

# Coping with climate change.

**Implications of the Yellow-Bellied Marmot's (*Marmota flaviventer*)  
body mass evolution in the last half-century.**



uOttawa

Comprehensive exam proposal

by

Augustin Birot (300444988)

2025-04-03

Committee members:

Julien Martin (Supervisor)

Vincent Careau (TAC member)

Roslyn Dakin (TAC member)

A proposal submitted as a partial requirement for a PhD degree  
at the University of Ottawa, Department of Biology

# Table of contents

|  |           |
|--|-----------|
| <b>Introduction</b>  | <b>3</b>  |
| Climate change . . . . .   | 3         |
| Life-history traits . . . . .  | 4         |
| The role of body mass . . . . .  | 4         |
| Body mass and hibernation . . . . .  | 5         |
| Expected effect of global warming on body mass . . . . .   | 6         |
| Adaptation, Evolution, Phenotypic plasticity . . . . .   | 7         |
| Quantitative Genetics and Animal Models . . . . .  | 8         |
| Traits coevolution . . . . .   | 9         |
| Detecting Individual variation in their plasticity in the wild . . . . .                             | 10        |
| Study system . . . . .   | 12        |
| Body mass increase in Yellow-Bellied Marmots . . . . .   | 14        |
| Data collection . . . . .  | 16        |
| Research objectives . . . . .  | 19        |
| <b>Chapter 1 - Structure of the body mass increase.</b>  | <b>20</b> |
| <b>Chapter 2 - Detecting individual variation in plasticity with DHGLMs.</b>                         | <b>24</b> |
| <b>Chapter 3 - Identifying predictors of increased body mass.</b>                                    | <b>28</b> |
| <b>Chapter 4 - Balance between body condition and experience as predictors of marmots' behavior.</b> | <b>30</b> |
| <b>Significance and impacts</b>  | <b>33</b> |
| <b>Potential side projects</b>   | <b>34</b> |
| <b>Expected Products</b>   | <b>37</b> |
| <b>Timeline</b>  | <b>38</b> |
| <b>References</b>  | <b>40</b> |

# **Introduction**

## **Climate change**

Climate change is unequivocally recognized as one of the most pressing challenges of our time. Its global impacts, such as melting polar ice caps and rising sea levels, are well documented and increasingly evident. This phenomenon is characterized by rising temperatures, changing season lengths, increased environmental variability and unpredictability, and a growing frequency and severity of droughts and extreme weather events (Intergovernmental Panel On Climate Change (Ipcc) 2022).

Climate change impacts on human society are, for example, well represented in the city of Ottawa. Temperature, snowing and raining trends in the Canadian capital over the last century, reveals worrying, but expected figures (*e.g.*, increasing temperature, less snow, more rain, Walsh and Patterson 2022), and future projections are not much more reassuring (*e.g.*, further increase in temperature, Zhai et al. 2019). One good illustration of that is the management of the Rideau canal ice skating rink. Indeed, in later years the opening of the world's longest ice staking risk has been more and more uncertain, and its future is unfortunately but, fatally, questionable.

But above all, as shown by countless studies, climate change deeply impacts the vast majority of Earth's ecosystems (Intergovernmental Panel On Climate Change (Ipcc) 2022). These profound ecological upheavals put numerous species at risk, which must act accordingly to avoid extinction, either by dispersing or adapting (Gienapp and Brommer 2014). It is crucial to improve our understanding of how natural population cope with this rapid and unpredictable changes in order to conduct efficient conservation policies.

Climate change have an important impact in alpine habitats, with more pronounced and severe drought, temperature variability and increase. These changes put these environments under higher risks and causes changes in plant communities at high elevation (Giorgi et al. 1997; Grabherr et al. 2010; Inouye and Wielgolaski 2003; Kittel et al. 2002; Ohmura 2012). These modifications are thus expected to have major impacts on food availability for a wide diversity of animals. Therefore, not only alpine animals should adjust to temperature and precipitation changes, but also to food availability potentially.

## **Life-history traits**

Life History Theory studies resources allocation between the life history traits of an individual. This theory relies on the fact that individuals in natural condition must contend with limited resources and therefore trade-offs must be made between competing functions such as growth, maintenance and reproduction (Bell 1980; Roff 1992). Stearns (1992) define a Life History Trait as phenotypic characteristics that will directly impact an individual's selective value, or "fitness" (i.e., individual's capacity to transmit their genes to the next generation, measured as the product of survival and reproductive success).

