University of Gothenburg and the University of Tasmania. I used two well-established ectotherm systems; the Swedish sand lizard and the Tasmanian spotted snow skink, to explore early-life effects on long-term life history traits. Both these systems are ideal models with decades of accumulated research detailing their physiology, life history and population structures. Leveraging this knowledge, I combined experimental manipulations and long-term mark-recapture data to examine the effects of early-life thermal conditions on key life history traits. I initially explored how incubation temperature affected sex determination and sex-specific telomere dynamics in neonate sand lizards. Sex is a crucial factor shaping life history strategies across all life stages. Telomeres, which protect chromosome ends, are vital components for organismal health, and their shortening has been linked to individual fitness and population structures. I showed that certain incubation temperatures can override chromosomal sex causing an overproduction of daughters. Additionally, incubation temperature influenced neonatal telomere maintenance, but sex was the strongest predictor of telomere dynamics. Female neonates had longer telomeres and better maintained them compared to males. This is likely explained by sex-specific selection on telomere length, in which it is a better predictor of fitness in females compared to males.

I then used longitudinal mark-recapture data to investigate the influence of early-life thermal conditions on the developmental rates of wild spotted snow skinks, and whether maturing decisions have costs to survival and reproduction later in life. Warmer early-life conditions caused females to mature earlier, grow larger, produce more offspring by midlife and live longer. This presented a life history paradox. To solve it, I applied survival trajectory models to the same long-term dataset to determine the latent costs of developmental rates. Specifically, whether females maturing early or large suffer increased rates of age-dependent declines in survival or fecundity (senescence). While maturing early did not cause increased rates of senescence, females that exhibited faster growth and matured large suffered significantly higher mortality rates later in life compared to smaller females maturing at the same age.

This thesis highlights the importance of considering variation in early-life conditions as drivers of individual heterogeneity in life history traits and resource allocation strategies. With constantly rising global temperatures, thermal effects on such traits have never been more relevant and can clearly affect the future health of ectotherm populations and influence their evolution.

Key words: life history, ectotherm, temperature, development, sex, telomere, senescence

Svensk summering

Livshistorieteorin avser att förklara den överväldigande mångfalden av resursallokeringsstrategier i naturen genom att undersöka hur evolutionära krafter optimerar organismens överlevnad och reproduktion inom deras miljö. En central del av denna teori är att resurser är begränsade och ökad investering i en egenskap kan minska resurser tillgängliga för en annan. Att förstå faktorer som påverkar resursallokering är därför av stor betydelse inom evolutionsbiologin. Hos växelvarma djur är temperatur den viktigaste yttre faktorn som visats påverka majoriteten av fysiologiska och beteendemässiga funktioner. Temperatur kan påverka egenskaper under alla livsstadier men förändringar som sker under utvecklingsstadiet är ofta permanenta med livslånga effekter som följd. Att förutsäga riktningen av effekter är en utmaning då de ofta skiljer mellan olika sammanhang och varierar betydligt mellan populationer. Denna avhandling ämnar bidra till vår förståelse av närliggande och långsiktig påverkan av temperaturförhållanden tidigt i livet på egenskaper som är kopplade till överlevnad och reproduktion.

Denna avhandling är resultatet av ett samarbete mellan Göteborgs universitet och the University of Tasmania. Jag genomförde studier på två ödlearter: svenska sandödlan och den tasmanska spotted snow skink. Båda arter har studerats under årtionden vilket lett till detaljerad beskrivning av deras fysiologi, livshistoria och populationsstruktur. Med hjälp av denna tidigare kunskap och en kombination av experimentella försök och långsiktiga fångst-återfångstdata undersöker jag hur temperaturförhållanden tidigt i livet påverkar viktiga livshistorieegenskaper.

Först undersökte jag hur inkubationstemperaturer påverkade könsbestämning och könsspecifik telomerdynamik hos sandödlor. Kön är en avgörande faktor som formar livshistoriska strategier genom alla livsstadier. Telomerer skyddar kromosomers ändar och utgör vitala cellulära komponenter och deras förkortning har visats påverka individuell överlevnad och fortplantningsförmåga, men även populationsstrukturer. Jag visade att vissa inkubationstemperaturer ledde till en överproduktion av döttrar. Dessutom påverkade inkubationstemperatur nykläckta sandödlors förmåga att underhålla sina telomerer. Kön hade dock den största påverkan på telomerdynamik, varvid honor hade längre telomerer och var bättre på att underhålla dem jämfört med hanar. Detta kan förklaras av könsspecifika selektionstryck på telomerlängd inom denna art, där telomerlängd mer exakt förutsäger överlevnad och reproduktionsframgång hos honor jämfört med hanar.

Därefter använde jag långsiktiga fångst-återfångstdata för att undersöka hur temperaturförhållanden tidigt i livet påverkar utvecklingshastigheten hos vilda spotted snow skinks och om tidig sexuell mognad eller mognad vid en stor storlek medför kostnader för överlevnad och reproduktion senare i livet. Varmare förhållanden tidigt i livet ledde honor att mogna tidigare och vid större storlek, producerar fler avkomor vid medelålder och leva längre. Detta skapade en livshistorisk paradox. För att lösa det, tillämpade jag överlevnadsmodeller på samma långsiktiga data för att undersöka dolda kostnader av utvecklingshastighet. Mer specifikt undersökte jag om honor som mognade tidigt eller vid större storlek påvisade lägre åldersberoende överlevnad eller reproduktionsförmåga (åldrande). Medan tidig mognad inte ledde till snabbare åldrande, honor som växte snabbare och mognade vid större storlek påvisade högre dödlighet senare i livet jämfört med mindre honor som mognade vid samma ålder.

Denna avhandling understryker vikten av att ta hänsyn till variation av förhållanden tidigt i livet som drivkrafter för individuell heterogenitet av livshistoriska egenskaper från födelse till död. Med ständigt ökande globala temperaturer har sådana temperatureffekter aldrig varit mer relevanta och kan påverka framtida hälsa hos populationer av växelvarma arter och deras evolution.

List of papers

- Paper I** Hansson, A., Wapstra, E., While, G. M., Lindsay, W. R., & Olsson, M. (2023). Context-dependent thermolability of sex determination in a lacertid lizard with heteromorphic sex chromosomes. *Biology Open*, 12, bio059967.
- Paper II** Hansson, A., Wapstra, E., While, G. M., & Olsson, M. (2023). Sex and early-life conditions shape telomere dynamics in an ectotherm. *Submitted to Journal of Experimental Biology*.
- Paper III** Hansson, A., Fitzpatrick, L. J., While, G. M., Olsson, M., & Wapstra, E. A predetermined fate – early-life conditions shape life histories in climatically distinct populations of a cold-climate ectotherm. *Manuscript*.
- Paper IV** Hansson, A., Fitzpatrick, L. J., While, G. M., Olsson, M., & Wapstra, E. Age and size at maturity predicts senescence in a cold-climate ectotherm. *Manuscript*.

Statement of authorship

The following people and institutions contributed to the publication of research undertaken as part of this thesis:

Alexander Hansson (candidate): Department of Biological and Environmental Sciences, University of Gothenburg & School of Natural Sciences, University of Tasmania

Mats Olsson (supervisor): Department of Biological and Environmental Sciences, University of Gothenburg

Erik Wapstra (supervisor): School of Natural Sciences, University of Tasmania

Geoffrey While (supervisor): School of Natural Sciences, University of Tasmania

Luisa Fitzpatrick (supervisor): School of Natural Sciences, University of Tasmania

Willow Lindsay: Department of Biological and Environmental Sciences, University of Gothenburg

Table of contents

1. Introduction	1
1.1. Life history traits, plasticity and constraints.....	2
1.1.1. Growth and development	4
1.1.2. Reproduction	5
1.1.3. Senescence and lifespan	8
1.2. Temperature and ectotherm life history traits	9
2. Research aims, study systems and main results	15
2.1. Sand lizard.....	19
2.1.1. Paper I – Sex determination	22
2.1.2. Paper II – Telomere dynamics	25
2.2. Spotted snow skink.....	28
2.2.1. Paper III – Early-life conditions shape life histories	31
2.2.2. Paper IV – Age and size at maturity predict senescence.....	34
4. Bridging hemispheres and closing words.....	38
5. Acknowledgements	46
6. References	47

1. Introduction

The theory of evolution is without a doubt the single most important theory in the study of life. It constitutes a unified theory of biology, giving an opportunity to explain everything in the natural world through one concept. Indeed, *"Nothing in biology makes sense except in the light of evolution"* (Theodosius Dobzhansky, 1973). Specifically, evolutionary biology aims to understand the processes that produced the overwhelming diversity of life from a single common ancestor. In biology, the term diversity is commonly used to describe the amount of variation on a genetic, species, or ecological level. Life histories play a central role in producing this variation, by shaping the fundamental patterns of growth, reproduction, and lifespan. Life history theory seeks to explain how evolutionary forces shape the survival and reproductive strategies of organisms so that they are optimised for a particular set of environmental conditions (Stearns, 1992; Roff, 1992; see Figure 1). However, things are not this simple, as variation in life history strategies are produced by trade-offs between survival and reproduction from birth to death—all governed by the finite availability of resources. These trade-offs strongly affect the rate of growth, reproduction and ageing of individuals, ultimately explaining variation in different strategies among populations of the same species and among species. Among-individual heterogeneity in life histories is of major interest in evolutionary research, as such variation is a fundamental prerequisite for evolution. All of which are directly associated with survival and reproduction and thus major components of fitness which quantifies the genetic contribution of an individual to the next generation relative to the average of such contributions in the population. This concept is the measurable force driving natural selection, and—like a prism—focuses random genetic mutations into directional evolutionary change.

"For a biologist the alternative to thinking in evolutionary terms is not to think at all"

Peter Medawar

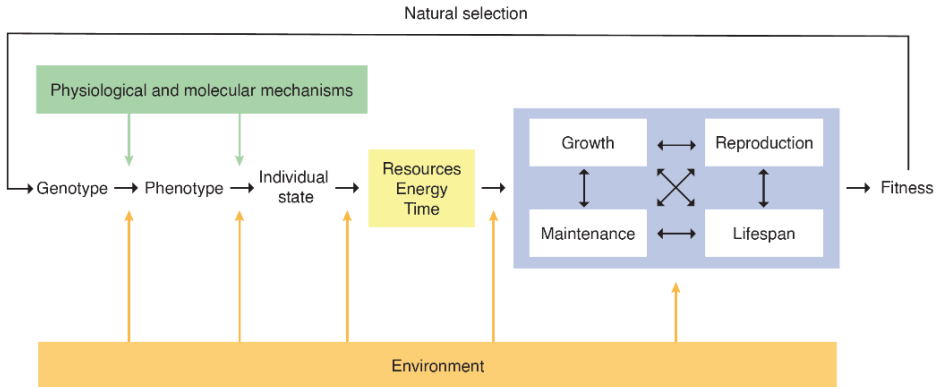


Figure 1. The life history of an individual comprises a series of steps through which the genetic instructions unfold to produce the phenotype which in turn will determine the condition of the individual and its capacity to acquire resources. These finite resources will then be allocated among main life history traits between which trade-offs occur. Physiological and environmental factors are expected to shape and constrain life history traits throughout life which ultimately determines the individual's genetic contribution to the next generation. Adapted from Ricklefs & Wikelski 2002.

1.1. Life history traits, plasticity and constraints

Variation in life history traits is constrained by one important feature; life history traits often compete for the finite pool of resources, making them subject to intrinsic trade-offs and other evolutionary constraints (Stearns, 1992; Roff, 1992). This means that if two life history traits share a common resource pool which is insufficient to sustain all the costs of both traits, a trade-off is unavoidable and thus an increment of resources allocated to one trait will necessitate a decrement of resources to the other trait (Figure 2). While this prediction is theoretically sound, it is often found wanting when tested empirically (van Noordwijk and de Jong, 1986). Positive correlations, rather than trade-offs, can occur among life history traits due to variation in individual resource acquisition; individuals with larger energy budgets, for example, may simply have both the greatest fecundity and survival (Reznick et al., 2000; Hamel et al., 2009; Wilson and Nussey, 2009). Studying the nature and extent of these trade-offs and how they vary depending on the prevailing environment is thus crucial for understanding life history variation more broadly.

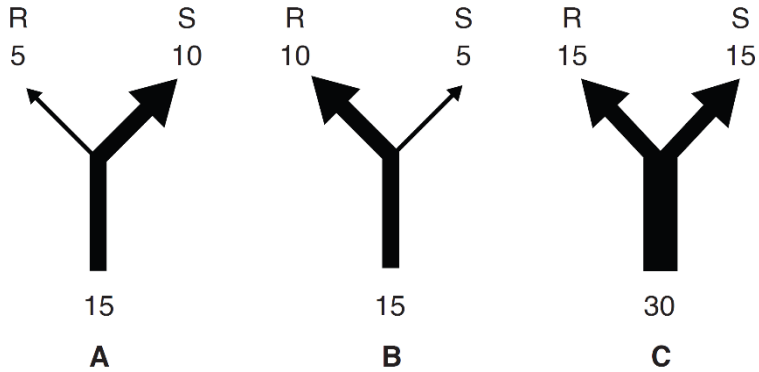


Figure 2. A simple representation of resource acquisition and allocation (adapted from Zera and Harshman, 2001). The base of each “Y allocation tree” illustrates the resources available to be allocated into two theoretical life history traits, R and S (reproduction and somatic maintenance). The “branches” represent the resources allocated into each trait. Trees A and B illustrates a trade-off, in which increased investment in one trait necessitates an equal reduction in the other when the amount of resources remain the same. Tree C illustrates the obviating effect of increasing the resource budget on a trade-off.

Understanding the proximate drivers of resource allocation strategies and life history trade-offs, and their context-dependency, is essential when attempting to predict evolutionary trajectories. Within species, however, evolutionary processes work much too slow to optimize individual fitness to fluctuations in environmental conditions. However, phenotypes may be flexible and influenced by environmental conditions (phenotypic plasticity). The plasticity of a specific genotype can be described mathematically as a range of phenotypes along an environmental gradient, called a reaction norm. The processes that promote plasticity are crucial to understand how organisms might adapt to rapid changes in their environment. Phenotypic plasticity has been observed in all major taxa, affecting the expression of, and relationships between, major life history traits, such as growth, somatic maintenance, reproduction, ageing, and lifespan, but explaining general patterns across species is difficult as reaction norms are often context-dependent (Holbrook and Schal, 2004; Hulme, 2008; Hulme and Bernard-Verdier, 2017; Penney et al., 2018; While et al., 2018). This context-dependency can make comparisons across studies difficult, even among same-species studies. Some contexts that alter reaction norms are obvious, such as life stage, while other can be more cryptic, such as parental genotype or level of

maternal investment, the latter itself having a propensity for context-dependence (Kim et al., 2017; Dew et al., 2018; Hall et al., 2020). These types of context-dependencies may limit interpretations and predictions of plasticity to the conditions under which it was evaluated.

1.1.1. Growth and development

Development is a key component of life history biology; it includes the period between conception and sexual maturity. This period of development will therefore incur a wide array of trade-offs among resource allocation towards growth, somatic maintenance and reproduction, all intimately tied to the organism and its environment. These trade-offs will ultimately shape the organism's life history. For example, the size of the adult of a species and the rate at which it reaches this size is produced by a variety of trade-offs between growth and mortality. Some of these include foraging and predation risk, growth and mature function, or growth and resistance to physiological stressors (Mangel and Stamps, 2001). Early growth is a particularly vulnerable stage of an organism's life, marked by often low ability of defence and competition for resources. Thus, rapid growth is expected to limit the time spent in this vulnerable stage. However, trade-offs do not allow for growth at the physiological maximum (Arendt, 1997), as evident by the fact that rapid growth early in life is associated with impaired performance, maintenance and reduced longevity (Metcalf and Monaghan, 2001; Olsson and Shine, 2002; Metcalfe and Monaghan, 2003). The benefits of increased growth rates will ultimately be a larger body size at maturation, and/or earlier maturation, both carrying potential short and long-term fecundity benefits. On the other hand, growing faster requires a higher metabolic rate, subsequently increasing metabolic-induced damage such as oxidative stress and potentially having detrimental effects on late-life survival and lifespan. Growth rate and lifespan are two fundamentally linked life history traits and trade-offs between them have been observed across the tree of life, forcing individuals to weigh short-term fitness gains against long-term ones (reviewed in Metcalfe and Monaghan, 2003).

1.1.2. Reproduction

Fitness, the individual's genetic contribution to future generations, is usually measured as the number of offspring and their size and quality. Reproduction is one of the most energetically demanding activities and resource allocation towards it will likely carry costs to future fecundity or longevity (Williams, 1966; Bell, 1980; Shine, 1980; Clutton-Brock, 1984; Reznick, 1985), possibly through a decrease in somatic protection, maintenance processes and survival rate (Kirkwood, 1977; Kirkwood and Rose, 1991). This makes reproduction a key consideration and its costs probably the most studied in life history biology. Importantly, current reproductive gains are often negatively and intimately linked to future reproductive gains (Stearns, 1976). Thus, reproductive investments can have major impacts on life history and it is clear that there is wide diversity in how organisms manage this trade-off, both among and within species.

When allocating resources toward reproduction, the organism is faced with important (evolutionary) considerations that will ultimately determine the lifetime reproductive success in their current environment. At what age and size is maturation optimised? How often should reproduction occur? How many offspring should be produced at each reproductive event and what should be invested per offspring? How many lifetime reproductive episodes? Reproductive strategies that optimise these outcomes will be fundamentally different between the sexes, in which female fecundity is to a much greater extent constrained by physical size (Vitt and Congdon, 1978; Shine, 1988; Honěk, 1993). The body size constraint on female fecundity is best represented by the fundamental relationship between the number and size of offspring, in which larger clutches or litters consist of smaller offspring (Zera and Harshman, 2001). The sex and factors that influence sexual differentiation of an individual will therefore have lifelong implications on their life history strategies (information on sex determination mechanisms is provided in Box 1).

Box 1. Sex determination mechanisms

The mechanisms that determine phenotypic sex are fundamentally important for the development and life history of the individual with broader consequences to population structures (West et al., 2002). Unsurprisingly, much scientific effort has therefore been directed to examining and mapping the various sex determination mechanisms across the animal kingdom. Vertebrate sex is determined genetically at conception by genes contained in sex chromosomes (genetic sex determination, GSD), by environmental cues (environmental sex determination, ESD)—most commonly by temperature during embryogenesis (temperature-dependent sex determination, TSD)—or via a combination of the two, where environment can override genotypic sex (GSD + EE) (Shine et al., 2002; Valenzuela et al., 2003; Sarre et al., 2004). Sex determination mechanisms of mammals and birds are highly conserved, where sex is determined by heteromorphic sex chromosomes at conception, with male heterogamety (XY) in mammals and female heterogamety (ZW) in birds. In contrast, reptiles show a remarkable diversity in sex determination systems including GSD (with XY or ZW), ESD, and GSD + EE (Janzen and Phillips, 2006; Uller et al., 2007; Bachtrog et al., 2014), and have proven vital to the study of the evolution of sex determination systems (Shine, 1999; Shine et al., 2002; Warner and Shine, 2008; Pen et al., 2010).

Temperature is the most studied environmental factor shown to influence sex determination in reptiles. Sex allocation theory maintains that parents should invest more in the reproduction of the sex that generates the greatest fitness return (Frank, 1990). In populations or species with sex-specific fitness returns from different thermal conditions, TSD should be favoured by selection (Charnov and Bull, 1977; Shine, 1999). Thus, the reproductive success of each sex should be optimized by thermal conditions that produces that sex in nature (Warner and Shine, 2008). While some reptiles produce exclusively one sex at certain temperatures, as shown in many turtles (Ewert et al., 1994), it is more common that the sex ratios are simply skewed, with a clear—albeit not absolute—bias (Valenzuela and Lance, 2004). The diversity of sex determination systems is well-documented in lizards, with agamids and geckos being notable for having variable sex determination systems even among closely related species (reviewed in Pokorná and Kratochvíl, 2009). Studies have even showed inconsistencies of sex determination mechanisms among experimental studies of the same species (Harlow, 2004; Uller et al., 2006; Hansson and Olsson, 2018).