However, this is a wide definition that could correspond to almost any traits as most phenotypic trait could impact either survival (e.g., body condition and time of nesting both predicts nesting females' survival probability in tufted ducks, *Aythya fuligula*, common pochard, *Aythya ferina* and northern shoveler, *Anas clypeata*, Blums et al. 2005; bold and active trinidadian guppies, *Poecilia reticulata*, survive longer against predators, Smith and Blumstein 2010) or reproductive sucess [e.g., ]. But conversely, one could argue that no trait would impact directly, *per se*, an individual fitness (e.g., horn size in bighorn sheeps is correlated with reproductive sucess , but is it a direct predictor? Or does it only impact fighting ability, which would be the direct predictor?).

Hence this definition encompass both all and no traits. Furthermore another objection with this definition is that with it, life-history traits both define and are defined by fitness, therefore making this reasoning tautological.

Reading the litterature, I realize that a lot of authors working on life history traits don't explicitely define them, therefore the community would benefit from a consensus on a clearer definition of Life History Trait. However, Life-History traits usually recognized as being individuals life-cycle features such as size at birth; age at maturity; size at maturity; number and size of offspring (Roff 1992; Stearns 1992).

## **The role of body mass**

We know that body mass is strongly related to both temperature acclimation (Kurz 2008; i.e., thermoregulation, Riesenfeld 1981) and food abundance (Acquarone et al. 2002). Consequently, climate change is expected to impact body mass, making it crucial to study how individuals will respond.

Body mass plays a critical role for most species. It affects individual metabolic rate (Darveau et al. 2002) as well as performance (e.g., foraging, exploration, fighting, competition ability). For instance, Weibel et al. (2004) showed a strong correlation between maximal metabolic rate and body mass in mammals.

Body mass also determines individuals energetic reserves, thereby impacting performance and resilience to environmental challenges by buffering against seasonal food scarcity (Heldstab 2017). More generally, body fat can be considered a buffer against harsh environments (Dendyter et al. 2022). Extending this reasoning to a wider timescale, we can expect that larger individuals may better buffer resource-poor years, increasing their resilience to environmental variability and unpredictability (Eimus and Fleming 2004).

From an ecological perspective, body mass influences population dynamics by affecting both survival and reproductive success. For example, body mass explains 89 % of hibernation survival in juvenile yellow-bellied marmots (*Marmota flaviventer*, Armitage 2014); individuals with heavier early-winter body mass have higher overall survival probability in adult male canvasbacks (*Aythya valisineria*, Haramis et al. 1986); winter body mass variation significantly impacts reproductive success in Norwegian moose (*Alces alces*, Milner et al. 2013); larger body size correlates with higher mating success in northern elephant seals (*Mirounga angustirostris*, Crocker et al. 2012); and individuals with greater energy reserves exhibit better reproductive capacity in bighorn sheep (*Ovis canadensis*, Festa-Bianchet et al. 1998). However, an excessively high body mass can become a handicap. Although certain costly traits have been theorized to be advantageous in sexual selection (Zahavi 1997), beyond a threshold, larger individuals may be counter-selected due to impaired performance (e.g., reduced ability to escape predators, Jebb et al. 2021).

While some authors might argue that body mass qualifies as a life-history-trait, since it influences survival and reproductive capacity, due to a lack of clear definition, this is not verified. It is more productive here to consider body mass as a central node influencing many characteristics, ultimately affecting global fitness. In this light, studying the evolution of body mass is essential to understand how natural populations respond to environmental changes.

## **Body mass and hibernation**

Within a year, food abundance can fluctuate drastically with season. Often, we see a harsh season, with lower food abundance and extreme temperatures (Williams et al. 2017). Species must adapt to that seasonal variation. Most usual strategies could be to migrate seasonally to

a milder environment (e.g., Alpine swift, *Tachymarptis melba*, Alerstam and Christie 2004; Meier et al. 2020); storing food before the harsh season (Jenkins and Busher 1979; e.g., Beavers, *Castor canadensis*, Smith et al. 1991); storing energy as fat during the good season (Denryter et al. 2022; e.g. bighorn sheep, *Ovis canadensis*, Stephenson et al. 2020); and eventually hibernating.

Hibernation is a coping mechanism consisting in reducing metabolism and body temperature to a minimum survival level, then emerge at the start of the favourable season. Beyond hibernators, two main strategies exist, they can either store food before hibernation, called “Food-storing hibernators” (e.g., chimpunks, *Tamias striatus*, Bieber et al. (2014)), or sustain on the energy they stocked in their white adipose tissue, or fat, those are the “Fat-storing hibernators” (Carey et al. 2003; Geiser 2013; Nedergaard and Cannon 1990). One of the most commonly known example of fat-storing hibernators being the Marmots (tribe: *Marmotini*, Armitage 2014)

Fat-storing hibernators must therefore forage sufficiently to gain enough fat in a short amount of time, as they are active only for a, usually small, part of the year. They rely on a highly efficient metabolism, allowing them to quickly gain fat that they need to survive through next hibernating season. Some fat-storing hibernators nearly double their weight during a 4 months active season (Armitage 2014; Carey et al. 2003). Hence, not only a prerequisite adaptation is the ability to store a lot of fat, but also a sufficiently efficient metabolism to gain weight quickly. These prerequisite represent a lot of challenges and specific adaptation. Body mass and metabolism are therefore highly constrained in hibernating species.

Additionally, for some species, reproduction occurs right at the onset of the active season (Armitage 2014). This means that before entering into hibernation, individuals must reach a body mass sufficient not only to survive, but also to have to reproduce directly after. Body mass is therefore a keystone LHT for hibernating species’ bio-demography.

### **Expected effect of global warming on body mass**

It has been theorized that changes in body size could be a third universal response to climate change, alongside modification in phenology and geographic range (Daufresne et al. 2009; Durant et al. 2007; Gardner et al. 2011; Visser and Both 2005).

This overall temperature increase is suspected to influence phenotypic traits such as body mass and size, though the precise direction of these changes remains uncertain. Some authors argue that a shrinking body size might be a universal response to climate change (Daufresne

et al. 2009). This hypothesis is based on Bergmann's rules, which states that smaller body size are favoured in warmer environment as a higher surface-to-volume ratio facilitates heat dissipation (Bergmann 1847). In other words, in warmer environments, an expected adaptive response would be a shrinking body size.

However, as noted by Gardner et al. (2011), a lack of large-scale comparative studies prevents us from confirming that this response is universal. In addition to that, in 2022, the IPCC's report stated that "evidence is weak for a consistent reduction in body size across taxonomic groups in terrestrial animals" (Intergovernmental Panel On Climate Change (Ipcc) 2022; Siepielski et al. 2019).

On the other hand, several studies at higher latitudes and altitudes yield opposite results (i.e., increasing body mass in response to climate change, Guillemain et al. 2010; Ozgul et al. 2010; Sheridan and Bickford 2011; Yom-Tov et al. 2008). In these regions, climate change is a synonym of milder conditions. Hence, individuals have access to a large food supply for a longer time and the severity of the harsh season is reduced, which overall is less energetically demanding. Ultimately, these new conditions enable individuals to grow larger.

Therefore, we expect changes in body mass and, we need to understand what is driving it and how it is happening.

## **Adaptation, Evolution, Phenotypic plasticity**

When an environment changes, inhabiting populations can avoid disappearance in several ways. They can disperse to another, more favourable, environment (Gienapp and Brommer 2014); they can modify their environment to correspond to specific needs (i.e., engineers species such as beavers, *castor canadensis*, Jones et al. 1994); or phenotypic changes can occur in the population, giving individuals better suited to their environment (Gienapp and Brommer 2014).

These phenotypic changes could happen in two ways: phenotypic plasticity, define as a change in phenotype expressed by a given genotype, which allows for rapid responses within an individual's lifetime, is highly flexible and does not involve any changes at the genetic level (Pigliucci 2001); and evolution, define as a change in alleles frequencies in a population over time. When an individual with a better-fitted phenotype for its new environment appears, it would have a higher survival and reproductive success. If this advantage relies on a heritable genetic difference, the new genotype is going to rapidly increase in proportion in the population, ultimately replacing the old one (Lynch and Walsh 1998).

Hence, evolution can be slow but will have effect on long-term, and a better answer to persistent ecological changes. However, if the change is transient, plasticity might be better suited. As noted by DeWitt et al. (1998) and Gardner et al. (2011), phenotypic plasticity solely is unlikely to be the most optimal long-term response to climate change as it is usually a transient answer to a temporary change, presenting costs and limits (DeWitt et al. 1998). Furthermore, if the optimal response to the new environment is a canalized phenotype (i.e., very low phenotypic variance), plasticity can even be maladaptive (Nussey et al. 2007). Therefore, the expected optimal answer to a long-term environmental change, as expected with climate change, is evolution.