The genetic sex of reptiles may be overridden by temperature during embryogenesis, causing a mismatch between genetic and phenotypic sex, so

called sex reversal. This phenomenon has only been definitively demonstrated, by comparing sex chromosomes and gonads, in three reptiles—all lizards—so far. These include two oviparous species (the bearded dragon, *Pogona vitticeps* [Quinn et al., 2007; Holleley et al., 2015; Castelli et al., 2020a] and the Eastern three-lined skink, *Bassiana duperreyi* [Shine et al., 2002; Radder et al., 2008; Quinn et al., 2009]), and one viviparous (the spotted snow skink, *Carinascincus ocellatus* [Wapstra et al., 2004; Pen et al., 2010; Cunningham et al., 2017; Hill et al., 2018; Hill et al., 2022]). These sex reversals all occur in the homogametic sex (i.e. XX males and ZZ females), which is in agreement with evolutionary theory due to second generation YY and WW chromosomal combinations being suboptimal or lethal (Bull, 1981). Furthermore, many other lizards determine sex based on a combination of genes and environmental cues, including the jacky dragon (*Amphibolurus muricatus*), the multi-ocellated racerunner (*Eremias multiocellata*), the Japanese gecko (*Gekko japonicus*), the yellow-bellied water skink (*Eulamprus heatwolei*), and the common collared lizard (*Crotaphytus collaris*) (Wang et al., 2015; Cornejo-Páramo et al., 2020; Wiggins et al., 2020; Whiteley et al., 2021a; Li et al., 2022). Despite only a few confirmed cases of sex reversals, they are hypothesized to be widespread in reptiles (Holleley et al., 2016; Schwanz and Georges, 2021). Moreover, phylogenetic inference has established TSD as an ancestral trait in reptiles (Janzen and Phillips, 2006) and thermosensitivity of sex determining genes in GSD species to be a conserved trait (Valenzuela, 2007).

One key reproductive trait that will dictate lifetime reproductive success is age at maturity. Early maturation can enhance the likelihood of realising fitness and increase the number of breeding attempts over a lifetime (Bell, 1980; Oli et al., 2002). Similarly, larger individuals may attain greater lifetime reproductive success compared to smaller counterparts due to factors such as increased fecundity (Honěk, 1993; Sand, 1996), competition for mates (Berglund et al., 1986; Tokarz, 1995), or better predator avoidance (Janzen et al., 2000; Sinclair et al., 2003). The age and size of maturation are outcomes influenced by a complex interplay of genetics and environmental factors. Because sexual maturity is an irreversible trait, the age and size at which it occurs are largely shaped by early-life conditions and resource acquisition that facilitate somatic growth and gonadal development (Adolph and Porter, 1996; Kearney, 2012). Importantly, maturing earlier and/or at a larger size are expected to reduce the resources available for maintenance and may therefore negatively impact future

health and the probability of surviving to the next breeding event or may reduce future fecundity (Partridge and Harvey, 1988; Stearns, 1989). Moreover, greater current fecundity may cause physical constraints on motility and subsequently increase predation risk (Shine, 1980; Bauwens and Thoen, 1981; Sinervo et al., 1991; Wapstra and O'Reilly, 2001).

1.1.3. Senescence and lifespan

The balance of resources allocated into life history traits will ultimately determine the organisms physiological and reproductive decline with advancing age (senescence). Senescence is commonly defined as a post-maturational process that, due to a diminished homeostasis and increased organism vulnerability, results in a reduction of the response to environmental stimuli (Troen, 2003; Vasto et al., 2007). The continuous decline of physiological capacity and reduction of the ability to respond to stress will lead to an increased susceptibility and vulnerability to disease. The rates of senescence reflect the amount of energy that has been allocated to traits such as growth, somatic protection and maintenance and reproduction. This allocation of energy is strongly affected by the rate of extrinsic mortality (e.g. predation and disease). Life history optimisation predicts that high extrinsic mortality levels will favour rapid maturation resulting in less resources for protection and maintenance causing faster senescence (Hamilton, 1966; Kirkwood and Holliday, 1979; Partridge and Barton, 1993, 1996, but the legitimacy of this prediction is debated [see Moorad et al., 2019]). However, senescence constitutes an evolutionary paradox as natural selection should oppose this progressive decrement of physiological capacity, although, it undoubtedly exists in nature (Medawar, 1952; Nussey et al., 2013). Evolutionary theory maintains that senescence occurs due to declining selection pressures on traits with age. Consequently, selection may favour genotypes that enhance early reproductive success even at the detriment of late-life fecundity or survival (see antagonistic pleiotropy theory of ageing by Williams, 1957 and the disposable soma theory of ageing by Kirkwood, 1977). While these theoretical predictions are well-supported by research at the species and population level (reviewed in Jones et al., 2014; Lemaître and Gaillard, 2017), the factors contributing to individual variation in ageing rates remain poorly understood. Nevertheless, some form of senescence, either declining fecundity (reproductive senescence) or increasing mortality rate

(actuarial senescence) with age, has been shown in a wide range of wild animal populations across the tree of life (Nussey et al., 2013; Jones et al., 2014; Lemaître and Gaillard, 2017). Furthermore, as predicted by life history theory and strategies to optimise fitness under different ecological niches (Holliday, 2006), ageing patterns are remarkably diverse across species (Colchero et al., 2019), but also among populations (Lemaître and Gaillard, 2017), and individuals (Cayuela et al., 2020; Tully et al., 2020).

"It is indeed remarkable that after a seemingly miraculous feat of morphogenesis a complex metazoan should be unable to perform the much simpler task of merely maintaining what is already formed"

George C. Williams

To detect and understand the evolutionary causes of senescence, it is first necessary to know of its proximate mechanistic processes. These mechanisms include those intrinsic to the organism, such as genetic and epigenetic factors, and those of extrinsic origin, like temperature, radiation, and other stressors (Robert, 2000). Identifying these processes will aid our understanding of individual life history strategies and how these change under variable environmental conditions. This, in turn, can help us to bridge the gap between proximate and ultimate explanations of current-future life history trade-offs.

1.2. Temperature and ectotherm life history traits

Environmental temperature is one of the most important drivers of phenotypic plasticity and life history variation among individuals, populations and species, and its effects are widespread and diverse. The effects of extrinsic temperatures on the organism are fundamentally influenced by physiological and behavioural adaptations that determine their internal temperature. Endothermic animals generate heat internally through metabolic processes to maintain a homeostatic body temperature. In contrast, ectothermic organisms rely on external heat sources, and their body temperature will, to a larger extent, reflect environmental temperature. Regardless of relying on internal or external

temperature, both endotherms and ectotherms protect their thermal optima through physiological (e.g. metabolism, structures or colours to increase, dissipate or absorb heat) and/or behavioural (e.g. panting, shade-seeking, basking, inactivity) adaptations (Seebacher and Franklin, 2005; Terrien et al., 2011; Rezende and Bacigalupe, 2015). Thus, while both endotherms and ectotherms are affected by ambient temperature, ectotherms are much more dependent on it (Taylor, 1981; Huey and Kingsolver, 1989). Virtually all physiological and behavioural functions are temperature-dependent in ectotherms, driven by the fundamental relationship between temperature and the rate of molecular reactions—in effect changing the rate at which time passes for the organism. Early life stages are generally those most sensitive to changes in temperature, in which small body sizes yield less thermal mass to buffer against overheating or freezing. Environmental temperature therefore plays a particularly important role in ectotherm development with consequences for life history variation.

Temperature distorts the relationship between physiological and chronological time in ectotherms

While temperature can cause plastic responses at any life stage, developmental plasticity is often most influential to overall long-term life history traits (Monaghan, 2008; Noble et al., 2017). Such temperature effects include those experienced by the mother (during gestation or preoviposition), the embryo, and experiences from birth to maturity. While environmental influence on plastic traits during adulthood often are reversible, environmentally induced changes during ontogeny often result in changes to traits and phenology that are irreversible (Lafuente and Beldade, 2019). Experiences during early development could, therefore, significantly and permanently alter individual life history trajectories (Monaghan, 2008; Noble et al., 2017). Early ontogeny is also associated with an increased sensitivity to the stress brought on by rapid changes in the environment (Albecker and McCoy, 2017; Pandori and Sorte, 2019). This makes this life stage not only the most influential to overall life history, but also the stage itself most easily affected by environmental factors. This sensitivity is largely due to high rates of cellular turnover associated with growth, and any environmental influence on these processes can be a major source of phenotypic variation within a species, potentially impacting individual fitness and thus having evolutionary significance. Rapid growth is subsequently associated with

metabolic-induced nucleic damage such as oxidative stress. Telomeres are structures at the ends of chromosomes that are particularly sensitive to such oxidation and can cause them to progressively shorten. The shortening of telomeres is associated with organismal health and longevity, and has recently been pointed out as causal drivers of life history variation (Casagrande and Hau, 2019; Giraudeau et al., 2019; Young, 2018, more information on telomere biology is provided in Box 2).

Box 2. Telomere biology

Telomeres are tandem non-coding nucleotide repeats and associated proteins located at the ends of eukaryote chromosomes. These structures are remarkably conserved across taxa, with all vertebrates possessing the sequence TTAGGG, suggesting that telomeres are evolutionarily ancient and an essential component of the cellular machinery (Meyne et al., 1989; Zakian, 1989; Blackburn, 1991). Telomeres serve two crucial functions in eukaryotic cells; firstly, they allow DNA repair mechanisms to distinguish true chromosome ends from double-stranded breaks, thereby preventing chromosome end-to-end fusion (Blackburn, 2000). Secondly, telomeres prevent the progressive loss of important coding sequences caused by the inability of DNA polymerase to fully replicate the terminal ends of chromosomes during mitosis, which is commonly referred to as the “end replication problem” (Olovnikov, 1973). In the absence of telomere elongation mechanisms, this results in the shortening of telomeres with each cell division. Telomere shortening is also influenced by intrinsic and extrinsic factors changing the conditions within the cell, most notably through oxidative stress that particularly targets this guanine-rich sequence with low redox-potential (von Zglinicki, 2002; Kawanishi and Oikawa, 2004).

Once telomeres become critically short, it triggers replicative senescence or apoptosis (Hayflick, 1965; Campisi, 1997; von Zglinicki et al., 2001). The accumulation of senescent cells and loss of cell lines are associated with impaired tissue renewal capacity and a decline in somatic function, causing symptoms of ageing (Hao et al., 2005; Shay and Wright, 2007; Aubert and Lansdorp, 2008; van Deursen, 2014). To limit or delay the detriment to the soma, there are a number of mechanisms that restore telomeres (Cesare and Reddel, 2010; Shay and Wright, 2019), the most widespread of which is telomerase, an enzyme that synthesise and replenish telomeric DNA (Greider and Blackburn, 1985; Gomes et al., 2010). Telomerase activity is highly variable among different cell types, life stages, and taxa (Monaghan, 2010). In

endotherms, telomerase is typically active in stem cells and the male germline while repressed in somatic tissues, whereas it can remain upregulated in somatic tissue throughout life in ectotherms (Olsson et al., 2018a). As a result, telomere dynamics (the length and change of telomeres across time) is incredibly diverse among ectotherms, in which telomeres may shorten with age in some species while remaining unchanged, or even lengthen, in others (Bronikowski, 2008; Simide et al., 2016; Olsson et al., 2018a; Burraco et al., 2020, Fitzpatrick et al., 2021). Importantly, telomere dynamics represent a balance between telomere shortening and elongation processes crucial to organismal health. Extreme rates of either can be detrimental to fitness. For example, excessive shortening is linked to a loss of cellular homeostasis and diminished survival at both cellular and organismal (and even population) level (Dupoué et al., 2017, 2022; Young, 2018), whereas high rates of elongation, via increased telomerase activity, raises the risk of immortalizing cancerous cells (Aviv et al., 2017).

Telomeres are in an evolutionary tug-of-war between shortening and elongation; too much of either can disrupt homeostasis

Investment in telomere maintenance might, like other forms of somatic maintenance, be a physiologically costly process that compete for resources with reproduction (Young, 2018; Casagrande and Hau, 2019). Thus, life history theory predicts that investments into telomere elongation, which promote longevity and future reproductive success, will come at the cost of current reproduction. Life history stages that are energy demanding, such as development and reproductive events, are predicted to further constrain this current-future life history trade-off (reviewed in Monaghan and Ozanne, 2018; Sudyka et al., 2019). Moreover, early-life environmental conditions that impair individual quality and negatively impact telomeres may similarly signal for a “faster” life history with increased investments in traits that maximise short-term fitness gains (Casagrande and Hau, 2019; Giraudeau et al., 2019). Few studies have empirically tested the costs of telomere maintenance, and subsequently its constraining role in current-future life history trade-offs. However, studies examining the effects of arousal from hibernation, endotoxic and hormonal stress in wild mice (*Glis glis*), laboratory mice (*Mus musculus*) and wild great tits (*Parus major*) support the hypothesis that telomere maintenance is energetically costly (Hoelzl et al., 2016; Criscuolo et al., 2018; Casagrande et al., 2020). Further support comes from the common trend of telomere shortening being greatest during life history stages that are metabolically demanding, such as growth and reproduction (Young, 2018; Burraco et al., 2020).

Levels of oxidative stress and telomere shortening is generally greatest during life history stages that demand high rates of cellular turnover such as rapid growth that characterise early life (Monaghan and Ozanne, 2018; Casagrande et al., 2020). Moreover, organisms are often most sensitive to extrinsic factors during ontogeny, often manifesting in long-lasting reaction norms (Lindström, 1999; Metcalfe and Monaghan, 2001). Temperature is the most influential extrinsic factor in ectotherms, influencing most life history traits by altering the rate of biological processes. These processes include telomere dynamics, which are influenced by elevated metabolic stress and cellular turnover associated with higher rates of metabolism, growth and reproduction (Vedder et al., 2017; Sudyka et al., 2019; Friesen et al., 2022) (Figure I). Studies have linked early-life telomere dynamics in ectotherms to central life history traits such as growth rate, reproductive success and lifespan, first and foremost via temperature (McLennan et al., 2016; Dupoue et al., 2022). Therefore, assuming that telomere maintenance—as an investment in future reproductive success—is a costly activity, it will compete for resources with traits promoting current growth and early reproduction (Stearns, 1989). This allocation of resources toward telomere maintenance has been linked to pace-of-life syndromes (Giraudeau et al., 2019; Pepke et al., 2022, 2023; Tissier et al., 2022), in which short telomeres may reduce life expectancy and thus drive the adoption a “faster” life history strategy. Telomeres, along with the early-life conditions that influence them, may therefore serve as critical ecological markers of life histories with significant implications for the evolution of species and populations.

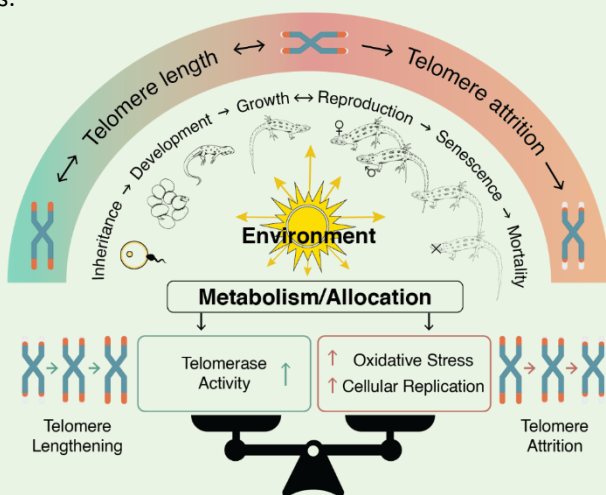


Figure I. An integrative conceptual view of physiological and environmental impacts on telomere dynamics across generations and throughout individual life stages (adapted from Friesen et al., 2022).

Telomere dynamics are commonly sex-specific which can provide valuable insights into both pace-of-life syndromes and the correlation between early-life telomeres and life history traits (Hämäläinen et al., 2018; Heidinger et al., 2021). In ectotherms, females often experience increased fecundity with age and size, meaning that the relative contribution to overall fitness of reproductive events can increase with age (Hoekstra et al., 2020). In such cases, selection should favour a longer lifespan by investing more resources into the soma (Vaupel et al., 2004), including telomeres. On the other hand, selective pressures may drive polygynous males towards adopting “faster” life histories that enhance sexual competitiveness including growth, early maturation and secondary sexual traits, at a cost to somatic maintenance and longevity (Clutton-Brock and Isvaran, 2007; Dammhahn et al., 2018).

2. Research aims, study systems and main results

I was provided a rare opportunity to take part in a conjoint double degree, with enrolment and supervision from both the University of Gothenburg (GU) and the University of Tasmania (UTas). This joint effort was built on the 20-year collaboration between my two main supervisors, Professor Mats Olsson (GU) and Professor Erik Wapstra (UTas). This thesis has been constructed to meet the expectations of both institutions and thus its structure and contents deviate slightly from the norm of each. I spent time at both institutions during which I undertook in considerable field and laboratory work at each. The fact that these universities are essentially located at opposite ends of the globe, and a pandemic that made travel impossible for large parts of my candidature, presented considerable logistic challenges to overcome. However, these difficulties were greatly outweighed by the opportunity to be part of these respected institutions and work on two incredible reptile systems on which my supervisors were hard at work before I was even born. Indeed, the view was great from their shoulders.

Developmental conditions often have long-term impacts on life history traits and may constitute important external sources of individual heterogeneity in life history strategies and fitness (Clark and Galef, 1995; Lindström, 1999; Monaghan, 2008). Determining such effects are therefore of great interest in evolutionary biology. The influence of early-life conditions on life history strategies are clearly recognised, however, predicting the specific direction of effects is not straightforward and often vary considerably both among and within species (Vedder and Bouwhuis, 2017; Cooper and Kruuk, 2018). Although theoretical life history models of resource allocation under variable environments are supported by an abundance of empirical research at the species and population level, the causes of individual heterogeneity in life history traits remain poorly understood. The overall aim of this thesis was therefore to address the importance of early-life thermal conditions and developmental rates in shaping life history traits central to survival and reproduction.

Two lizards, a world apart

To investigate long-lasting effects of early-life conditions and developmental rates on life history traits, I studied well-established ectotherm systems from

two hemispheres (Figure 3), the Swedish sand lizard (*Lacerta agilis*) and the Tasmanian spotted snow skink (*Carinascincus* (formerly *Niveoscincus*) *ocellatus*). Both systems have over 20 years of accumulated research providing in-depth information on their physiology, reproductive behaviour, ecology and population structures (see below sections). The sand lizard is an egg-laying species (oviparous) and the spotted snow skink is live-bearing (viviparous). These two reptile systems each provide distinct and tangible research opportunities, both experimental and longitudinal. The four research papers in this thesis are ordered based on experimental and longitudinal work. In **Paper I** and **Paper II**, I examine proximate effects of incubation temperature on neonate sand lizards. **Paper III** and **Paper IV** focus on the influence of natural climate fluctuations over 20 years on developmental rates and subsequent consequences to the life history of spotted snow skinks.

In **Paper I** and **II**, I examine the influence of developmental temperature on neonate sex and sex-specific telomere dynamics in sand lizards. The large knowledge base on this species, especially in Swedish sand lizards, including observations of facultative alterations to sex ratios, clearly defined sex chromosomes and sex-specific fitness returns from longer telomeres, make this system ideally suited for determining—and highlighting the evolutionary importance of—thermal influence on sex and early-life telomere dynamics (see box 3). Furthermore, oviparous reptiles are excellent models to study proximate effects of the developmental environment. The egg can easily be translocated to experimental treatments in a controlled manner. Moreover, eggs can be split among such treatments following a “split-clutch” experimental design, in which sibling eggs from the same clutch are divided among the treatments. This design helps to minimise the risk of confounding parental and treatment effects (Via, 1993).

In **Paper III** and **IV**, I investigate the influence of individual developmental rates as influenced by temperature and activity time early in life on age and size at maturity of wild spotted snow skinks, and whether maturing decisions have costs to survival and reproduction later in life. Furthermore, I also examined whether these early-life effects differed between two populations with different geography, climate and life history strategies. This was only possible due to the previous two-decade long field mark-recapture study on two spotted snow skink populations. These longitudinal data enabled me to conduct robust analyses of

individual females' life history traits, from birth to death. The previous field and experimental research on the spotted snow skink also provided important insights into population-specific thermal physiology and behaviours (see Box 4) that I leveraged, together with meteorological data, to make ecologically realistic estimates of activity time early in life. Furthermore, because the spotted snow skink is viviparous with highly synchronous reproduction, makes it ideally suited as a longitudinal study system. Females can be captured close to parturition and then released immediately after, ultimately spending only about two weeks in the laboratory. This minimises our potential impact on the animals and maintain their ecology as close to natural as possible.

Together, these two reptile systems are ideally suited for investigating both the proximate effects of experimental developmental conditions on crucial life history traits and the lifelong consequences of developmental rates on patterns of survival and reproduction.

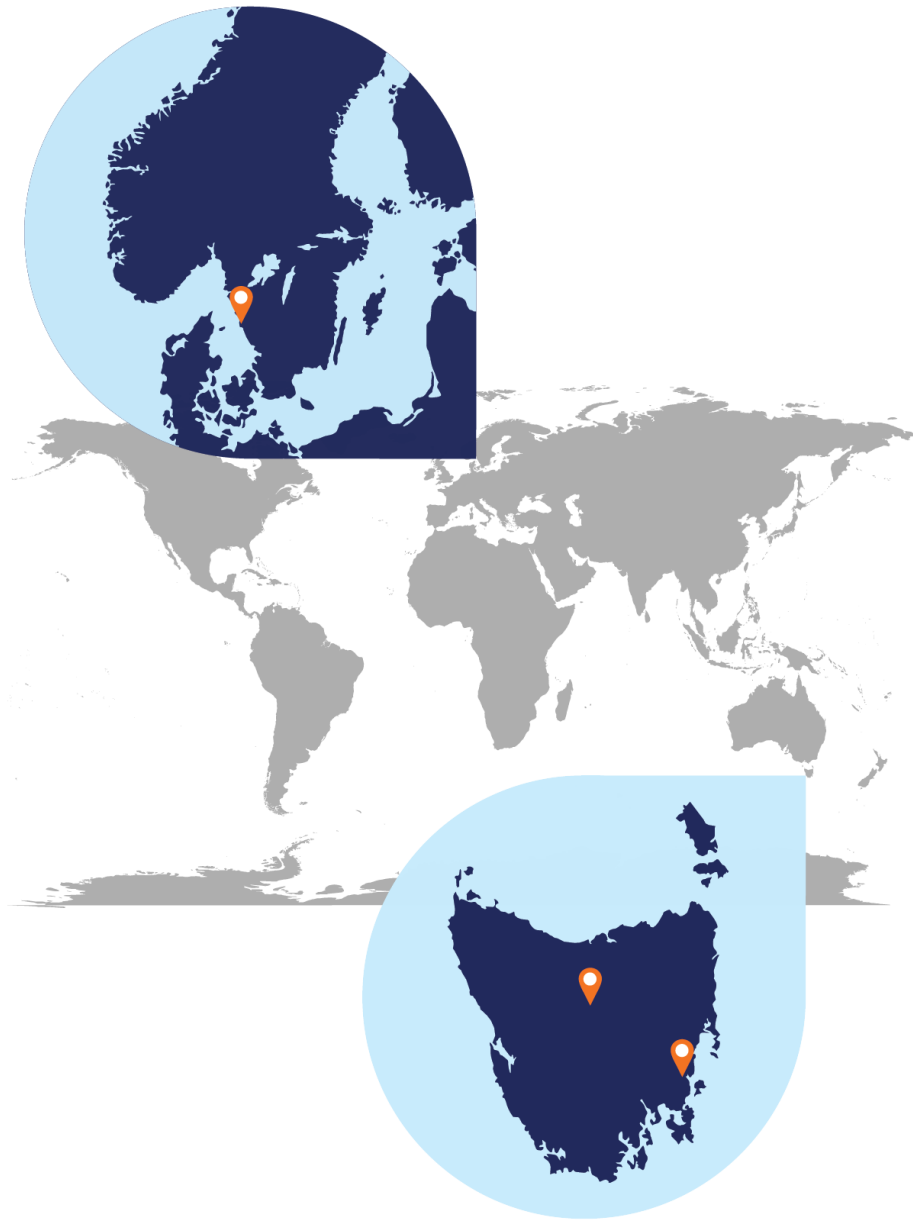


Figure 3. Map of the Swedish sand lizard and Tasmanian spotted snow skink populations that were the focus of my thesis. The points indicate proximate locations of each population, including St. Keholmen (57°29' N 11°56' E) and the spotted snow skink lowland (42°33' S, 147°50' E) and highland (41°50' S, 146°34' E) population.

2.1. Sand lizard

The sand lizard (*Lacerta agilis*) is a small ground-dwelling oviparous lacertid lizard weighing up to 20 g with an average snout-vent length of ca. 80 mm. With multiple subspecies, *L. agilis* has one of the largest distribution ranges of any reptile, occupying a major part of temperate Eurasia. It is distributed between France in the west to Mongolia in the east and from Turkey in the south to Sweden in the north (Bischoff, 1984; Bülbül et al., 2019; Andres et al., 2014; Roitberg et al., 2015). This makes the sand lizard the most northern-occurring oviparous lizard in Europe. In Sweden, the sand lizard is red-listed as a vulnerable species and therefore has a high conservation interest (Niesel, 2007; IUCN 2010).

Swedish sand lizard research has been spearheaded by Mats Olsson and colleagues since the late 1980s, resulting in invaluable information on the species' ecology, life history, genetic makeup and the viability of populations. In Sweden, sand lizards occur in highly fragmented populations throughout the southern half of the country with generally low genetic variation compared to continental Europe (Gullberg et al., 1998; Gullberg et al., 1999) and little to no inter-population gene-flow (Olsson et al., 1996a). Females emerge from hibernation in April-May, closely followed by ovulation and copulation (Olsson and Madsen, 1996; Olsson et al., 1996b; Olsson et al., 2011a). Males are polygynous and compete for females through nuptial colouration, aggressive contests, sperm competition and mate guarding (Olsson, 1994; Olsson et al., 1996a; Olsson et al., 1996b; Lindsay et al., 2016). Females lay a single clutch of 4–15 eggs sired by one to three males each year but can, under favourable conditions, produce a second seasonal clutch (Olsson and Shine, 1997b; Olsson and shine, 1997a; Olsson et al., 2011a). Key phenological traits, including ovulation and oviposition date, are highly variable among females and years depending on environmental conditions; mainly temperature and opportunity for activity (Olsson and Shine, 1997b; Olsson and Shine, 1997c; Ljungström et al., 2015). Sand lizards reach sexual maturity after about three years in males and four years in females, have an average lifespan of 5–6 years but can live up to 10 years (Olsson, 1992).

A large body of longitudinal and experimental work on the Swedish sand lizard has been focused on a coastal population, Asketunnan (57°22' N, 11°59' E), 50

km south of Gothenburg and near the northern limit of the species' range. This population suffers from low genetic variation and show negative effects, including effects on hatching success (on average 86 to 89%) and increased risk of hatchling malformations at 10–20% incidence (Olsson et al., 1996a; Bererhi et al., 2019; Lindsay et al., 2020; Bererhi et al., 2023). In recent years, this population has declined and scientific efforts have been redirected to a small island (ca. 360 × 270 m) population approximately 20 km north of Asketunnan, St. Keholmen (57°29' N 11°56' E) (e.g. Olsson et al., 2018b; Lindsay et al., 2020). This island population was experimentally founded (established ca. 20 years ago) and before that did not contain any lizards. The founders were the product of a captive outbreeding experiment in 1999 and 2000 (Olsson et al., 2018b), in which Asketunnan males and females were bred with individuals captured in Swedish provinces (Skåne and Halland) further south. The climate in these southern populations is warmer and sand lizards are more continuously distributed (Berglind, 2015). The offspring (454 individuals) that were the product of this outbreeding experiment were then released within a week of hatching at St. Keholmen. The island is separated from the mainland by about 100 m of shallow water and comprises a mosaic of connected habitats, including rocky screes, heathlands and both dry and wet grasslands.



Post-ovipositional sand lizard female in the “swamp” at St. Keholmen

In the sand lizard section of this thesis (**Paper I** and **II**), we captured gravid females in spring 2018–2020 from this island population and brought them back to the facilities at the University of Gothenburg. Once laid, eggs were split

among thermal treatments (according to a split-clutch design) to test the effects of developmental temperature and post-hatching growth on offspring sex and telomere dynamics. Full methods are contained in each paper which are each written as stand-alone papers. In Box 3, I have summarised the literature for the sand lizard that have a specific importance to these two studies.

Box 3. Previous sand lizard findings relevant to this thesis

The incubation period (time from oviposition to hatching) differ drastically between eggs incubated at the same temperature from St. Keholmen. In extreme cases, eggs have shown to hatch after only 55% of the normal incubation period (Olsson et al., 2018b). This heterogeneity in incubation period is largely due to females retaining eggs in uteri and delaying oviposition (Shine et al., 2018). Egg retention varies seasonally and among females, and is likely a cold-climate adaptation, allowing females to maintain much higher temperatures of their clutch through behavioural thermoregulation than would normally be experienced by oviposited eggs. This is supported by incubation periods being shorter for eggs laid late in the season and in cooler years (Shine et al., 2018). High maternal temperatures can increase the developmental time close to 25°C; the optimal incubation temperature that minimises developmental abnormalities and asymmetries in this species (Zakharov, 1989).

Accurately sexing neonate sand lizards was essential for this thesis. Sand lizard hatchlings are easily sexed with no negative effects on the animal by gently everting the male hemipenes with a pair of tweezers (Harlow, 1996; Olsson and shine, 2003). A method that has been reconfirmed by mark-recapture studies to have 100% repeatability in this species (Olsson et al., 2004; Olsson et al., 2005a; Olsson et al., 2011b).

Sand lizards (as in all lacertids [Pokorná and Kratochvíl, 2009]) have clearly defined heteromorphic sex chromosomes (ZZ/ZW) with female heterogamety (Srikulnath et al., 2014; Lisachov et al., 2020). Consequently, the production of daughters is associated with an increased risk of inviability due to harmful paternal recessive genes on the Z chromosome (Olsson et al., 2004; Olsson et al., 2005b). Hence, females should favour the production of daughters when mating with high-quality males. Consistent with this, female sand lizards facultatively overproduce daughters when mated with high-quality males that exhibit brighter coloration, or higher genetic quality (i.e. more MHC polymorphic, Madsen et al., 2000; Olsson et al., 2003).

Sand lizards, like many ectotherms, continue to grow post-maturity with body size eventually reaching an asymptote. In this species, growth plateaus at 6–7 years of age (Olsson and Shine, 1996; Bererhi et al., 2023). Fecundity in female sand lizards is strongly and positively associated with body size (Olsson and Shine, 1996). Reproductive events later in life are, therefore, predicted to have a greater relative contribution to lifetime fitness compared to earlier reproduction. Selection should, therefore, favour greater investments into somatic maintenance that promote longevity in female sand lizards. This is supported by females being the longer-lived sex in this species (Olsson, 1988; Srijbosch and Creemers, 1988). Further support comes from the sex-specific telomere dynamics in sand lizards. Telomeres lengthen with age in females while in males, most have telomeres that either shorten or remain unchanged with increasing age (Olsson et al., 2010; Olsson et al., 2011b; Axelsson et al., 2020). Telomere length is also a better predictor of lifetime reproductive success and lifespan in females compared to males (Olsson et al., 2011c). Telomere length is therefore a trait under sexually diversifying selection in sand lizards. Thus, females may maximise their lifetime reproductive success by investing in telomere maintenance that promotes longevity, while males instead divert more resources into short-term reproductive gains through a polygynous mating behaviour. Determining the factors that influence early-life telomere length and dynamics is not trivial because, besides potential ties to individual life history, telomeres have been linked to population extirpations in a lizard—*Zootoca vivipara*—closely related to the sand lizard (Dupoue et al., 2017; Dupoue et al., 2022).

2.1.1. Paper I – Sex determination

Phenotypic sex is fundamentally important for the life history of an individual and the sex ratio structure of populations (West et al., 2002). Sex determination mechanisms of birds and mammals are highly conserved, in which sex is largely determined at conception by sex genes located on heterogametic sex chromosomes. Across reptile taxa, however, sex is determined based on sex genes, environmental cues, or a combination of the two (Janzen and Phillips, 2006; Bachtrog et al., 2014). Recently, environmental involvement in the sex determination of reptiles with sex genes have been proposed to be widespread spanning multiple reptilian lineages (Holleley et al., 2016; Capel, 2017; Schwanz and Georges, 2021). To date, such sex determination systems have only been observed in skinks and agamids. In **Paper I**, I test whether this

hypothesis expands to lacertids (with female heterogamety) by examining the influence of incubation temperature on offspring sex. Additionally, I investigated the presence of sex-specific physiological benefits from different developmental temperatures to examine whether thermolabile sex determination is a trait under selection. Specifically, I used 561 eggs and hatchlings from 78 mothers over three years (2018–2020) to examine whether incubation temperature (23, 25, 27°C) can override the clearly defined sex genes in sand lizards and cause an overproduction of one sex.

The 27°C temperature treatment produced significantly more females compared to the 23°C treatment (70% and 50% females, respectively) but only in 2018. A similar, albeit non-significant, female bias occurred in 2020, with a production of 69% females in the 27°C treatment and 53% females in the 23°C treatment (Figure 4).

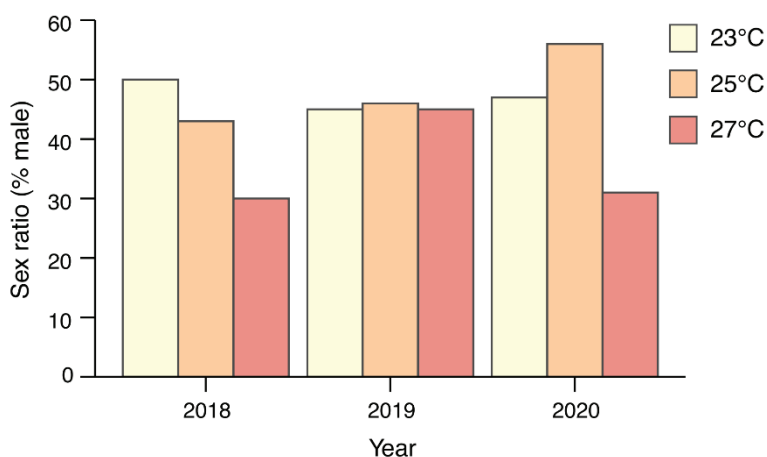


Figure 4. Percentage of males produced in the three temperature treatments (23, 25, 27°C) in each of the years (2018–2020) of the study.

I also examined sex-specific effects of incubation temperature on conversion of yolk into tissue in 2019 and 2020. This showed that females may benefit more than males from warmer developmental temperature, in which warm-incubated daughters more efficiently converted yolk into tissue (Figure 5). Moreover, neonates from energy-efficient embryos also grew at a faster rate post-hatching (Figure 6).

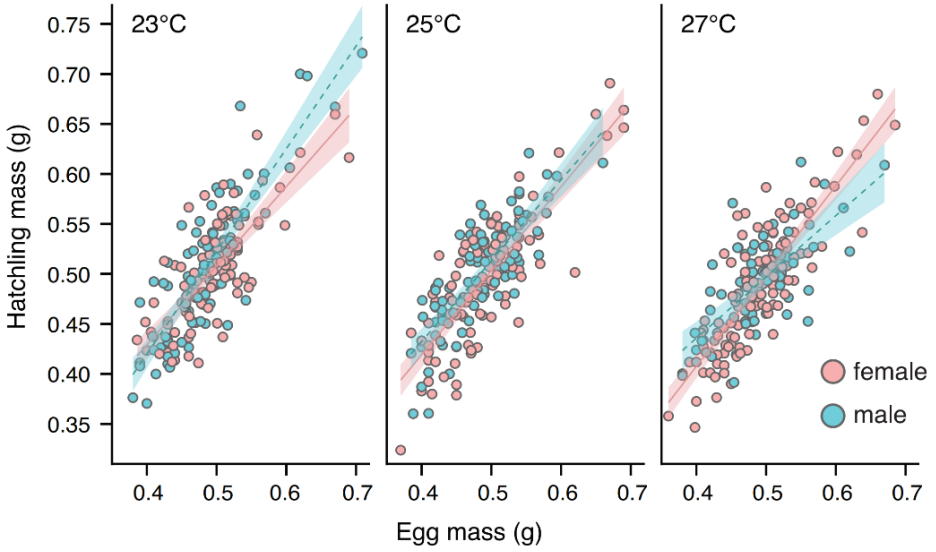


Figure 5. An interaction plot illustrating the within-treatment (23, 25, 27°C) relationship between egg mass and hatchling mass of male (blue) and female (red) hatchlings. The slopes are derived from linear regression analyses, and the shaded regions indicate standard error range.

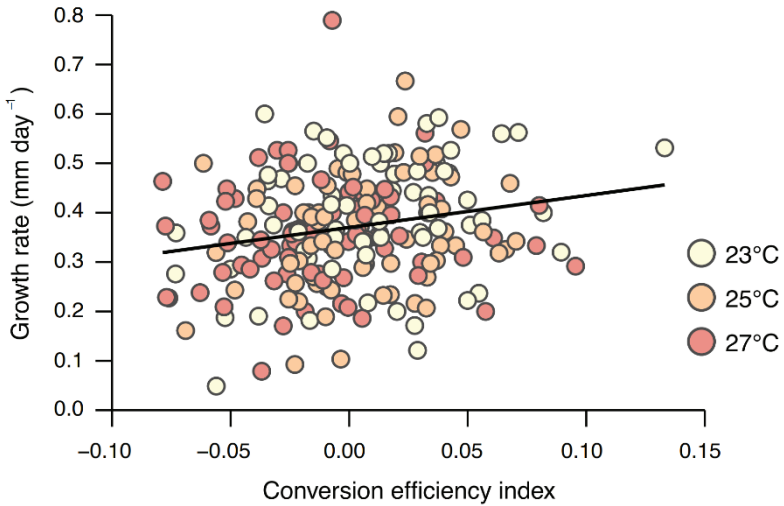


Figure 6. The relationship between egg conversion efficiency and neonate growth rate.

These results suggest a context-dependent thermolabile sex determination in sand lizards that may be maintained by selection through sex-specific environmental optima. Sex-specific environmental optima are the most accepted evolutionary explanation of environmental influence on sex determination (Charnov and Bull, 1977; Shine et al., 1995; Shine, 1999; Warner and Shine, 2008).

2.1.2. Paper II – Telomere dynamics

Telomere dynamics are remarkably diverse across ectothermic species. Unfortunately, the literature on telomere dynamics is heavily biased towards mammals and birds while limited attention has been given to non-model ectothermic species (Olsson et al., 2018a; Olsson et al., 2018c). However, the available information shows that telomeres can shorten with age in some species, while in others they can lengthen with age or remain stable (Bronikowski, 2008; Simide et al., 2016; Olsson et al., 2018a; Burraco et al., 2020; Fitzpatrick et al., 2021). Due to this, ectotherm telomere biology has been likened to a treasure chest for the study of the evolution of telomere dynamics and their association with life history (Olsson et al., 2018a). Importantly, in species that compensate for telomere shortening in adulthood, telomere dynamics early in life can prove the most influential to lifetime telomere dynamics (Monaghan and Ozanne, 2018; Friesen et al., 2022). It is during this life stage that organisms generally grow the fastest and are the most sensitive to extrinsic factors, both of which are associated with increased telomere erosion and subsequent long-term effects on survival and reproductive success (Monaghan, 2014; Olsson et al., 2018a; Marasco et al., 2022; Pepke et al., 2022). In **Paper II**, I contribute to the research on ectotherm telomere biology by investigating the impacts of incubation temperature and post-hatching growth on the telomere dynamics of neonate sand lizards. Additionally, I explored sex-specific patterns of telomere dynamics early in life in this species in which telomere length has shown to predict survival and reproductive success in a sex-specific manner.

While incubation temperature did not impact telomere length at hatching, it had subsequent effects on the telomere maintenance capacity of neonates. Specifically, telomere maintenance capacity was overall inversely related to

incubation temperature (Figure 7) and telomeres only shortened in neonates incubated at 27°C.