Phenotypic plasticity and evolution are not mutually exclusive. For example, highly plastic traits, like body mass, can change considerably during an individual's life in response to environmental fluctuations both within and between years. At the same time, these traits can also evolve at the population level over similar time scales. Plasticity in itself for such traits can also evolve, indeed, individual, and even genetic-based, variation in phenotypic plasticity can occur within population, meaning that there is a potential for selection and therefore evolution on phenotypic plasticity itself (Pigliucci 2005).

Long-term consequences of these processes differ substantially, since evolutionary changes are measured across generations and tend to be more permanent than plastic adjustments made across an individual lifespan. As a result, determining how much each mechanism contributes to long-term changes is challenging but essential for understanding adaption and evolution in response to climate change in natural population.

## Quantitative Genetics and Animal Models

Since an observed phenotypic change is not necessarily due to evolution (i.e., phenotypic plasticity), estimating existence of evolution in natural conditions can be complicated. Fortunately, quantitative genetic provides robust and well-established methods to decompose the total phenotypic variance ( $V_P$ ) into its genetic ( $V_A$ ) and environmental ( $V_E$ ) components:  $V_P = V_A + V_E$  (Lynch and Walsh 1998; Wilson et al. 2010). Knowing the genetic component of the phenotypic variance allows us to investigate genetic, and so evolutionary, changes through time.

A well-known statistical method to decompose the phenotypic variance into its genetic and environmental components is the so-called Animal Model (Kruuk 2004). This method allows a robust estimation of the genetic variance in a trait affected by a large number of genes, each

with small effects (Kruuk et al. 2014; i.e., a “quantitative trait,” Lynch and Walsh 1998). An Animal model is a specific kind of mixed model fitting individual identity as a random effect and assuming that individuals are not independent but genetically related. The genetic relatedness is most of the time extracted from the population pedigree (i.e., parental links between each individual in the population, Lynch and Walsh (1998)).

This method has the advantage of being relatively simple to employ, enabling genetic variance parameters estimation directly from phenotypic data. Only parental links between individuals need to be known, making this method easily applicable to wild populations (Kruuk 2004; Lynch and Walsh 1998).

As emphasized by Kruuk et al. (2014), there is a pressing need for quantitative genetics studies on long-term wildlife populations, as the most common problem in such studies is the lack of statistical power, which can be resolved thanks to the quantity of data brought by long-term studies. Such studies would improve our understanding of the relationship between animals and their environment, as well as the genotype-phenotype-environment relationship, especially in a context of global change.

## **Traits coevolution**

A well-recognized challenge, when studying evolution in natural context, is to consider the genetic correlation between several traits (Gould and Lewontin 1979; Roff 1992). Indeed, when genetically correlated to another trait, a trait does not evolve independently and its evolution can either drive changes in other traits or be driven by other traits. Genetic correlations are often seen as constraints narrowing the range of possibility and reachable outcomes in the adaptive landscape but can also speed up the process of reaching and optimum (Arnold et al. 2001; Gould and Lewontin 1979; Teplitsky et al. 2014).

When studying the evolution of a specific trait (especially ones having important phenotypic consequences), failing to account for its link with other traits is an oversimplification. This failure can bias not only our understanding of the causes and consequences of phenotypic change, but also the estimations of its evolutionary potential (Teplitsky et al. 2014; Walsh and Blows 2009). To effectively study traits’ evolution, it is essential to consider that selection generally acts on multiple traits simultaneously, as a phenotype is the result of a combination of various traits (Phillips and Arnold 1989).

A continuation of this reasoning is the extended Pace Of Life Syndrome suggesting that life-history strategy, physiological and behavioural traits coevolve in response to the environment

(Dammhahn et al. 2018; Réale et al. 2010).

So, if climate change lead to life history traits changes, it should be expected that other key physiological or behavioural trait will coevolve with it. For example, it has been observed that some behavioural types will be consistently associated with specific Life-History strategies (Biro and Stamps 2008; *e.g.*, individual with faster life-cycle will tend to be bolder, Stamps 2007; Wolf et al. 2007).