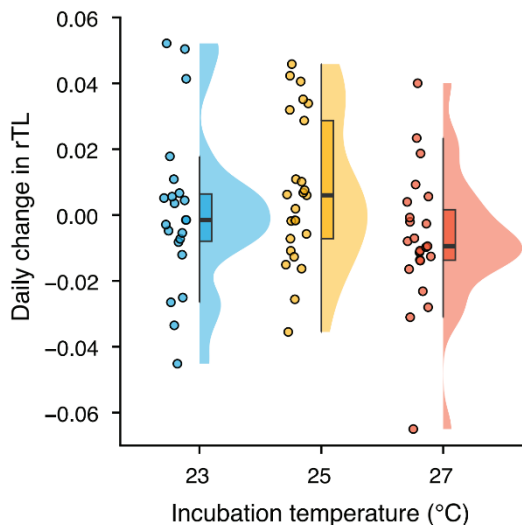


Figure 7. Effects of incubation temperature on daily change in relative telomere length (RTL) of neonate sand lizards.

Sex was the strongest predictor of telomere dynamics in neonates. Females hatched with on average 34% longer telomeres compared to their male counterparts (Figure 8a). Neonate telomere maintenance capacity also showed important sex-specific effects, with females on average lengthened their telomeres whereas males' telomeres on average shortened (Figure 8b). The daily rates of telomere lengthening and shortening would after 60 days correspond to a 7.1% increase and 11.5% decrease in the telomere lengths of females and males, respectively. Moreover, long telomeres, regardless of sex or treatment, shortened faster than short telomeres.

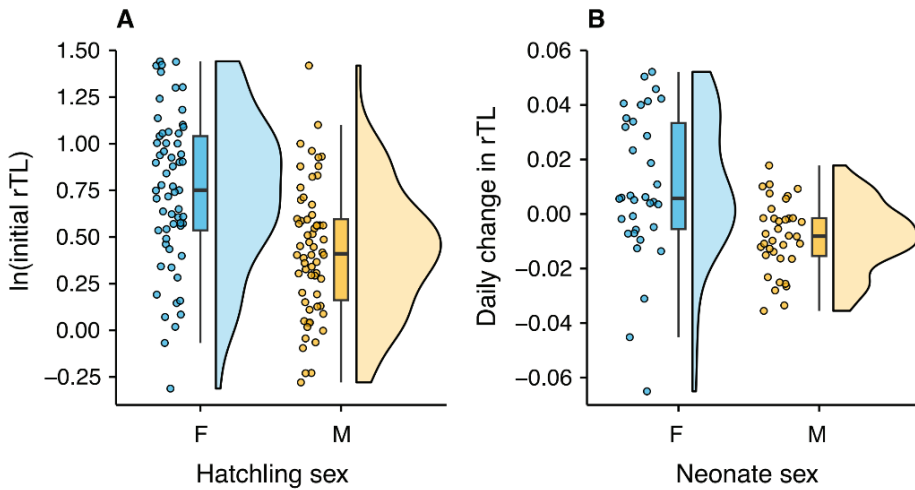


Figure 8. Sex-specific telomere dynamics in neonate sand lizards, including (A) the difference between the sexes in their initial relative telomere length (rTL), and (B) the difference in daily change in telomere length between the sexes. Note that initial telomere lengths (A) are log-transformed.

Our results showed an impressive telomere maintenance capacity in female neonates, enough to achieve telomere elongation despite potential high rates of shortening due to rapid growth and having longer telomeres than males. I suggest that selection drives this sexual dimorphism in telomere maintenance, in which female sand lizards, with size-dependent fecundity and longer lifespan (Olsson, 1988; Strijbosch and Creemers, 1988; Olsson and Shine, 1996), maximise their fitness by investing in traits that promote longevity, while males invest in short-term reproductive gains through polygynous mating behaviour. This is supported by previous work on adult sand lizards showing that telomere length was a stronger predictor of lifetime reproductive success in females compared to males (Olsson et al., 2011c).

2.2. Spotted snow skink

The spotted snow skink (*Carinascincus ocellatus*) is a small scincid lizard with an adult body weight of between 3–12 g and a snout-vent length of 60–80 mm. They are viviparous, producing a litter of offspring annually across their geographic range. The spotted snow skink is endemic to Tasmania, Australia, distributed throughout the island spanning a 1200 m altitudinal and climatic gradient from warm coastal areas to cold alpine regions (Wapstra, 1998; Wapstra et al., 1999; Cliff et al., 2015). Since the mid 1990s, Erik Wapstra and colleagues have researched the spotted snow skink, culminating in wide knowledge of the species' ecology and life history, with special attention to population differences along an altitudinal gradient.

Females reproduce annually and most copulations occur in Austral autumn followed by female sperm storage over winter (Jones et al., 1997). Secondary matings, ovulations and fertilisation occur shortly after emergence from winter hibernation in Austral spring (September–November), with parturition following a 3–4 month long temperature-dependent gestation period (Wapstra et al., 1999). The timing of ovulations is highly synchronous among females within populations (Wapstra et al., 1999). Mature females produce an annual litter of 1–8 offspring, that mature after 2–4 years and live on average 4–5 years but can live up to 12 years in the wild (Wapstra et al., 2001; Wapstra and Swain, 2001; Cunningham et al., 2018).

Considerable scientific effort has been dedicated for over 20 years—and continues to be dedicated—to monitoring two populations of spotted snow skinks in contrasting environments near the limits of the species' altitudinal range; specifically, one warm lowland population on the east coast (42°33' S, 147°50' E, 30 m altitude) and one highland alpine population on the Central Plateau (41°50' S, 146°34' E, 1150 m altitude). Both populations are surrounded by unsuitable habitat and physical barriers including unsuitable vegetation, roads, lakes and rivers causing low rates of immigration or emigration in either population (Cadby et al., 2010; Uller et al., 2011; Cunningham et al., 2018). The two populations are genetically isolated (see Cliff et al., 2015; Hill et al., 2018 for details on the extent of gene flow between sites).



Spotted snow skink basking at the lowland site near Orford

During Austral summers between the years 2000–2023, our research group has performed a mark-recapture study in which gravid females close to parturition were brought back to facilities at the University of Tasmania. These records cover phenotypic metrics and life history traits of more than 900 unique lowland females and their over 4400 offspring, and more than 1000 unique highland females and their over 6500 offspring.

In the section of the thesis dedicated to the spotted snow skink (**Paper III** and **IV**), I use this powerful dataset on longitudinal life history information of females from the lowland and highland populations to explore how natural climate variation and developmental rates influence crucial life history traits throughout life. Within Box 4, I have assembled information on the spotted snow skink and the two populations that are particularly important to the two studies at hand.

Box 4. Spotted snow skink information relevant to this thesis

In the ongoing mark-recapture field study, female spotted snow skinks are captured near the end of pregnancy. Gestation therefore occurs in the wild and females experience local weather and climate conditions. Females are brought in to the UTas facilities for approximately a two-week period and field collection

continues until no more females are left (see Cunningham et al., 2020). Once in the laboratory, they are held under standardised conditions in plastic terraria with a shelter, a basking rock and a basking light. After parturition, neonate spotted snow skinks are assigned a permanent ID by toe clipping, which allows for accurate identification of females that survive to maturity and are captured at their first reproductive event. The vast majority of gravid females are captured each year at the two sites and, by their unique toe clips, we can identify their information at birth. Thus, our data includes birth information of both sexes, but longitudinal life history data is focused on females.

The two populations experience substantially different thermal conditions, both during the activity season and crucial life history events (Wapstra et al., 2001; Yuni et al., 2018), with lower temperatures throughout the year at the highland site. Highland females therefore have a shorter activity season compared to lowland females. Consequently, key phenological traits are delayed about a month in the highland population compared to the lowland site, including spring emergence, ovulation and birth (Wapstra et al., 1999; Cadby et al., 2010; Uller et al., 2011; Cunningham et al., 2020). Furthermore, there is extensive evidence of local adaptation at each site, including variation in size at birth and age and size at maturity (Wapstra et al., 2001; Wapstra and Swain, 2001; Pen et al., 2010), reproductive investment (Wapstra and Swain, 2001; Cadby et al., 2011), thermoregulatory behaviour (Uller et al., 2011; Cadby et al., 2014), phenology (Cunningham et al., 2020) and sex determination mechanisms (Pen et al., 2010; Cunningham et al., 2017; Hill et al., 2022). Specifically, highland females are generally larger, invest more in reproduction (relative to body size), and maintain higher body temperatures when basking opportunity is low compared to lowland females (Uller et al., 2011; Cadby et al., 2014; Caldwell et al., 2017).

While spotted snow skinks continue to grow post-maturity (eventually reaching an asymptote), growth rate is greatest during the neonatal stage and drastically decreases post-maturity (Wapstra et al., 2001). Fecundity is size-dependent in both populations but size-corrected fecundity (relative fecundity) increases more steeply with increasing size in highland females compared to their lowland counterparts (Wapstra and Swain, 2001; Wapstra and O'Reilly, 2001).

2.2.1. Paper III – Early-life conditions shape life histories

The age and size at which organisms reach sexual maturity are pivotal life history traits that influence individual fitness, population structure, and demographic rates (Roff, 1992; Stearns, 1992). Early maturation might enhance the likelihood of realising fitness and/or increase the potential for more breeding attempts over a lifetime (Bell, 1980; Oli et al., 2002). Conversely, individuals maturing at a larger size—either by faster growth rates or delayed maturity—may attain greater survival and lifetime reproductive success compared to their smaller counterparts (Honěk, 1993; Sand, 1996; Janzen et al., 2000; Sinclair et al., 2003). Female fecundity is often closely associated with size in ectotherms and despite growth often continuing post-maturity, growth rates are greatest during ontogeny and can predict maximum adult size (Kearney, 2012). Developmental rates are closely tied to temperature in ectotherms, in which conditions during relatively short timeframes early in life may significantly alter the time to and size at which ectotherms mature. Determining the effect of early life conditions on age and size at maturity is therefore crucial to understanding lifelong patterns of survival and reproduction. In **Paper III**, I test whether the amount of time suitable for activity early in life (as determined by thermal conditions) affected developmental rates and the age and size at which lowland and highland spotted snow skink females matured. I also explored trade-offs between maturing early vs. late and small vs. large, and whether age and size at maturity predict long-term survival and reproductive success. Specifically, I analysed 20 years of longitudinal data on female life history traits from two climatically distinct populations. I used hourly temperature data and population-specific thermoregulatory behaviours to make robust estimates of the amount of time suitable for activity during the first two years of life of individual females. Finally, I explored the potential long-term fitness consequences of age and size at maturity by examining the trade-off between these traits, and whether these traits predict long-term survival and reproductive success.

Increased activity time during the first two years of life caused females to mature faster compared to those that experienced reduced activity time (Figure 9a,b). In contrast, females that experienced more warm temperatures during winter hibernation matured later compared to those experiencing colder winters. This was, however, only observed in the warm lowland population (Figure 9c).

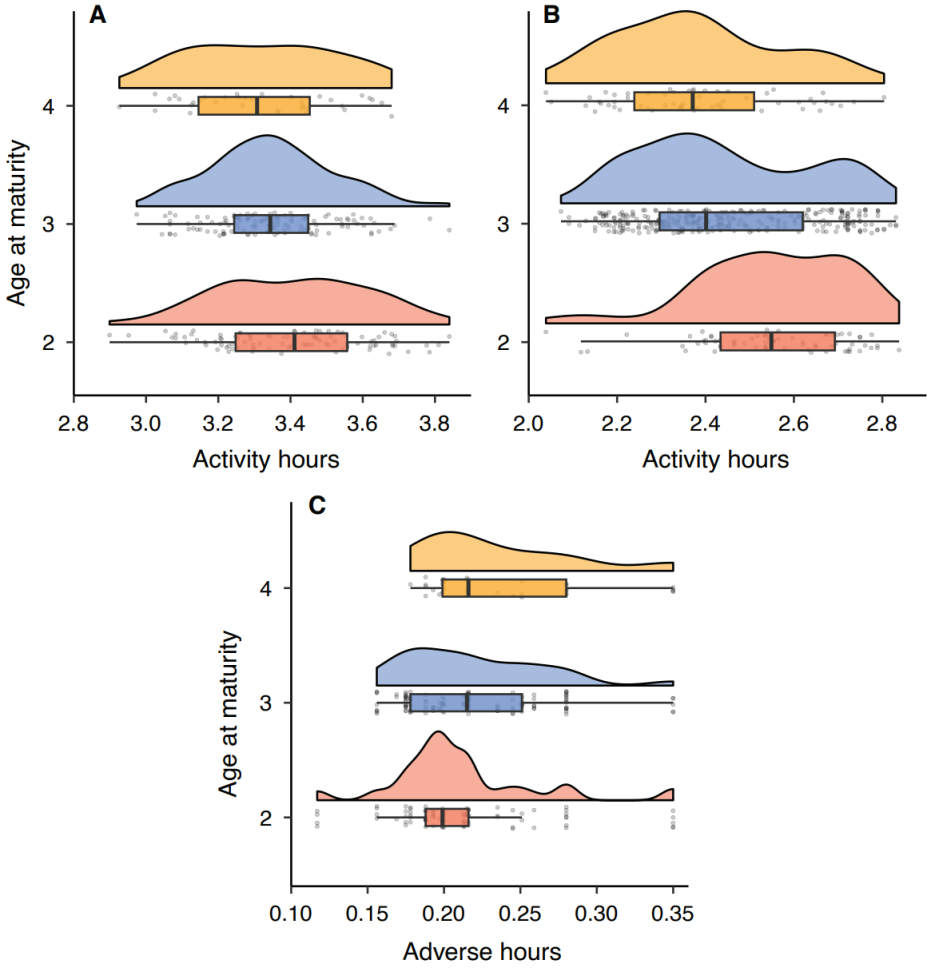


Figure 9. Number of hours suitable for activity during the activity (A, B) and hibernation (C) season experienced during the first two years of life of lowland (A, C) and highland (B) females maturing at ages 2, 3 and 4. Box plots display the median, interquartile range and minimum/maximum values. Above each box plot is a density plot.

The influence of thermal conditions early in life on size at maturity was population-specific. Highland females that experienced more time suitable for activity, either during the activity or hibernation season, matured at larger sizes compared to females with less activity time. There was no such effect on size at maturity in lowland females. Finally, females that matured earlier did so at on

average a smaller size, but maintained post-maturity growth rates high enough to surpass the body size of later-maturing females within one year (Figure 10).

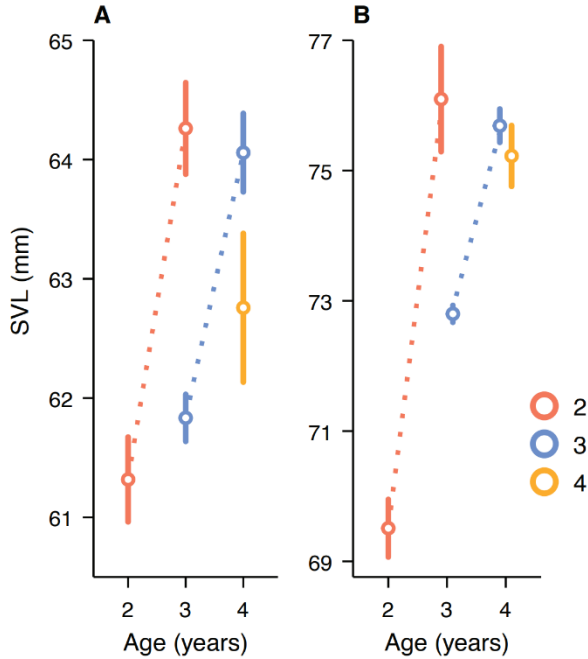


Figure 10. The snout-vent length (SVL) of lowland (A) and highland (B) females at maturity and at the second reproductive event. Colours indicate age at maturity, open circles display the mean, and solid lines the standard error range.

Females in both populations who reached maturity earlier also produced a greater number of offspring upon reaching the average lifespan of the species compared to females who matured a year later. Additionally, more early-maturing females in the highlands survived to their fifth reproductive year compared to those that matured a year later (26% and 9% survival, respectively). No effect on survival was shown in lowland females (Table 1).

Table 1. The number of females that survived 4 years post-maturity and the average (\pm SE) number of offspring females maturing at ages 2 and 3 produced by age 5.

Life history trait	Age at maturity	
	2	3
<i>Lowland</i>		
Survival	10 (of 97)	22 (of 129)
Total offspring	11.08 \pm 0.90	6.53 \pm 0.35
<i>Highland</i>		
Survival	18 (of 70)	30 (of 326)
Total offspring	14.50 \pm 0.65	10.76 \pm 0.39

The lack of evidence for a trade-off suggests that individual variation in age and size at maturity is largely driven by thermal constraints early in life. This is supported by our findings of a positive correlation between developmental rate and long-term fecundity and survival. Warmer (good) conditions early in life may increase energy assimilation rates and energy budget in this cold-climate species, allowing greater allocation of resources into growth, maintenance and reproduction (Reznick et al., 2000; Hamel et al., 2009; Wilson and Nussey, 2009).

2.2.2. Paper IV – Age and size at maturity predict senescence

Increasing developmental rates can have positive effects on multiple life history traits simultaneously such as age and size at maturity. As mentioned above, these traits can have important implications for individual fitness. However, because resources are finite, life history theory maintains that the greater developmental rates necessary to mature early and/or at a large body size should come at the cost of somatic maintenance with detrimental effects on late-life survival and reproduction (Arendt, 1997). In **Paper IV**, I use longitudinal life history data on female spotted snow skinks to explore the latent costs of developmental rate. Specifically, I examined patterns of actuarial and reproductive senescence in females that matured at different ages and sizes in

populations with divergent life history traits. The consideration of such costs becomes increasingly relevant in species like the spotted snow skink that continue to grow post-maturity and exhibit size-dependent fecundity with weak actuarial senescence post-midlife (Wapstra et al., 2001; Wapstra and Swain, 2001; Colchero et al., 2019).

To achieve this, I applied Bayesian survival trajectory analyses to two decades of longitudinal mark-recapture life history data from the same two populations of spotted snow skinks as used in **Paper III**. The effect of age and size at maturity on reproductive senescence was determined by testing their relationship with age-dependent fecundity (adjusted for size) throughout life.

Age and size at maturity were crucial in determining rates of actuarial senescence. Both lowland and highland females that developed faster and matured early (age 2 and 3 in lowlands and highlands, respectively) experienced a significantly slower rate of actuarial senescence later in life compared to females that matured a year later (Figure 11). In contrast, females that grew faster and matured at larger sizes, independent of age at maturity, suffered significantly higher mortality rates later in life compared to smaller-maturing females (Figure 12).

Ectotherms generally mature early and small when reared under warmer conditions while generally maturing later at larger sizes in colder conditions (Atkinson, 1994; Berrigan and Charnov, 1994; Adolph and Porter, 1996; Angilletta et al., 2004; Verberk et al., 2021). Maturing early may, therefore, be indicative of favourable developmental conditions that also contribute to positive effects on survival and lifespan. I propose that the contrasting effects of size at maturity on senescence rate can be attributed to strong selective pressures on body size in females, through their size-dependent fecundity (Jones et al., 1997; Wapstra and O'Reilly; Wapstra and Swain, 2001). Favourable developmental conditions may, therefore, cause females to opportunistically invest in growth while compromising maintenance and late-life survival. This strategy of opportunistically allocating resources during favourable conditions to maximise immediate reproduction, even at the expense of future reproduction, has been demonstrated across taxa; e.g., birds (Spagopoulou et al., 2020), reptiles (Olsson and Shine, 2002) and insects (Hunt et al., 2004; Hooper et al., 2017; Crosland et al., 2022).