As such, changes in such traits are expected to go along with other changes, therefore synonym of greater impacts on the global phenotype. A robust method to study such changes are Multivariate Animal models (i.e., an Animal model with multiple phenotypic traits as dependant variables) which allows us to estimate the genetic covariance between each trait (Kruuk 2004).

However, such models are heavily data-hungry, and the main reason that significant results with such methods are quite rare today is that only a few studies have enough data to support the statistical power required for these complex models (Lynch and Walsh 1998). That limitation in statistical power is expected to be addressed by long-term study datasets (Charmantier et al. 2014).

## **Detecting Individual variation in their plasticity in the wild**

Plasticity is usually studied using Reaction Norm framework (Nussey et al. 2007; Via et al. 1995), i.e., studying the value of a phenotypic trait (*e.g.*, body mass) in response to an environmental proxy (*e.g.*, temperature, precipitation). A plastic response correspond to a different phenotypic value associated to a different environment. In this framework, a trait is plastic if the slope of the reaction norm is different from 0 (Nussey et al. 2007).

A reaction norm has two parameters: Elevation, which is the expected phenotypic value in the average environment; and the slope, corresponding to the linear change of the phenotype over the environmental gradient. In statistical terms, these parameters correspond respectively to the “Intercept” and the “Slope” of the linear regression of the phenotype over the environment.

This is how phenotypic plasticity is usually studied. However, as emphasized by Nussey et al. (2007), a lot of information is loss when plasticity is only studied at the population level (i.e., fixed linear model of the phenotype over the environment). First using a linear mixed model is crucial to estimate different elevations for each individual, this allows the model to account

for the individual variability in their phenotype in the average environment. However, that kind of model doesn't allow estimating individual-level difference in their plastic response to the environment, which can be biologically significant and must be accounted for.

Nussey et al. (2007) proposed a framework to estimate that individual variance in plasticity, which is now fairly accepted and used: Random Regression. Let's go back to the Linear Mixed Models (LMMs), the most classical type of mixed models is to add a random individual term on the intercept to estimate the "individual variance" by allowing the model to fit one intercept per individual, however with this model, the slope is the same for each individual. Now, if we add a random term also on the slope, not only the model fit one intercept per individual, but also one slope (so, one reaction norm) per individual, estimating thus the individual variance in the phenotype expected in the average environment (elevation) but also the individual variation in phenotypic variation (slope) which is commonly called the individual by environment interaction and noted  $I * E$ .

Once we've estimated this between-individual variance in plasticity, we can use quantitative genetic methods using Random Regression Animal Model: "RRAM" (Nussey et al. 2007) to decompose this variance into its genetic and environmental parts in order to get the between-individual genetic variation in plasticity, commonly referred to as  $G * E$ . From that, we can estimate the heritable variation in reaction norm's slope and have an idea of the evolutionary potential of a trait's phenotypic plasticity itself.

From a theoretical point of view, this method allows for proper estimations of a trait's  $I * E$  and  $G * E$ . However, as underlined by Ramakers et al. (2023), an important limitation is the environmental proxy used for the reaction norm. Indeed, if this latter isn't appropriate (i.e., too far from the real predictor of the trait's plastic response), an important part of the actual individual variation in their plasticity is missed, this is what Ramakers et al. (2023) called the "hidden  $I * E$ ".

Furthermore, it is often impossible to identify the real driver of plasticity in natural conditions, as natural environments are exceptionally complex systems, and individuals generally have to react to a combination of environmental variables rather than one. Therefore, the real driver of plasticity is often unknown, unmeasurable and a combination of a lot of different variables. Another method is to use Environment Specific Mean phenotype (ESM) (Finlay and Wilkinson 1963; Ramakers et al. 2023). Although they have shown that this method is indeed efficient, they emphasized that we still need a really good knowledge of the study system, and specific conditions to be an effective approach. Although the ESM method is

helpful, it is far from perfect and more work is needed to deal with this  $I * E$  detection problem in natural environments.

The good news is that a promising, fairly new, statistical method could bring new interesting insights to that matter: the “Double Hierarchical Generalized Linear Model” (DHGLM). DHGLM is a type of mixed model estimating, fitting a model on both the mean and the dispersion of a trait (Lee and Nelder 2006). In addition to the standard mixed model, a DHGLM directly model the variation in the residual as a function of fixed and random effects. In other words, a DHGLM can estimate the *among-individual variance in the residual variance*, hereafter referred to as  $V_{V_e}$ .