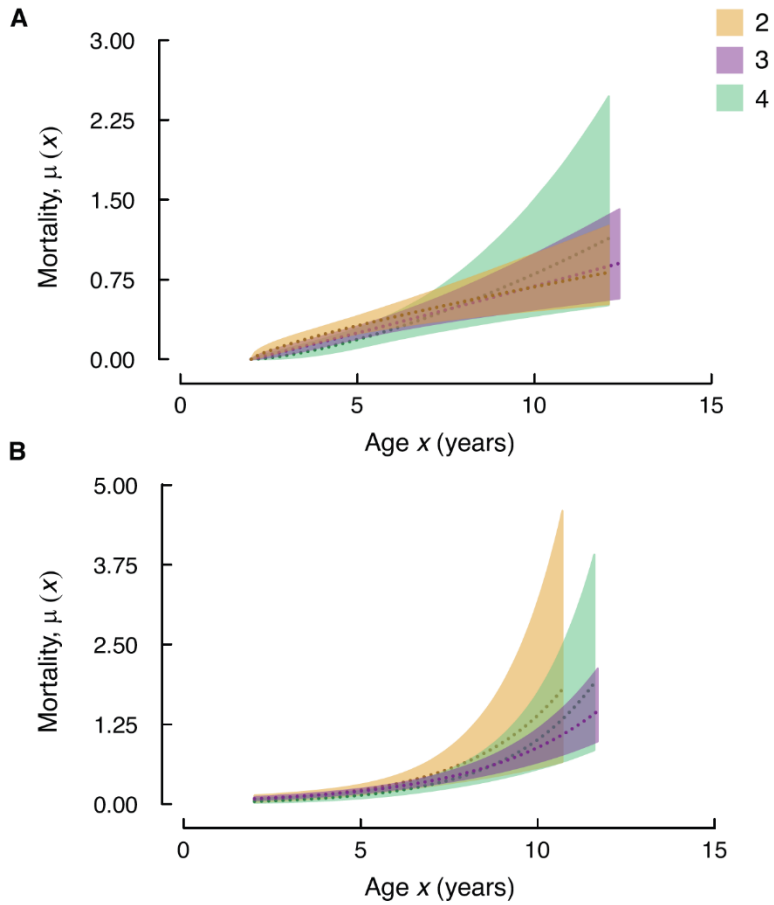


Figure 11. Variation in age-specific mortality rate among lowland (A) and highland (B) females maturing at different ages (age 2 to 4). Mortality functions were fit with a Weibull function in lowland females and a Gompertz function in highland females. Trajectories of age-specific mortality rates are shown with 95% confidence intervals (shaded areas).

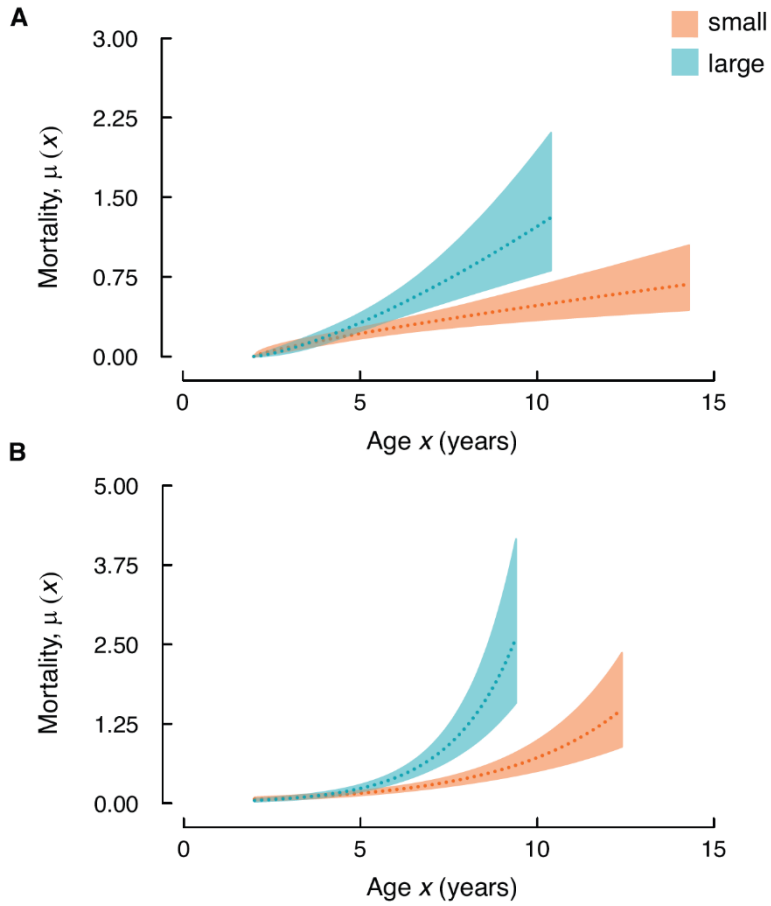


Figure 12. Variation in age-specific mortality rate among lowland (A) and highland (B) females maturing small or large (determined as the lower (small), and upper (large) 50% quantiles of snout-vent lengths). Mortality functions were fit with a Weibull function in lowland females and a Gompertz function in highland females. Trajectories of age-specific mortality rates are shown with 95% confidence intervals (shaded areas).

4. Bridging hemispheres and closing words

It is well established that developmental conditions constitute important sources of among-individual variation in life history traits and are recognised as mediators of lifelong patterns of growth, fecundity and survival (Clark and Galef, 1995; Lindström, 1999; Monaghan, 2008). Understanding the proximate drivers of life history trade-offs, and their context-dependencies, is therefore essential to predict evolutionary trajectories. In this thesis, I examine proximate drivers of traits associated with survival and reproduction (see Figure 13) and demonstrate the complexities associated with the study of individual heterogeneity of life history traits, using both experimental and longitudinal studies.

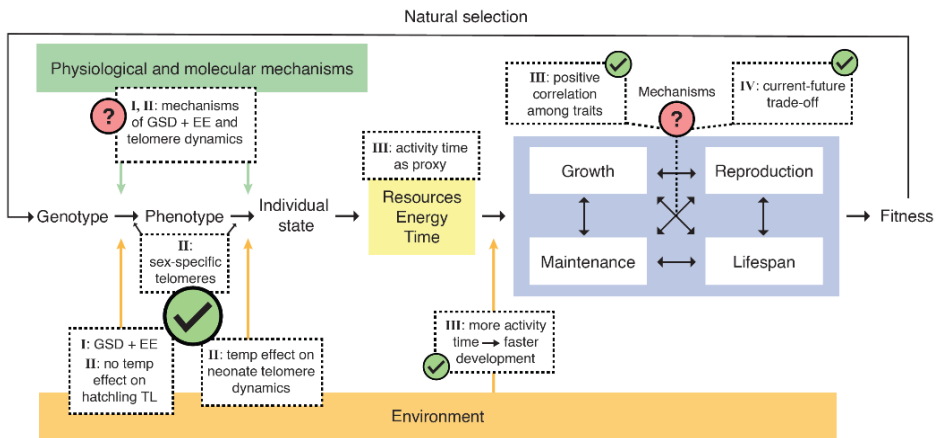


Figure 13. Figure 1 revisited. An overview of the physiological and environmental factors that shape life histories explored in this thesis, as well as questions that remain unanswered.

Recent reviews have proposed that environmental influence on the sex determination of species with sex chromosomes may be widespread in reptiles (Holleley et al., 2016; Capel, 2017; Schwanz and Georges, 2021). An increasing number of documented cases of GSD + EE in reptiles give credence to this hypothesis (see Box 1). The dismissal of additional complexity to the sex determination mechanism of reptiles based only on the presence of sex

chromosomes has, therefore, clearly been proven presumptuous. Look no further than to the thermosensitive sex determination of the spotted snow skink that simultaneously possess sex chromosomes (Wapstra et al., 2004; Pen et al., 2010; Cunningham et al., 2017; Hill et al., 2018; Hill et al., 2022). Lacertids all have sex chromosomes and therefore have formerly been assigned genetic sex determination (Janzen and Paukstis, 1991; Pokorna and Kratochvíl, 2009). In **Paper I**, I present the first evidence for thermolabile sex determination in the widespread occurring sand lizard (Figure 13). Thermosensitive sex determination was previously observed in a closely related species to the sand lizard, *Podarcis pityusensis* (Eichenberger, 1981). However, this conclusion was based on the single brief description of one male to 10–15 females produced at 29°C and has subsequently been dismissed as anecdotal (see Harlow, 2004; Pokorna and Kratochvíl, 2009). A more recent study exposed sand lizard eggs to different fluctuating thermal treatments, all with a mean temperature of 27°C (Li et al., 2013). The study found no treatment effects on sex, but their treatments did cause an overall female biased sex ratio (39.6% males) similar to the overall sex ratio produced from eggs incubated at 27°C in **Paper I** (36.2% males). This earlier work on lacertids, together with my work suggest that investigation of thermal influence on sex determination in lacertids is, indeed, warranted. The year-dependent effect shown in **Paper I** suggests an additional layer of complexity to lacertid sex determination which must be taken into consideration. I emphasise the significance of this, in which single-year studies might be insufficient to draw meaningful conclusions of negative results, and the biological importance of positive results might easily be overstated.

The mechanistic processes by which chromosomal sex can be bypassed by environmental cues remain largely unknown. A promising candidate explanation of this process is the acquisition of a thermosensitive gene dosage in the homogametic sex, in which extreme temperatures may inactivate the sex-determining gene (Quinn et al., 2007; Ezaz et al., 2009; Quinn et al., 2011; Schwanz and Georges, 2021). Thermal extremes may similarly alter gene expression of aromatase, the enzyme tasked with converting testosterone to oestrogens, causing a hormonally induced sex differentiation-cascade (Sarre et al., 2004). Involvement of aromatase in sex determination is conserved across taxa regardless of sex determination systems, including in fish, amphibians, reptiles and birds (Crews et al., 1989; Elbrecht and Smith, 1992; Wallace et al., 1999; Baroiller and D'Cotta, 2001). Moreover, recent studies have proposed a

novel mechanism by which environmental cues may be sensed via calcium and reactive oxygen species signalling, which then may, via epigenetics, transduce these cues into changes to sexual differentiation (Castelli et al., 2020b; Whiteley et al., 2021b).

The importance of determining the causes, mechanisms, and prevalence of sex reversals is undeniable. With extreme thermal events, it can cause the loss of the Y or W chromosome in as little as one generation by the production of "Trojan gene carriers", in which expected heterogamety is not realized, resulting in next-generation crossings between XX males and XX females, or ZZ males and ZZ females (Stelkens and Wedekind, 2010; Holleley et al., 2015). In the bearded dragon (*Pogona vitticeps*), sex reversed females (ZZ) produced viable offspring whose sex determination was solely determined by temperature (Holleley et al., 2015). Sex reversals may, therefore, present a viable pathway for a rapid transition between GSD and ESD. However, it has been hypothesised that sex reversal can be evolutionarily stable and may exist in GSD populations without becoming fixed (Wild et al., 2022). Chromosomal loss might be buffered against by heritable variation in thermal sex determination thresholds, immigration, or by decreased fitness of sex-reversed individuals (Holleley et al., 2016; Schwanz et al., 2019). However, we still know very little about the prevalence of reptile sex reversals, the mechanisms by which they occur, or how reversals influence individual life histories and population structures. Future research should embrace these unknowns. Sex reversals under extreme thermal conditions might also shift cohort sex ratios. If these are male-biased, this may have negative population effects either by limiting recruitment rate caused by fewer females, but may also impact individual female's survival and fecundity through increased aggressive intra-sexual interactions (Le Galliard et al., 2005). Alternatively, a female-biased sex ratio may enhance population viability in the short-term until males become limited which may also increase the risk of population collapse (Milner-Gulland et al., 2003; Bessa-Gomes et al., 2004; Wapstra et al., 2009). Climate change presents both directional change but also increased frequency of extreme weather events, and as my results in **Paper I** varied between years there is much we are yet to understand about reptilian sex determination.

Understanding sex-specific evolutionary constraints and life history strategies is crucial to determine and predict individual fitness and population structures

and trajectories. Telomere dynamics early in life, in particular, have proven important to organismal health and longevity, more so than that experienced in adulthood (Heidinger et al., 2012; Boonekamp et al., 2013; Monaghan and Ozanne, 2018). Sexually dimorphic telomere dynamics are not uncommon (see Remot et al., 2020 for the inconsistency of this sexual dimorphism) and the study of which have provided valuable insight into sex-specific life history optima and differential reproductive strategies (Barrett and Richardson, 2011; Hämäläinen et al., 2018; Heidinger et al., 2021). Most commonly, females have longer telomeres and better maintain their telomeres. This is the pattern previously observed in sand lizard adults (Olsson et al., 2010; Olsson et al., 2011b; Axelsson et al., 2020). In **Paper II**, I expand on this, showing that this sexual dimorphism is present already at hatching. Neonate females also exhibited an impressive capacity for rapid lengthening of their telomeres in the first weeks post-hatching (Figure 13). This despite the expected negative relationship between early-life growth and telomere length which is taxonomically conserved across fish, amphibians, birds and mammals (Brümmendorf et al., 2002; McLennan et al., 2016; Burraco et al., 2017; Vedder et al., 2017). A candidate proximate explanation for sex-specific variation in telomere dynamics is the influence of sex hormones on oxidative stress. Oestrogen regulates antioxidant genes and is itself a powerful antioxidant that reduces oxidative stress (Viña et al., 2005). In contrast, testosterone is associated with an increased susceptibility to oxidative stress (Alonso-Alvarez et al., 2007; Tobler and Sandell, 2009). Evolutionary explanations of sexually dimorphic telomere dynamics centre around differential reproductive costs, roles and strategies. Males in polygynous ectothermic taxa generally exhibit a faster pace-of-life and shorter lifespan compared to females. This is presumably caused by higher costs of sexual competition (e.g. sexual ornamentation, fighting, guarding and sperm competition) that subsequently decrease investments into somatic maintenance (Clutton-Brock and Isvaran, 2007). The remarkable difference in telomere maintenance between male and female neonates I present in **Paper II**, is likely driven by on-going selection on telomere length. Telomere length is positively, and more strongly, related to reproductive success and longevity in females compared to males (Olsson et al., 2011c). In contrast, the spotted snow skink—that has less sexually dimorphic morphology and more cryptic male reproductive strategies compared to sand lizards—does not exhibit sex differences in telomere length at birth (Fitzpatrick et al., 2021). Sex-specific telomere dynamics, may therefore reflect sex roles, in which polygynous and

aggressive males favour short-term reproduction gains and partner acquisition, whereas females with indeterminate growth and size-dependent fecundity favour longevity and invest more in early-life maintenance.

Telomerase—the telomere-replenishing enzyme typically repressed in endotherm somatic tissues and often upregulated in ectotherms throughout life—is currently missing in the study of ectotherm telomere dynamics and their association with life history traits (Olsson et al., 2018a; Fitzpatrick et al., 2021; Friesen et al., 2022). Although telomerase may compensate for adult telomere attrition, the high cellular turnover rates and oxidative stress associated with rapid growth early in life may saturate the capacity of telomerase. This has been shown in the fish, *Oryzias latipes*, in which yearly rates of telomere shortening was over six times greater during the first months of life compared to that during adulthood, despite having considerable telomerase activity throughout life (Hatakeyama et al., 2008). In the same fish, telomerase activity varies between life stages and closely follows telomere shortening, peaking at the end of adolescence (Hatakeyama et al., 2016). Furthermore, elevated telomerase activity has shown to accompany tissue regeneration, requiring high cell proliferation rates, in zebra fish (*Danio rerio*) and the anole lizard, *Anolis carolinensis* (Anchelin et al., 2011; Alibardi, 2015). The activity of telomerase is, therefore, necessary to understand telomere dynamics and the physiological stress imposed on the organism; especially if telomerase itself carries high energetic production costs as part of somatic maintenance (Young, 2018). The limited data on telomerase activity in ectotherm vertebrates suggest that it is highly variable across species and life stages (Gomes et al., 2010; Olsson et al., 2018a; Friesen et al., 2022), and its regulation may reflect sex roles and resource allocation strategies (Frydrychová et al., 2023). Telomerase is therefore a prime candidate to study costs of growth and reproduction to future fecundity and survival, and may constitute a pleiotropic regulator that link early-life traits and conditions to senescence (Smith et al., 2021). The sand lizard is an ideal model to explore this novel research field, in which previous studies together with my findings in **Paper I**, highlight the complexity of telomere dynamics. Sand lizard telomere dynamics are sexually dimorphic throughout life, inherited in a sex-specific manner (both on the side of parents and offspring), influenced by epigenetics, and predict offspring survival and adult fitness (Olsson et al., 2010; Olsson et al., 2011b, 2011c; Axelsson et al., 2020). Future studies should embrace this complexity to examine the role of telomere shortening and

telomerase activity as constraints on development and reproduction and mediators of resource allocation strategies and current–future life history trade-offs. This importance is elevated by recent work that points out telomeres as causal drivers of life history strategies, signalling for optimal strategies based on environmental and ecological cues (Eisenberg, 2011; Casagrande and Hau, 2019; Giraudeau et al., 2019; Sudyka, 2019; Young, 2018; Tobler et al., 2022).

Higher developmental rates are expected to be accompanied by increased replicative and oxidative stress and lower relative investments in somatic maintenance, which may have deleterious effects on late-life reproduction and survival. The benefits of increased developmental rates are well-understood and include earlier maturation and/or a larger size at maturation, both with potential positive effects on short-term and long-term fecundity. In **Paper III**, I clearly demonstrate these positive effects, in which females with more time suitable for activity during ontogeny matured earlier, grew larger, produced more offspring and had greater survival to midlife; a lesser Darwinian demon springs to mind. However, increased activity time early in life is expected to increase energy budgets by affecting energy assimilation rates (Angilletta, 2001; Kearney, 2012). My results in **Paper III** demonstrate that a greater input of resources into the resource allocation “tree” may facilitate increased investments into multiple life history traits simultaneously (see Figure 2). The apparent lack of life history trade-offs in **Paper III** mimics common observations of positive correlation among life history traits (Reznick et al., 2000; Hamel et al., 2009; Wilson and Nussey, 2009; Vedder and Bouwhuis, 2017; Cooper and Kruuk, 2018) and highlights the complexity of studying life history trade-offs in free-ranging populations. The life history “paradox” presented in **Paper III** was solved in **Paper IV**, but only with a rare longitudinal dataset on female life history traits over decades and entire lifespans. Faster growth in females during ontogeny that resulted in a larger age-corrected size at maturity was associated with increased rates of late-life mortality. This clearly shows that caution must be taken when drawing conclusions on constraints and trade-offs among life history traits, and longitudinal studies might, however impractical, be essential.

One important question remains unanswered in **Paper III** and **Paper IV**. What are the relative contributions of reproductive investment before and after reaching the average lifespan in the population? The fact is that an individual female’s chances of surviving to age $x + n$ years decline with each additional

year, even under stochastic mortality (Wensink et al., 2017). Consequently, growing fast and maturing early and/or large, even at the detriment to late-life survival, may still optimise fitness. The reproductive gains from commencing reproduction earlier and with a higher fecundity may outweigh the reproductive losses caused by an increased mortality rate late in life (see Baudisch and Scott, 2019 for information on age-dependent fecundity trajectories). Furthermore, reproductive output is not the end-all of female fitness. In ectothermic species with asymptotic growth, fecundity—measured as the number and size of offspring produced—often increases with age through continued post-maturity growth and size-dependent fecundity. This common measure of fecundity does not, however, consider offspring recruitment or fitness. A recent study found that older and larger woodlouse females produced more and larger offspring, but those offspring had subsequently lower fitness compared to those produced by younger females (Depeux et al., 2020). Offspring from older woodlouse females suffered greater mortality rates and produced smaller clutches or did not reproduce at all. Thus, while older females may produce more and/or larger offspring, those offspring may yet be of lesser quality (Priest et al., 2007; Monaghan et al., 2020). Telomeres are candidate mediators of such age-dependent transgenerational effects on offspring quality, in which offspring telomere dynamics may be inherited from the parents and in turn predict longevity or reproductive success (reviewed in Monaghan and Metcalfe, 2019; Heidinger and Young, 2020). Such effects are likely to be highly diverse across taxa due to differential age-dependent telomere dynamics, sexual dimorphisms and epigenetic effects. For instance, in the sand lizard, offspring survival increases approximately linearly with paternal telomere length (Olsson et al., 2011b). Moreover, male telomere erosion is age-dependent and only manifests in older males, and offspring telomere length declines with paternal age. In contrast, in the spotted snow skink, maternal telomere length that can lengthen with age is inherited by the offspring and subsequently offspring born from older females may have longer telomeres (Fitzpatrick et al., 2021). Thus, it may be necessary for future studies to consider telomere dynamics, as heritable epigenetic pathways that influence offspring fitness, when examining age-dependent patterns of reproduction. Such considerations are especially important in species with previously observed negligible or negative reproductive senescence

In closing, sex, sex-specific resource allocation, telomere dynamics, developmental rates and senescence are integral parts of an individual's life history decisions, ultimately influencing their genetic contribution to the next generation. In this thesis, I present evidence for important early-life drivers of short-term and long-term individual heterogeneity in traits related to reproduction and survival. The molecular mechanisms that cause this variation, however, remain largely unknown and should be prioritized going forward. This includes the molecular pathways that cause environmental cues to override genetic sex, the combined effects of growth and environmental stressors on telomere dynamics and telomerase activity, and the physiological costs associated with telomere maintenance. Longitudinal studies on individual telomere dynamics and telomerase activity throughout life in wild populations are especially needed. The treasure chest of ectotherm telomeres has only recently been opened and initial data show their exciting ties to sexual roles, life history strategies and trade-offs, and the health and death of populations. The experiences encountered early in life can undeniably have significant and lasting impacts on individual life histories. Tomorrow's individual may, indeed, be shaped by the events of yesterday.

5. Acknowledgements

First and foremost, I want to thank my two main supervisors, **Mats Olsson** and **Erik Wapstra** for their support throughout these years. Mats, I cannot believe it has been seven years since you took me on as a master student, after which you asked me if I wanted to pursue a PhD, and despite not being able to hire me, I clearly recall your “let’s get you a PhD” attitude. After many explored avenues, we ended up with the simplest of all, a conjoint PhD with a university on the other side of the world. Erik, thank you for agreeing to supervise me and for the incredible job in doing so. I am also grateful to you and **Julianne** for opening your home to me when I first arrived in Tasmania. Mats and Erik, I cannot thank you enough.

After my neat project plan got annihilated by a pandemic and a new one made, **Geoffrey While** joined my supervisory team. Geoff, thank you for stepping up, and I am especially grateful for your invaluable help in advancing my writing skills. Later in my PhD, **Luisa Fitzpatrick** also came on and assumed the role as an unofficial co-supervisor. Thank you, Lu.

I also want to thank my examiner, **Staffan Andersson**, for his guidance and always making the time for my questions.

I consider myself fortunate to have met such incredible people at two universities. I want to thank all my friends and colleagues at GU for their support, lunchtime chats and game nights: **Oskar** (our dungeon master), **James** (for all the years of splendid banter), **Darragh** (for never forgetting to complement my outfit), **Niklas** (my twin), **Mette**, **Willow**, **Badreddine**, **Joshua**, **Magnus**, **Daniel**, **Rute**, **Jonathan**, **Mårten**, **Leon**, **Charlotte**, **Laima**, **Agathe**, **Lucas**, **Nicklas**, and **Varpu**. I also want to thank all my friends and colleagues at UTas for their support, office chats, and the memories: **Dierdre**, **Peta**, **Tori**, **Luisa** (that’s two thanks now), **Alix**, **Paul** (surf’s up dude!), **Mara**, **Kirsty**, **Elize**, **Helena**, **Javier**, **Carles**, **Jamie** and **Jen**. To anyone I might have missed, you are no less important!

Thank you, **mom** and **dad**, for always being there.

Lastly, I want to thank **Gilma**, my partner and best friend. I am forever grateful for your endless support and for the 16 wonderful years we have shared.

This project was funded by the Swedish Science Council, the Australian Research Council, the Holsworth Wildlife Research Endowment, the Helge Ax:son Johnsons Foundation, the Nilsson-Ehle Endowments, the Adlerbert scholarships and the Herbert & Karin Jacobssons Foundation.

6. References

- Adolph, S. C., & Porter, W. P. (1996). Growth, seasonality, and lizard life histories: age and size at maturity. *Oikos*, 77, 267–278.
- Agasyan, A., Avci, A., Tuniyev, B., Lymberakis, P., Andrén, C., Cogalniceanu, D., Wilkinson, J., Ananjeva, N., Üzümlü, N., Orlov, N., Podloucky, R., Tuniyev, S., Kaya, U., Crnobrnja Isailovic, J., Vogrin, M., Corti, C., Pérez Mellado, V., Sá-Sousa, P., Cheylan, M., ... Schmidt, B. (2010). *Lacerta agilis*. The IUCN Red List of Threatened Species 2010.
- Albecker, M. A., & McCoy, M. W. (2017). Adaptive responses to salinity stress across multiple life stages in anuran amphibians. *Frontiers in Zoology*, 14, 40.
- Alibardi, L. (2015). Immunolocalization of the telomerase-1 component in cells of the regenerating tail, testis, and intestine of lizards. *Journal of Morphology*, 276, 748–758.
- Alonso-Alvarez, C., Bertrand, S., Faivre, B., & Sorci, G. (2007). Increased susceptibility to oxidative damage as a cost of accelerated somatic growth in zebra finches. *Functional Ecology*, 21, 873–879.
- Anchelin, M., Murcia, L., Alcaraz-Pérez, F., García-Navarro, E. M., & Cayuela, M. L. (2011). Behaviour of telomere and telomerase during aging and regeneration in zebrafish. *PLoS ONE*, 6, e16955.
- Andres, C., Franke, F., Bleidorn, C., Bernhard, D., & Schlegel, M. (2014). Phylogenetic analysis of the *Lacerta agilis* subspecies complex. *Systematics and Biodiversity*, 12, 43–54.
- Angilletta, M. J. (2001). Thermal and physiological constraints on energy assimilation in a widespread lizard (*Sceloporus undulatus*). *Ecology*, 82, 3044–3056.
- Angilletta, M. J. (2004). Temperature, growth rate, and body size in ectotherms: fitting pieces of a life-history puzzle. *Integrative and Comparative Biology*, 44, 498–509.
- Arendt, J. D. (1997). Adaptive intrinsic growth rates: an integration across taxa. *The Quarterly Review of Biology*, 72, 149–177.
- Atkinson, D. (1994). Temperature and organism size—a biological law for ectotherms? *Advances in Ecological Research*, 25, 1–58.
- Aubert, G., & Lansdorp, P. M. (2008). Telomeres and aging. *Physiological Reviews*, 88, 557–579.

- Aviv, A., Anderson, J. J., & Shay, J. W. (2017). Mutations, cancer and the telomere length paradox. *Trends in Cancer*, 3, 253–258.
- Axelsson, J., Wapstra, E., Miller, E., Rollings, N., & Olsson, M. (2020). Contrasting seasonal patterns of telomere dynamics in response to environmental conditions in the ectothermic sand lizard, *Lacerta agilis*. *Scientific Reports*, 10, 182.
- Bachtrog, D., Mank, J. E., Peichel, C. L., Kirkpatrick, M., Otto, S. P., Ashman, T.-L., Hahn, M. W., Kitano, J., Mayrose, I., Ming, R., Perrin, N., Ross, L., Valenzuela, N., Vamosi, J. C., & The Tree of Sex Consortium. (2014). Sex determination: why so many ways of doing it? *PLoS Biology*, 12, e1001899.
- Baroiller, J. F., & D'Cotta, H. (2001). Environment and sex determination in farmed fish. *Comparative Biochemistry and Physiology Part C: Toxicology & Pharmacology*, 130, 399–409.
- Barrett, E. L. B., & Richardson, D. S. (2011). Sex differences in telomeres and lifespan. *Aging Cell*, 10, 913–921.
- Baudisch, A., & Stott, I. (2019). A pace and shape perspective on fertility. *Methods in Ecology and Evolution*, 10, 1941–1951.
- Bauwens, D., & Thoen, C. (1981). Escape tactics and vulnerability to predation associated with reproduction in the lizard *Lacerta vivipara*. *The Journal of Animal Ecology*, 50, 733.
- Bell, G. (1980). The costs of reproduction and their consequences. *The American Naturalist*, 116, 45–76.
- Bererhi, B., Lindsay, W. R., Schwartz, T. S., Wapstra, E., & Olsson, M. (2023). Limited effects of inbreeding on breeding coloration. *Journal of Heredity*, 114, 143–151
- Bererhi, B., Wapstra, E., Schwartz, T. S., & Olsson, M. (2019). Inconsistent inbreeding effects during lizard ontogeny. *Conservation Genetics*, 20, 865–874.
- Berglind, S.-Å., Gullberg, A., & Olsson, M. (2015). Action plan for the Swedish sand lizard 2014–2017 (in Swedish: 'Åtgärdsprogram för sandödla, 2014–2017', Rapport 6597, December 2013). The Swedish Environmental Protection Agency.
- Berglund, A., Rosenqvist, G., & Svensson, I. (1986). Mate choice, fecundity and sexual dimorphism in two pipefish species (Syngnathidae). *Behavioral Ecology and Sociobiology*, 19, 301–307.

- Berrigan, D., & Charnov, E. L. (1994). Reaction norms for age and size at maturity in response to temperature: a puzzle for life historians. *Oikos*, 70, 474–478.
- Bessa-Gomes, C., Legendre, S., & Clobert, J. (2004). Allee effects, mating systems and the extinction risk in populations with two sexes. *Ecology Letters*, 7, 802–812.
- Bischoff B. (1984). *Lacerta agilis* Linnaeus 1798 – Zauneidechse. Handbuch der reptilien und amphibien Europas (Böhme, W., ed.), Band 2/1, Echsen II, pp. 23–68. Wiesbaden: AULA-Verlag.
- Blackburn, E. H. (1991). Structure and function of telomeres. 350, 569–573.
- Blackburn, E. H. (2000). Telomere states and cell fates. *Nature*, 408, 53–56.
- Boonekamp, J. J., Mulder, G. A., Salomons, H. M., Dijkstra, C., & Verhulst, S. (2014). Nestling telomere shortening, but not telomere length, reflects developmental stress and predicts survival in wild birds. *Proceedings of the Royal Society B: Biological Sciences*, 281, 20133287.
- Bronikowski, A. M. (2008). The evolution of aging phenotypes in snakes: a review and synthesis with new data. *AGE*, 30, 169–176.
- Brümmendorf, T. H., Mak, J., Sabo, K. M., Baerlocher, G. M., Dietz, K., Abkowitz, J. L., & Lansdorp, P. M. (2002) Longitudinal studies of telomere length in feline blood cells: implications for hematopoietic stem cell turnover in vivo. *Experimental Hematology*. 30, 1147–1152.
- Bülbül, U., Koç, H., Özkan, H., Öztürk, İ., & Kutrup, B. (2019). New locality record of *Lacerta agilis* (Squamata: Lacertidae) in Turkey. *Turkish Journal of Biodiversity*, 2, 52–56.
- Bull, J. J. (1981). Evolution of environmental sex determination from genotypic sex determination. *Heredity*, 47, 173–184.
- Burraco, P., Comas, M., Reguera, S., Zamora-Camacho, F. J., & Moreno-Rueda, G. (2020). Telomere length mirrors age structure along a 2200-m altitudinal gradient in a Mediterranean lizard. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology*, 247, 110741.
- Burraco, P., Díaz-Paniagua, C., & Gomez-Mestre, I. (2017). Different effects of accelerated development and enhanced growth on oxidative stress and telomere shortening in amphibian larvae. *Scientific Reports*, 7, 7494.
- Cadby, C. D., Jones, S. M., & Wapstra, E. (2011). Potentially adaptive effects of maternal nutrition during gestation on offspring phenotype of a viviparous reptile. *Journal of Experimental Biology*, 214, 4234–4239.

- Cadby, C. D., While, G. M., Hobday, A. J., Uller, T., & Wapstra, E. (2010). Multi-scale approach to understanding climate effects on offspring size at birth and date of birth in a reptile. *Integrative Zoology*, 5, 164–175.
- Cadby, C., Jones, S., & Wapstra, E. (2014). Geographical differences in maternal basking behaviour and offspring growth rate in a climatically widespread viviparous reptile. *Journal of Experimental Biology*, 217, 1175–1179.
- Caldwell, A. J., While, G. M., & Wapstra, E. (2017). Plasticity of thermoregulatory behaviour in response to the thermal environment by widespread and alpine reptile species. *Animal Behaviour*, 132, 217–227.
- Campisi, J. (1997). The biology of replicative senescence. *European Journal of Cancer*, 33, 703–709.
- Capel, B. (2017). Vertebrate sex determination: evolutionary plasticity of a fundamental switch. *Nature Reviews Genetics*, 18, 675–689.
- Casagrande, S., & Hau, M. (2019). Telomere attrition: metabolic regulation and signalling function? *Biology Letters*, 15, 20180885.
- Casagrande, S., Stier, A., Monaghan, P., Loveland, J. L., Boner, W., Lupi, S., Trevisi, R., & Hau, M. (2020). Increased glucocorticoid concentrations in early life cause mitochondrial inefficiency and short telomeres. *Journal of Experimental Biology*, 223, jeb.222513.
- Castelli, M. A., Georges, A., Cherryh, C., Rosauer, D. F., Sarre, S. D., Contador-Kelsall, I., & Holleley, C. E. (2020a). Evolving thermal thresholds explain the distribution of temperature sex reversal in an Australian dragon lizard. *Diversity and Distributions*, 27, 427–438.
- Castelli, M. A., Whiteley, S. L., Georges, A., & Holleley, C. E. (2020). Cellular calcium and redox regulation: the mediator of vertebrate environmental sex determination? *Biological Reviews*, 95, 680–695.
- Cayueta, H., Lemaître, J., Bonnaire, E., Pichenot, J., & Schmidt, B. R. (2020). Population position along the fast–slow life-history continuum predicts intraspecific variation in actuarial senescence. *Journal of Animal Ecology*, 89, 1069–1079.
- Cesare, A. J., & Reddel, R. R. (2010). Alternative lengthening of telomeres: models, mechanisms and implications. *Nature Reviews Genetics*, 11, 319–330.
- Charnov, E. L., & Bull, J. (1977). When is sex environmentally determined? *Nature*, 266, 828–830.

- Clark, M. M., & Galef, B. G. (1995). Prenatal influences on reproductive life history strategies. *Trends in Ecology & Evolution*, 10, 151–153.
- Cliff, H. B., Wapstra, E., & Burridge, C. P. (2015). Persistence and dispersal in a Southern Hemisphere glaciated landscape: The phylogeography of the spotted snow skink (*Niveoscincus ocellatus*) in Tasmania. *BMC Evolutionary Biology*, 15, 121.
- Clutton-Brock, T. H. (1984). reproductive effort and terminal investment in iteroparous animals. *The American Naturalist*, 123, 212–229.
- Clutton-Brock, T. H., & Isvaran, K. (2007). Sex differences in ageing in natural populations of vertebrates. *Proceedings of the Royal Society B: Biological Sciences*, 274, 3097–3104.
- Colchero, F., Jones, O. R., Conde, D. A., Hodgson, D., Zajitschek, F., Schmidt, B. R., Malo, A. F., Alberts, S. C., Becker, P. H., Bouwhuis, S., Bronikowski, A. M., Vleeschouwer, K. M., Delahay, R. J., Dummermuth, S., Fernández-Duque, E., Frisenvænge, J., Hesselsøe, M., Larson, S., Lemaître, J., ... Gaillard, J. (2019). The diversity of population responses to environmental change. *Ecology Letters*, 22, 342–353.
- Cooper, E. B., & Kruuk, L. E. B. (2018). Ageing with a silver-spoon: a meta-analysis of the effect of developmental environment on senescence. *Evolution Letters*, 2, 460–471.
- Cornejo-Páramo, P., Dissanayake, D. S. B., Lira-Noriega, A., Martínez-Pacheco, M. L., Acosta, A., Ramírez-Suástegui, C., Méndez-de-la-Cruz, F. R., Székely, T., Urrutia, A. O., Georges, A., & Cortez, D. (2020). Viviparous reptile regarded to have temperature-dependent sex determination has old XY chromosomes. *Genome Biology and Evolution*, 12, 924–930.
- Criscuolo, F., Sorci, G., Behaim-Delarbre, M., Zahn, S., Faivre, B., & Bertile, F. (2018). Age-related response to an acute innate immune challenge in mice: proteomics reveals a telomere maintenance-related cost. *Proceedings of the Royal Society B: Biological Sciences*, 285, 20181877.
- Crosland, A., Rigaud, T., Balourdet, A., & Moret, Y. (2022). “Born with a silver spoon in the mouth has bad sides too”: experimentally increasing growth rate enhances individual quality but accelerates reproductive senescence in females of the mealworm beetle, *Tenebrio molitor*. *Frontiers in Ecology and Evolution*, 10, 915054.

- Crews, D., Wibbels, T., & Gutzke, W. H. N. (1989). Action of sex steroid hormones on temperature-induced sex determination in the snapping turtle (*Chelydra serpentina*). *General and Comparative Endocrinology*, 76, 159–166.
- Cunningham, G. D., Fitzpatrick, L. J., While, G. M., & Wapstra, E. (2018). Plastic rates of development and the effect of thermal extremes on offspring fitness in a cold-climate viviparous lizard. *Journal of Experimental Zoology Part A: Ecological and Integrative Physiology*, 329, 262–270.
- Cunningham, G. D., While, G. M., Olsson, M., Ljungström, G., & Wapstra, E. (2020). Degrees of change: between and within population variation in thermal reaction norms of phenology in a viviparous lizard. *Ecology*, 101, e03136.
- Cunningham, G. D., While, G. M., & Wapstra, E. (2017). Climate and sex ratio variation in a viviparous lizard. *Biology Letters*, 13, 20170218.
- Dammhahn, M., Dingemanse, N. J., Niemelä, P. T., & Réale, D. (2018). Pace-of-life syndromes: a framework for the adaptive integration of behaviour, physiology and life history. *Behavioral Ecology and Sociobiology*, 72, 62
- Depeux, C., Lemaître, J., Moreau, J., Dechaume-Moncharmont, F., Laverre, T., Pauhac, H., Gaillard, J., & Beltran-Bech, S. (2020). Reproductive senescence and parental effects in an indeterminate grower. *Journal of Evolutionary Biology*, 33, 1256–1264.
- van Deursen, J. M. (2014). The role of senescent cells in ageing. *Nature*, 509, 439–446.
- Dew, R. M., Shell, W. A., & Rehan, S. M. (2018). Changes in maternal investment with climate moderate social behaviour in a facultatively social bee. *Behavioral Ecology and Sociobiology*, 72, 69.
- Dobzhansky, T. (1973). Nothing in biology makes sense except in the light of evolution. *The American Biology Teacher*, 35, 125–129.
- Dupoué, A., Blaimont, P., Angelier, F., Ribout, C., Rozen-Rechels, D., Richard, M., Miles, D., De Villemereuil, P., Rutschmann, A., Badiane, A., Aubret, F., Lourdais, O., Meylan, S., Cote, J., Clobert, J., & Le Galliard, J.-F. (2022). Lizards from warm and declining populations are born with extremely short telomeres. *Proceedings of the National Academy of Sciences*, 119, e2201371119.

- Dupoué, A., Rutschmann, A., Le Galliard, J. F., Clobert, J., Angelier, F., Marciaud, C., Ruault, S., Miles, D., & Meylan, S. (2017). Shorter telomeres precede population extinction in wild lizards. *Scientific Reports*, 7, 16976.
- Eichenberger, P. (1981). Smaragdhagedissen (*Lacerta viridis*) kweken op bestelling. *Lacerta*, 39, 72–76.
- Eisenberg, D. T. A. (2010). An evolutionary review of human telomere biology: the thrifty telomere hypothesis and notes on potential adaptive paternal effects. *American Journal of Human Biology*, 23, 149–167.
- Elbrecht, A., & Smith, R. (1992). Aromatase enzyme activity and sex determination in chickens. *Science*, 255, 467–470.
- Ewert, M. A., Jackson, D. R., & Nelson, C. E. (1994). Patterns of temperature-dependent sex determination in turtles. *Journal of Experimental Zoology*, 270, 3–15.
- Ezaz, T., Sarre, S. D., O’Meally, D., Marshall Graves, J. A., & Georges, A. (2009). Sex chromosome evolution in lizards: independent origins and rapid transitions. *Cytogenetic and Genome Research*, 127, 249–260.
- Fitzpatrick, L. J., Olsson, M., Pauliny, A., While, G. M., & Wapstra, E. (2021). Individual telomere dynamics and their links to life history in a viviparous lizard. *Proceedings of the Royal Society B: Biological Sciences*, 288, 20210271.
- Frank, S. A. (1990). Sex allocation theory for birds and mammals. *Annual Review of Ecology and Systematics*, 21, 13–55.
- Friesen, C. R., Wapstra, E., & Olsson, M. (2022). Of telomeres and temperature: Measuring thermal effects on telomeres in ectothermic animals. *Molecular Ecology*, 31, 6069–6086.
- Frydrychová, R. Č., Konopová, B., Peska, V., Brejcha, M., & Sábová, M. (2023). Telomeres and telomerase: active but complex players in life-history decisions. *Biogerontology*.
- Le Galliard, J. F., Fitze, P. S., Ferriere, R., & Clobert, J. (2005). From the cover: sex ratio bias, male aggression, and population collapse in lizards. *Proceedings of the National Academy of Sciences*, 102, 18231–18236.
- Giraudeau, M., Angelier, F., & Sepp, T. (2019). Do telomeres influence pace-of-life-strategies in response to environmental conditions over a lifetime and between generations? *BioEssays*, 41, 1800162.
- Gomes, N. M. V., Shay, J. W., & Wright, W. E. (2010). Telomere biology in Metazoa. *FEBS Letters*, 584, 3741–3751.

- Greider, C. W., & Blackburn, E. H. (1985). Identification of a specific telomere terminal transferase activity in tetrahymena extracts. *Cell*, 43, 405–413.
- Gullberg, A., Olsson, M., & Tegelström, H. (1998). Colonization, genetic diversity, and evolution in the Swedish sand lizard, *Lacerta agilis* (Reptilia, Squamata). *Biological Journal of the Linnean Society*, 65, 257–277.
- Gullberg, Olsson, & Tegelström. (1999). Evolution in populations of Swedish sand lizards: Genetic differentiation and loss of variability revealed by multilocus DNA fingerprinting. *Journal of Evolutionary Biology*, 12, 17–26.
- Hall, J. M., Mitchell, T. S., Thawley, C. J., Stroud, J. T., & Warner, D. A. (2020). Adaptive seasonal shift towards investment in fewer, larger offspring: evidence from field and laboratory studies. *Journal of Animal Ecology*, 89, 1242–1253.
- Hämäläinen, A., Immonen, E., Tarka, M., & Schuett, W. (2018). Evolution of sex-specific pace-of-life syndromes: causes and consequences. *Behavioral Ecology and Sociobiology*, 72, 50.
- Hamel, S., Côté, S. D., Gaillard, J.-M., & Festa-Bianchet, M. (2009). Individual variation in reproductive costs of reproduction: high-quality females always do better. *Journal of Animal Ecology*, 78, 143–151.
- Hamilton, W. D. (1966). The moulding of senescence by natural selection. *Journal of Theoretical Biology*, 12, 12–45.
- Hansson, A., & Olsson, M. (2018). Incubation temperature and parental identity determine sex in the Australian agamid lizard *Ctenophorus pictus*. *Ecology and Evolution*, 8, 9827–9833.
- Hao, L.-Y., Armanios, M., Strong, M. A., Karim, B., Feldser, D. M., Huso, D., & Greider, C. W. (2005). Short telomeres, even in the presence of telomerase, limit tissue renewal capacity. *Cell*, 123, 1121–1131.
- Harlow, P.S. (1996). A harmless technique for sexing hatchling lizards. *Herpetological Review*, 27, 71–72.
- Harlow, P. (2004). Temperature-dependent sex determination in lizards. In N. Valenzuela, & V. Lance (Eds.), *Temperature-dependent sex determination in vertebrates* (pp. 42–52). Smithsonian Books, Washington, DC.

- Hatakeyama, H., Nakamura, K.-I., Izumiya-Shimomura, N., Ishii, A., Tsuchida, S., Takubo, K., & Ishikawa, N. (2008). The teleost *Oryzias latipes* shows telomere shortening with age despite considerable telomerase activity throughout life. *Mechanisms of Ageing and Development*, 129, 550–557.
- Hatakeyama, H., Yamazaki, H., Nakamura, K.-I., Izumiya-Shimomura, N., Aida, J., Suzuki, H., Tsuchida, S., Matsuura, M., Takubo, K., & Ishikawa, N. (2016). Telomere attrition and restoration in the normal teleost *Oryzias latipes* are linked to growth rate and telomerase activity at each life stage. *Aging*, 8, 62–75.
- Hayflick, L. (1965). The limited in vitro lifetime of human diploid cell strains. *Experimental Cell Research*, 37, 614–636.
- Heidinger, B. J., Blount, J. D., Boner, W., Griffiths, K., Metcalfe, N. B., & Monaghan, P. (2012). Telomere length in early life predicts lifespan. *Proceedings of the National Academy of Sciences*, 109, 1743–1748.
- Heidinger, B. J., Kucera, A. C., Kittilson, J. D., & Westneat, D. F. (2021). Longer telomeres during early life predict higher lifetime reproductive success in females but not males. *Proceedings of the Royal Society B: Biological Sciences*, 288, 20210560.
- Heidinger, B. J., & Young, R. C. (2020). Cross-generational effects of parental age on offspring longevity: are telomeres an important underlying mechanism? *BioEssays*, 42, 1900227.
- Hill, P. L., Burridge, C. P., Ezaz, T., & Wapstra, E. (2018). Conservation of sex-linked markers among conspecific populations of a viviparous skink, *Niveoscincus ocellatus*, exhibiting genetic and temperature-dependent sex determination. *Genome Biology and Evolution*, 10, 1079–1087.
- Hill, P., While, G. M., Burridge, C. P., Ezaz, T., Munch, K. L., McVarish, M., & Wapstra, E. (2022). Sex reversal explains some, but not all, climate-mediated sex ratio variation within a viviparous reptile. *Proceedings of the Royal Society B: Biological Sciences*, 289, 20220689.
- Hoekstra, L. A., Schwartz, T. S., Sparkman, A. M., Miller, D. A. W., & Bronikowski, A. M. (2020). The untapped potential of reptile biodiversity for understanding how and why animals age. *Functional Ecology*, 34, 38–54.

- Hoelzl, F., Cornils, J. S., Smith, S., Moodley, Y., & Ruf, T. (2016). Telomere dynamics in free-living edible dormice (*Glis glis*): the impact of hibernation and food supply. *Journal of Experimental Biology*, 219, 2469–2474.
- Holbrook, G. L., & Schal, C. (2004). Maternal investment affects offspring phenotypic plasticity in a viviparous cockroach. *Proceedings of the National Academy of Sciences*, 101, 5595–5597.
- Holleley, C. E., O’Meally, D., Sarre, S. D., Marshall Graves, J. A., Ezaz, T., Matsubara, K., Azad, B., Zhang, X., & Georges, A. (2015). Sex reversal triggers the rapid transition from genetic to temperature-dependent sex. *Nature*, 523, 79–82.
- Holleley, C. E., Sarre, S. D., O’Meally, D., & Georges, A. (2016). Sex reversal in reptiles: reproductive oddity or powerful driver of evolutionary change? *Sexual Development*, 10, 279–287.
- Holliday, R. (2006). Aging is no longer an unsolved problem in biology. *Annals of the New York Academy of Sciences*, 1067, 1–9.
- Honěk, A. (1993). Intraspecific variation in body size and fecundity in insects: a general relationship. *Oikos*, 66, 483–492.
- Hooper, A. K., Spagopoulou, F., Wylde, Z., Maklakov, A. A., & Bonduriansky, R. (2017). Ontogenetic timing as a condition-dependent life history trait: high-condition males develop quickly, peak early, and age fast. *Evolution*, 71, 671–685.
- Huey, R. B., & Kingsolver, J. G. (1989). Evolution of thermal sensitivity of ectotherm performance. *Trends in Ecology & Evolution*, 4, 131–135.
- Hulme, P. E. (2008). Phenotypic plasticity and plant invasions: is it all Jack? *Functional Ecology*, 22, 3–7.
- Hulme, P. E., & Bernard-Verdier, M. (2018). Comparing traits of native and alien plants: can we do better? *Functional Ecology*, 32, 117–125.
- Hunt, J., Brooks, R., Jennions, M. D., Smith, M. J., Bentsen, C. L., & Bussière, L. F. (2004). High-quality male field crickets invest heavily in sexual display but die young. *Nature*, 432, 1024–1027.
- Janzen, F. J., & Paukstis, G. L. (1991). Environmental sex determination in reptiles: ecology, evolution, and experimental design. *The Quarterly Review of Biology*, 66, 149–179.

- Janzen, F. J., & Phillips, P. C. (2006). Exploring the evolution of environmental sex determination, especially in reptiles. *Journal of Evolutionary Biology*, 19, 1775–1784.
- Janzen, F. J., Tucker, J. K., & Paukstis, G. L. (2000). Experimental analysis of an early life-history stage: avian predation selects for larger body size of hatchling turtles. *Journal of Evolutionary Biology*, 13, 947–954.
- Jones, O. R., Scheuerlein, A., Salguero-Gómez, R., Camarda, C. G., Schaible, R., Casper, B. B., Dahlgren, J. P., Ehrlén, J., García, M. B., Menges, E. S., Quintana-Ascencio, P. F., Caswell, H., Baudisch, A., & Vaupel, J. W. (2014). Diversity of ageing across the tree of life. *Nature*, 505, 169–173.
- Jones, S. M., Wapstra, E., & Swain, R. (1997). Asynchronous male and female gonadal cycles and plasma steroid concentrations in a viviparous lizard, *Niveoscincus ocellatus* (Scincidae), from Tasmania. *General and Comparative Endocrinology*, 108, 271–281.
- Kawanishi, S., & Oikawa, S. (2004). Mechanism of telomere shortening by oxidative stress. *Annals of the New York Academy of Sciences*, 1019, 278–284.
- Kearney, M. (2012). Metabolic theory, life history and the distribution of a terrestrial ectotherm. *Functional Ecology*, 26, 167–179.
- Kim, S.-Y., Metcalfe, N. B., Da Silva, A., & Velando, A. (2017). Thermal conditions during early life influence seasonal maternal strategies in the three-spined stickleback. *BMC Ecology*, 17, 34.
- Kirkwood, T. B. L. (1977). Evolution of ageing. *Nature*, 270, 301–304.
- Kirkwood, T. B. L., & Holliday, R. (1979). The evolution of ageing and longevity. *Proceedings of the Royal Society of London. Series B, Biological Sciences*, 205, 531–546.
- Kirkwood, T. B. L., & Rose, M. R. (1991). Evolution of senescence: late survival sacrificed for reproduction. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, 332, 15–24.
- Lafuente, E., & Beldade, P. (2019). Genomics of developmental plasticity in animals. *Frontiers in Genetics*, 10, 720.
- Lemaître, J.-F., & Gaillard, J.-M. (2017). Reproductive senescence: new perspectives in the wild. *Biological Reviews*, 92, 2182–2199.
- Li, S., Xu, Z., Luo, L., Ping, J., Zhou, H., Xie, L., & Zhang, Y. (2022). Latitudinal variation in the pattern of temperature-dependent sex determination in the Japanese gecko, *Gekko japonicus*. *Animals*, 12, 942.

- Li, H., Zhou, Z.-S., Ding, G.-H., & Ji, X. (2011). Fluctuations in incubation temperature affect incubation duration but not morphology, locomotion and growth of hatchlings in the sand lizard *Lacerta agilis* (Lacertidae). *Acta Zoologica*, 94, 11–18.
- Lindsay, W. R., Madsen, T., Wapstra, E., Lillie, M., Loeb, L., Ujvari, B., & Olsson, M. (2020). Long term effects of outbreeding: experimental founding of island population eliminates malformations and improves hatching success in sand lizards. *Biological Conservation*, 249, 108710.
- Lindsay, W. R., Wapstra, E., Silverin, B., & Olsson, M. (2016). Corticosterone: a costly mediator of signal honesty in sand lizards. *Ecology and Evolution*, 6, 7451–7461.
- Lindström, J. (1999). Early development and fitness in birds and mammals. *Trends in Ecology & Evolution*, 14, 343–348.
- Lisachov, A. P., Giovannotti, M., Pereira, J. C., Andreyushkova, D. A., Romanenko, S. A., Ferguson-Smith, M. A., Borodin, P. M., & Trifonov, V. A. (2020). Chromosome painting does not support a sex chromosome turnover in *Lacerta agilis* Linnaeus, 1758. *Cytogenetic and Genome Research*, 160, 134–140.
- Ljungström, G., Wapstra, E., & Olsson, M. (2015). Sand lizard (*Lacerta agilis*) phenology in a warming world. *BMC Evolutionary Biology*, 15, 206.
- Madsen, T., Olsson, M., Wittzell, H., Stille, B., Gullberg, A., Shine, R., Andersson, S., & Tegelström, H. (2000). Population size and genetic diversity in sand lizards (*Lacerta agilis*) and adders (*Vipera berus*). *Biological Conservation*, 94, 257–262.
- Mangel, M., & Stamps, J. (2001). Trade-offs between growth and mortality and the maintenance of individual variation in growth. *Evolutionary Ecology Research*, 3, 583–593.
- Marasco, V., Smith, S., & Angelier, F. (2022). How does early-life adversity shape telomere dynamics during adulthood? Problems and paradigms. *BioEssays*, 44, 2100184.
- McLennan, D., Armstrong, J. D., Stewart, D. C., Mckelvey, S., Boner, W., Monaghan, P., & Metcalfe, N. B. (2016). Interactions between parental traits, environmental harshness and growth rate in determining telomere length in wild juvenile salmon. *Molecular Ecology*, 25, 5425–5438.

- Medawar, P.B. (1952). An unsolved problem of biology. Lewis, London.
- Metcalfe, N. B., & Monaghan, P. (2001). Compensation for a bad start: grow now, pay later? *Trends in Ecology & Evolution*, 16, 254–260.
- Metcalfe, N. B., & Monaghan, P. (2003). Growth versus lifespan: perspectives from evolutionary ecology. *Experimental Gerontology*, 38, 935–940.
- Meyne, J., Ratliff, R. L., & Moyzis, R. K. (1989). Conservation of the human telomere sequence (TTAGGG)_n among vertebrates. *Proceedings of the National Academy of Sciences*, 86, 7049–7053.
- Milner-Gulland, E. J., Bukreeva, O. M., Coulson, T., Lushchekina, A. A., Kholodova, M. V., Bekenov, A. B., & Grachev, I. A. (2003). Reproductive collapse in saiga antelope harems. *Nature*, 422, 135.
- Monaghan, P. (2008). Early growth conditions, phenotypic development and environmental change. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 363, 1635–1645.
- Monaghan, P. (2010). Telomeres and life histories: the long and the short of it. *Annals of the New York Academy of Sciences*, 1206, 130–142.
- Monaghan, P. (2014). Organismal stress, telomeres and life histories. *Journal of Experimental Biology*, 217, 57–66.
- Monaghan, P., Maklakov, A. A., & Metcalfe, N. B. (2020). Intergenerational transfer of ageing: parental age and offspring lifespan. *Trends in Ecology & Evolution*, 35, 927–937.
- Monaghan, P., & Metcalfe, N. B. (2019). The deteriorating soma and the indispensable germline: gamete senescence and offspring fitness. *Proceedings of the Royal Society B: Biological Sciences*, 286, 20192187.
- Monaghan, P., & Ozanne, S. E. (2018). Somatic growth and telomere dynamics in vertebrates: relationships, mechanisms and consequences. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 373, 20160446.
- Moorad, J., Promislow, D., & Silvertown, J. (2019). Evolutionary ecology of senescence and a reassessment of Williams’ ‘extrinsic mortality’ hypothesis. *Trends in Ecology & Evolution*, 34, 519–530.
- Niesel, J. (2007). Inventering av sandödlor, *Lacerta agilis*, i Västra Götalands län 2006–2007. (Länsstyrelsen i Västra Götalands län).
- van Noordwijk, A. J., & de Jong, G. (1986). Acquisition and allocation of resources: their influence on variation in life history tactics. *The American Naturalist*, 128, 137–142.

- Noble, D. W. A., Stenhouse, V., & Schwanz, L. E. (2018). Developmental temperatures and phenotypic plasticity in reptiles: a systematic review and meta-analysis. *Biological Reviews*, 93, 72–97.
- Nussey, D. H., Froy, H., Lemaitre, J.-F., Gaillard, J.-M., & Austad, S. N. (2013). Senescence in natural populations of animals: widespread evidence and its implications for bio-gerontology. *Ageing Research Reviews*, 12, 214–225.
- Oli, M. K., Hepp, G. R., & Kennamer, R. A. (2002). Fitness consequences of delayed maturity in female wood ducks. *Evolutionary Ecology Research*, 4, 563–576.
- Olovnikov, A. M. (1973). A theory of marginotomy. *Journal of Theoretical Biology*, 41, 181–190.
- Olsson M. (1988). Ecology of a Swedish population of the sand lizard (*Lacerta agilis*) - preliminary report. *Mertensiella*, 1, 86–91.
- Olsson, M. (1992). Sexual selection and reproductive strategies in the sand lizard, *Lacerta agilis*. PhD thesis, University of Gothenburg, Sweden.
- Olsson, M. (1994). Why are sand lizard males (*Lacerta agilis*) not equally green? *Behavioral Ecology and Sociobiology*, 35, 169–173.
- Olsson, M., Gullberg, A., & Tegelstrom, H. (1996a). Malformed offspring, sibling matings, and selection against inbreeding in the sand lizard (*Lacerta agilis*). *Journal of Evolutionary Biology*, 9, 229–242.
- Olsson, M., Gullberg, A., & Tegelström, H. (1996b). Mate guarding in male sand lizards (*Lacerta agilis*). *Behaviour*, 133, 367–386.
- Olsson, M., Loeb, L., Lindsay, W., Wapstra, E., Fitzpatrick, L., & Shine, R. (2018b). Extreme plasticity in reproductive biology of an oviparous lizard. *Ecology and Evolution*, 8, 6384–6389.
- Olsson, M., & Madsen, T. (1996). Costs of mating with infertile males selects for late emergence in female sand lizards (*Lacerta agilis* L.). *Copeia*, 1996, 462–464.
- Olsson, M., Madsen, T., Nordby, J., Wapstra, E., Ujvari, B., & Wittsell, H. (2003). Major histocompatibility complex and mate choice in sand lizards. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 270, S254–S256.
- Olsson, M., Madsen, T., Uller, T., Wapstra, E., & Ujvari, B. (2005b). The role of Haldane's rule in sex allocation. *Evolution*, 59, 221–225.

- Olsson, M., Pauliny, A., Wapstra, E., & Blomqvist, D. (2010). Proximate determinants of telomere length in sand lizards (*Lacerta agilis*). *Biology Letters*, 6, 651–653.
- Olsson, M., Pauliny, A., Wapstra, E., Uller, T., Schwartz, T., & Blomqvist, D. (2011b). Sex differences in sand lizard telomere inheritance: paternal epigenetic effects increases telomere heritability and offspring survival. *PLoS ONE*, 6, e17473.
- Olsson, M., Pauliny, A., Wapstra, E., Uller, T., Schwartz, T., Miller, E., & Blomqvist, D. (2011c). Sexual differences in telomere selection in the wild. *Molecular Ecology*, 20, 2085–2099.
- Olsson, M., & Shine, R. (1996). Does reproductive success increase with age or with size in species with indeterminate growth? a case study using sand lizards (*Lacerta agilis*). *Oecologia*, 105, 175–178.
- Olsson, M., & Shine, R. (1997a). Advantages of multiple matings to females: a test of the infertility hypothesis using lizards. *Evolution*, 51, 1684–1688.
- Olsson, M., & Shine, R. (1997c). The limits to reproductive output: offspring size versus number in the sand lizard (*Lacerta agilis*). *The American Naturalist*, 149, 179–188.
- Olsson, M., & Shine, R. (1997b). The seasonal timing of oviposition in sand lizards (*Lacerta agilis*): why early clutches are better. *Journal of Evolutionary Biology*, 10(3), 369–381.
- Olsson, M., & Shine, R. (2002). Growth to death in lizards. *Evolution*, 56, 1867–1870.
- Olsson, M., & Shine, R. (2003). Female-biased natal and breeding dispersal in an alpine lizard, *Niveoscincus microlepidotus*: natal dispersal in a lizard. *Biological Journal of the Linnean Society*, 79, 277–283.
- Olsson, M., Ujvari, B., Madsen, T., Uller, T., & Wapstra, E. (2004). Haldane rules: costs of outbreeding at production of daughters in sand lizards. *Ecology Letters*, 7, 924–928.
- Olsson, M., Wapstra, E., & Friesen, C. (2018a). Ectothermic telomeres: it's time they came in from the cold. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 373, 20160449.
- Olsson, M., Wapstra, E., & Friesen, C. R. (2018c). Evolutionary ecology of telomeres: a review. *Annals of the New York Academy of Sciences*, 1422, 5–28.

- Olsson, M., Wapstra, E., Schwartz, T., Madsen, T., Ujvari, B., & Uller, T. (2011a). In hot pursuit: fluctuating mating system and sexual selection in sand lizards. *Evolution*, 65, 574–583.
- Olsson, M., Wapstra, E., & Uller, T. (2005a). Differential sex allocation in sand lizards: bright males induce daughter production in a species with heteromorphic sex chromosomes. *Biology Letters*, 1, 378–380.
- Pandori, L. L. M., & Sorte, C. J. B. (2019). The weakest link: sensitivity to climate extremes across life stages of marine invertebrates. *Oikos*, 128, 621–629.
- Partridge, L., & Barton, N. H. (1993). Optimality, mutation and the evolution of ageing. 362, 305–311.
- Partridge, L., & Barton, N. H. (1996). On measuring the rate of ageing. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 263, 1365–1371.
- Partridge, L., & Harvey, P. H. (1988). The ecological context of life history evolution. *Science*, 241, 1449–1455.
- Pen, I., Uller, T., Feldmeyer, B., Harts, A., While, G. M., & Wapstra, E. (2010). Climate-driven population divergence in sex-determining systems. *Nature*, 468, 436–438.
- Penney, H. D., Beirão, J., & Purchase, C. F. (2018). Phenotypic plasticity during external embryonic development is affected more by maternal effects than multiple abiotic factors in brook trout. *Evolutionary Ecology Research*, 19, 171–194.
- Pepke, M. L., Kvalnes, T., Ranke, P. S., Araya-Ajoy, Y. G., Wright, J., Sæther, B., Jensen, H., & Ringsby, T. H. (2022). Causes and consequences of variation in early-life telomere length in a bird metapopulation. *Ecology and Evolution*, 12, e9144.
- Pepke, M. L., Ringsby, T. H., & Eisenberg, D. T. A. (2023). The evolution of early-life telomere length, pace-of-life and telomere-chromosome length dynamics in birds. *Molecular Ecology*, 32, 2898–2912.
- Pokorná, M., & Kratochvíl, L. (2009). Phylogeny of sex-determining mechanisms in squamate reptiles: are sex chromosomes an evolutionary trap? *Zoological Journal of the Linnean Society*, 156, 168–183.
- Priest, N. K., Mackowiak, B., & Promislow, D. E. L. (2002). The role of parental age effects on the evolution of aging. *Evolution*, 56, 927–935.

- Quinn, A. E., Georges, A., Sarre, S. D., Guarino, F., Ezaz, T., & Graves, J. A. M. (2007). Temperature sex reversal implies sex gene dosage in a reptile. *Science*, 316, 411–411.
- Quinn, A. E., Radder, R. S., Sarre, S. D., Georges, A., Ezaz, T., & Shine, R. (2009). Isolation and development of a molecular sex marker for *Bassiana duperreyi*, a lizard with XX/XY sex chromosomes and temperature-induced sex reversal. *Molecular Genetics and Genomics*, 281, 665–672.
- Quinn, A. E., Sarre, S. D., Ezaz, T., Marshall Graves, J. A., & Georges, A. (2011). Evolutionary transitions between mechanisms of sex determination in vertebrates. *Biology Letters*, 7, 443–448.
- Radder, R. S., Quinn, A. E., Georges, A., Sarre, S. D., & Shine, R. (2008). Genetic evidence for co-occurrence of chromosomal and thermal sex-determining systems in a lizard. *Biology Letters*, 4, 176–178.
- Remot, F., Ronget, V., Froy, H., Rey, B., Gaillard, J.-M., Nussey, D. H., & Lemaître, J.-F. (2020). No sex differences in adult telomere length across vertebrates: a meta-analysis. *Royal Society Open Science*, 7, 200548.
- Rezende, E. L., & Bacigalupe, L. D. (2015). Thermoregulation in endotherms: physiological principles and ecological consequences. *Journal of Comparative Physiology B*, 185, 709–727.
- Reznick, D. (1985). Costs of reproduction: an evaluation of the empirical evidence. *Oikos*, 44, 257–267.
- Reznick, D., Nunney, L., & Tessier, A. (2000). Big houses, big cars, superfleas and the costs of reproduction. *Trends in Ecology & Evolution*, 15, 421–425.
- Ricklefs, R. E., & Wikelski, M. (2002). The physiology/life-history nexus. *Trends in Ecology & Evolution*, 17, 462–468.
- Robert, L. (2000). Cellular and molecular mechanisms of aging and age related diseases. *Pathology & Oncology Research*, 6, 3–9.
- Roff, D.A. (1992) *The Evolution of Life Histories*. Chapman & Hall, New York.
- Roitberg, E. S., Eplanova, G. V., Kotenko, T. I., Amat, F., Carretero, M. A., Kuranova, V. N., Bulakhova, N. A., Zinenko, O. I., & Yakovlev, V. A. (2015). Geographic variation of life-history traits in the sand lizard, *Lacerta agilis*: testing Darwin's fecundity-advantage hypothesis. *Journal of Evolutionary Biology*, 28, 613–629.

- Sand, H. (1996). Life history patterns in female moose (*Alces alces*): the relationship between age, body size, fecundity and environmental conditions. *Oecologia*, 106, 212–220.
- Sarre, S. D., Georges, A., & Quinn, A. (2004). The ends of a continuum: genetic and temperature-dependent sex determination in reptiles. *BioEssays*, 26, 639–645.
- Schwanz, L. E., & Georges, A. (2021). Sexual development and the environment: conclusions from 40 years of theory. *Sexual Development*, 15, 7–22.
- Schwanz, L. E., Georges, A., Holleley, C. E., & Sarre, S. D. (2020). Climate change, sex reversal and lability of sex-determining systems. *Journal of Evolutionary Biology*, 33, 270–281.
- Seebacher, F., & Franklin, C. E. (2005). Physiological mechanisms of thermoregulation in reptiles: a review. *Journal of Comparative Physiology B*, 175, 533–541.
- Shay, J. W., & Wright, W. E. (2007). Hallmarks of telomeres in ageing research. *The Journal of Pathology*, 211, 114–123.
- Shay, J. W., & Wright, W. E. (2019). Telomeres and telomerase: three decades of progress. *Nature Reviews Genetics*, 20, 299–309.
- Shine, R. (1980). “Costs” Of reproduction in reptiles. *Oecologia*, 46, 92–100.
- Shine, R. (1988). Constraints on reproductive investment: a comparison between aquatic and terrestrial snakes. *Evolution*, 42, 17–27.
- Shine, R. (1999). Why is sex determined by nest temperature in many reptiles? *Trends in Ecology & Evolution*, 14, 186–189.
- Shine, R., Elphick, M. J., & Donnellan, S. (2002). Co-occurrence of multiple, supposedly incompatible modes of sex determination in a lizard population. *Ecology Letters*, 5, 486–489.
- Shine, R., Elphick, M. & Harlow, P. (1995). Sisters like it hot. *Nature*, 378, 451–452.
- Shine, R., Wapstra, E., & Olsson, M. (2018). Seasonal shifts along the oviparity–viviparity continuum in a cold-climate lizard population. *Journal of Evolutionary Biology*, 31, 4–13.
- Simide, R., Angelier, F., Gaillard, S., & Stier, A. (2016). Age and heat stress as determinants of telomere length in a long-lived fish, the siberian sturgeon. *Physiological and Biochemical Zoology*, 89, 441–447.

- Sinclair, A. R. E., Mduma, S., & Brashares, J. S. (2003). Patterns of predation in a diverse predator–prey system. *Nature*, 425, 288–290.
- Sinervo, B., Hedges, R., & Adolph, S. C. (1991). Decreased sprint speed as a cost of reproduction in the lizard *Sceloporus occidentalis*: variation among populations. *Journal of Experimental Biology*, 155, 323–336.
- Smith, S., Hoelzl, F., Zahn, S., & Criscuolo, F. (2021). Telomerase activity in ecological studies: what are its consequences for individual physiology and is there evidence for effects and trade-offs in wild populations. *Molecular Ecology*, 31, 6239–6251.
- Spagopoulou, F., Teplitsky, C., Chantepie, S., Lind, M. I., Gustafsson, L., & Maklakov, A. A. (2020). Silver-spoon upbringing improves early-life fitness but promotes reproductive ageing in a wild bird. *Ecology Letters*, 23, 994–1002.
- Srikulnath, K., Matsubara, K., Uno, Y., Nishida, C., Olsson, M., & Matsuda, Y. (2014). Identification of the linkage group of the Z sex chromosomes of the sand lizard (*Lacerta agilis*, Lacertidae) and elucidation of karyotype evolution in lacertid lizards. *Chromosoma*, 123, 563–575.
- Stearns, S. C. (1976). Life-history tactics: a review of ideas. *the Quarterly Review of Biology*, 51, 3–47.
- Stearns, S. C. (1989). Trade-offs in life-history evolution. *Functional Ecology*, 3, 259–268.
- Stearns, S.C. (1992) *The Evolution of Life Histories*. Oxford University Press, Oxford.
- Stelkens, R. B., & Wedekind, C. (2010). Environmental sex reversal, Trojan sex genes, and sex ratio adjustment: conditions and population consequences. *Molecular Ecology*, 19, 627–646.
- Strijbosch, H., & Creemers, R. C. M. (1988). Comparative demography of sympatric populations of *Lacerta vivipara* and *Lacerta agilis*. *Oecologia*, 76, 20–26.
- Sudyka, J. (2019). Does reproduction shorten telomeres? towards integrating individual quality with life-history strategies in telomere biology. *BioEssays*, 41, 1900095.
- Taylor, F. (1981). Ecology and evolution of physiological time in insects. *The American Naturalist*, 117, 1–23.
- Terrien, J., Perret, M., & Aujard, F. (2011). Behavioral thermoregulation in mammals: a review. *Frontiers in Bioscience*, 16, 1428–1444.

- Tissier, M. L., Bergeron, P., Garant, D., Zahn, S., Criscuolo, F., & Réale, D. (2022). Telomere length positively correlates with pace-of-life in a sex- and cohort-specific way and elongates with age in a wild mammal. *Molecular Ecology*, 31, 3812–3826.
- Tobler, M., Gómez-Blanco, D., Hegemann, A., Lapa, M., Neto, J. M., Tarka, M., Xiong, Y., & Hasselquist, D. (2022). Telomeres in ecology and evolution: a review and classification of hypotheses. *Molecular Ecology*, 31, 5946–5965.
- Tobler, M., & Sandell, M. I. (2008). Sex-specific effects of prenatal testosterone on nestling plasma antioxidant capacity in the zebra finch. *Journal of Experimental Biology*, 212, 89–94.
- Tokarz, R. R. (1995). Mate choice in lizards: a review. *Herpetological Monographs*, 9, 17–40.
- Troen B.R. (2003). The biology of aging. *The Mount Sinai Journal of Medicine*, 70, 3–22.
- Tully, T., Le Galliard, J., & Baron, J. (2020). Micro-geographic shift between negligible and actuarial senescence in a wild snake. *Journal of Animal Ecology*, 89, 2704–2716.
- Uller, T., Mott, B., Odierna, G., & Olsson, M. (2006). Consistent sex ratio bias of individual female dragon lizards. *Biology Letters*, 2, 569–572.
- Uller, T., Pen, I., Wapstra, E., Beukeboom, L. W., & Komdeur, J. (2007). The evolution of sex ratios and sex-determining systems. *Trends in Ecology & Evolution*, 22, 292–297.
- Uller, T., While, G. M., Cadby, C. D., Harts, A., O'Connor, K., Pen, I., & Wapstra, E. (2011). Altitudinal divergence in maternal thermoregulatory behaviour may be driven by differences in selection on offspring survival in a viviparous lizard: thermoregulation and offspring survival. *Evolution*, 65, 2313–2324.
- Valenzuela, N. (2007). Relic thermosensitive gene expression in a turtle with genotypic sex determination: relic thermal gene expression in GSD turtles. *Evolution*, 62, 234–240.
- Valenzuela, N., Adams, D. C., & Janzen, F. J. (2003). Pattern does not equal process: exactly when is sex environmentally determined? *The American Naturalist*, 161, 676–683.
- Valenzuela N. & Lance V.A. (2004). Temperature dependent sex determination in vertebrates. *Smithsonian Books*, Washington, DC.

- Vasto, S., Candore, G., Balistreri, C. R., Caruso, M., Colonna-Romano, G., Grimaldi, M. P., Listi, F., Nuzzo, D., Lio, D., & Caruso, C. (2007). Inflammatory networks in ageing, age-related diseases and longevity. *Mechanisms of Ageing and Development*, 128, 83–91.
- Vedder, O., & Bouwhuis, S. (2017). Heterogeneity in individual quality in birds: overall patterns and insights from a study on common terns. *Oikos*, 127, 719–727.
- Vedder, O., Verhulst, S., Bauch, C., & Bouwhuis, S. (2017). Telomere attrition and growth: a life-history framework and case study in common terns. *Journal of Evolutionary Biology*, 30, 1409–1419.
- Verberk, W. C. E. P., Atkinson, D., Hoefnagel, K. N., Hirst, A. G., Horne, C. R., & Siepel, H. (2021). Shrinking body sizes in response to warming: explanations for the temperature–size rule with special emphasis on the role of oxygen. *Biological Reviews*, 96, 247–268.
- Via, S. (1993). Adaptive phenotypic plasticity: target or by-product of selection in a variable environment? *The American Naturalist*, 142, 352–365.
- Viña, J., Borrás, C., Gambini, J., Sastre, J., & Pallardó, F. V. (2005). Why females live longer than males? Importance of the upregulation of longevity-associated genes by oestrogenic compounds. *FEBS Letters*, 579, 2541–2545.
- Vitt, L. J., & Congdon, J. D. (1978). Body shape, reproductive effort, and relative clutch mass in lizards: resolution of a paradox. *The American Naturalist*, 112, 595–608.
- Vaupel, J. W., Baudisch, A., Dölling, M., A. Roach, D., & Gampe, J. (2004). The case for negative senescence. *Theoretical Population Biology*, 65, 339–351.
- Wallace, H., Badawy, G. M. I., & Wallace, B. M. N. (1999). Amphibian sex determination and sex reversal. *Cellular and Molecular Life Sciences*, 55, 901–909.
- Wang, C., Tang, X., Xin, Y., Yue, F., Yan, X., Liu, B., An, B., Wang, X., & Chen, Q. (2015). Identification of sex chromosomes by means of comparative genomic hybridization in a lizard, *Eremias multiocellata*. *Zoological Science*, 32, 151–156.
- Wapstra, E. (1998) Life history and reproductive variation in the spotted skink, *Niveoscincus ocellatus* (Gray 1845). PhD thesis, University of Tasmania, Australia.

- Wapstra, E., Olsson, M., Shine, R., Edwards, A., Swain, R., & Joss, J. M. P. (2004). Maternal basking behaviour determines offspring sex in a viviparous reptile. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 271, S230–S232.
- Wapstra, E., & O'Reilly, J. M. (2001). Potential 'costs of reproduction' in a skink: Inter- and intrapopulational variation. *Austral Ecology*, 26, 179–186.
- Wapstra, E., & Swain, R. (2001). Geographic and annual variation in life-history traits in a temperate zone Australian skink. *Journal of Herpetology*, 35, 194–203.
- Wapstra, E., Swain, R., Jones, S. M., & O'Reilly, J. (1999). Geographic and annual variation in reproductive cycles in the Tasmanian spotted snow skink, *Niveoscincus ocellatus* (Squamata: Scincidae). *Australian Journal of Zoology*, 47, 539–550.
- Wapstra, E., Swain, R., & O'Reilly, J. M. (2001). Geographic variation in age and size at maturity in a small Australian viviparous skink. *Copeia*, 2001, 646–655.
- Wapstra, E., Uller, T., Sinn, D. L., Olsson, M., Mazurek, K., Joss, J., & Shine, R. (2009). Climate effects on offspring sex ratio in a viviparous lizard. *Journal of Animal Ecology*, 78, 84–90.
- Warner, D. A., & Shine, R. (2008). The adaptive significance of temperature-dependent sex determination in a reptile. *Nature*, 451, 566–568.
- Wensink, M. J., Caswell, H., & Baudisch, A. (2016). The rarity of survival to old age does not drive the evolution of senescence. *Evolutionary Biology*, 44, 5–10.
- West, S. A., Reece, S. E., & Sheldon, B. C. (2002). Sex ratios. *Heredity*, 88, 117–124.
- While, G. M., Noble, D. W. A., Uller, T., Warner, D. A., Riley, J. L., Du, W., & Schwanz, L. E. (2018). Patterns of developmental plasticity in response to incubation temperature in reptiles. *Journal of Experimental Zoology Part A: Ecological and Integrative Physiology*, 329, 162–176.
- Whiteley, S. L., Georges, A., Weisbecker, V., Schwanz, L. E., & Holleley, C. E. (2021a). Ovotestes suggest cryptic genetic influence in a reptile model for temperature-dependent sex determination. *Proceedings of the Royal Society B: Biological Sciences*, 288, 20202819.

- Whiteley, S. L., Holleley, C. E., Wagner, S., Blackburn, J., Deveson, I. W., Marshall Graves, J. A., & Georges, A. (2021b). Two transcriptionally distinct pathways drive female development in a reptile with both genetic and temperature dependent sex determination. *PLOS Genetics*, 17, e1009465.
- Wiggins, J. M., Santoyo-Brito, E., Scales, J. B., & Fox, S. F. (2020). Gene dose indicates presence of sex chromosomes in collared lizards (*Crotaphytus collaris*), a Species with temperature-influenced sex determination. *Herpetologica*, 76, 27–30.
- Wild, K. H., Roe, J. H., Schwanz, L., Georges, A., Sarre, S. D., & Alexander, A. (2022). Evolutionary stability inferred for a free ranging lizard with sex-reversal. *Molecular Ecology*, 31, 2281–2292.
- Williams, G. C. (1957). Pleiotropy, natural selection, and the evolution of senescence. *Evolution*, 11, 398–411.
- Williams, G. C. (1966). Natural selection, the costs of reproduction, and a refinement of Lack's principle. *The American Naturalist*, 100, 687–690.
- Wilson, A. J., & Nussey, D. H. (2009). What is individual quality? An evolutionary perspective. *Trends in Ecology & Evolution*, 25, 207–214.
- Young, A. J. (2018). The role of telomeres in the mechanisms and evolution of life-history trade-offs and ageing. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 373, 20160452.
- Yuni, L. P. E. K., Jones, S. M., & Wapstra, E. (2018). Thermal biology of the spotted snow skink, *Niveoscincus ocellatus*, along an altitudinal gradient. *Australian Journal of Zoology*, 66, 235–246.
- Zakharov, V. (1989). Future prospects for population phenogenetics. *Soviet Scientific Reviews Series F: Physiology and Genetics of Biology*, 4, 1–79.
- Zakian, V. A. (1989). Structure and function of telomeres. *Annual Review of Genetics*, 23, 579–604.
- Zera, A. J., & Harshman, L. G. (2001). The physiology of life history trade-offs in animals. *Annual Review of Ecology and Systematics*, 32, 95–126.
- von Zglinicki, T. (2002). Oxidative stress shortens telomeres. *Trends in Biochemical Sciences*, 27, 339–344.
- von Zglinicki, T., Burkle, A., & Kirkwood, T. B. (2001). Stress, DNA damage and ageing—An integrative approach. *Experimental Gerontology*, 36, 1049–1062.