We are confident that DHGLM can become an important approach in the toolbox used to detect  $I * E$ . Indeed, when  $I * E$  are not modelled in a DHGLM via a random slope because the  $E$  is unknown for example, then the variation due to  $I * E$  will be captured by the among-individual variance in the residual variance  $V_{V_e}$ .

Although a non-zero value for  $V_{V_e}$  isn't necessarily due to the presence of  $I * E$  in the system, it would justify further investigations by testing different environmental proxies. In contrast, except in very specific conditions, almost impossible in natural conditions (i.e., perfect contrary effect), a  $V_{V_e}$  equal to 0 indicate that the relative contribution to the residual variance in phenotype isn't significantly different between each individual, and so that there's no individual variation in plasticity in the studied system.

An important feature of this method is that it should be free from the problems of bad environmental proxies as it detects  $I * E$  from the structure of the residual variance in phenotype. And obviously, as for the random regression with the RRAM, we can use quantitative genetics to also detect  $G * E$  by using a “Double Animal Model” (DAM).

This is a very promising method, however, as most new statistical methods, it is poorly understood and rarely used. Hence, a general framework, including clear applications showing how DHGLM should be used to detect  $I * E$  would be really helpful for the community, especially with the rising need to study efficiently phenotypic plasticity, and its evolution, in natural condition in a context of climate change.

## Study system

Since 1962, a wild population of Yellow-Bellied Marmots (*Marmota flaviventer*, Figure 1) is monitored continuously, initiated by Kenneth Armitage, and now co-lead by Julien Martin

and Daniel Blumstein, at the Rocky Mountain Biological Laboratory (RMBL) in Gothic, Colorado, USA ( $38^{\circ}56'34''$  –  $38^{\circ}59'13''$  N /  $106^{\circ}58'60''$  –  $107^{\circ}0'45''$  W). This study is the second-longest long-term monitoring of a wild mammal population in the world.



Figure 1: Yellow-Bellied Marmot, *Marmota flaviventer*, Yosemite, CA, USA. Picture by [Davidofoc](#).

Yellow-bellied marmots is a ground-dwelling sciurid (Rodentia, Sciuridae) inhabiting alpine habitats in western North America. Their life cycle is divided between an “active season” representing approximately a third of the year (from May to September) where individuals must reproduce and accumulate enough fat reserves in order to survive hibernation over the remainder of the year (September to May) (Armitage 2014).

Marmots experiences high seasonal fluctuation in body mass, with a critical threshold to be reached before the onset of hibernation in order to first, survive through the next active season and second, have enough energy left for reproduction (which occurs in the first weeks of the active season, Armitage 1965, 2014). Hence, body mass is a critical life-history traits for the marmots.

Yellow-bellied marmots lives in colonies usually composed by one or more matrilineal with including multiple adult females, their offsprings, and one or two adult males (Armitage 2014). Our population is composed of 7 main and 31 smaller colonies divided between an “up” and a “down valley” sections differing by 300m elevation (Fig. 2; up valley: 3,000 m; down valley: 2,700 m).

The altitude differences between the two valleys implies some differences in weather like delayed snowmelt and vegetation growth onset, or temperature differences up to 2 °C (Armitage 2014; Blumstein et al. 2004). In consequence of these weather differences, a delayed emergence up to two weeks in the up-valley can be observed (Blumstein 2009; Monclús et al. 2014). These two different condition offers an amazing opportunity to test the impact of environmental differences on several factors while working in natural conditions.

The marmots’ hibernation life-cycle is highly environment-dependent. Indeed, their phenology (*i.e.*, onset and end of the active season) seems to be mediated mostly by weather variable such as temperature and snow cover (Armitage 2014), as for the rest of high-altitude ecosystems (Inouye and Wielgolaski 2003).

### **Body mass increase in Yellow-Bellied Marmots**

An important body mass increase has been observed in this population over the past half-century, estimated around 600 g, representing almost 20% of total individuals’ body mass (Biro, Blumstein & Martin, Manuscript in progress, Fig 3a). Previous studies concluded that most of the change was due to phenotypic plasticity (Ozgul et al. 2010). This would a potential expectation under climate change since the active season is getting longer and population faces milder winter conditions (e.g., higher temperature, less snow). Hence, marmots have more time to forage and gain weight, and the hibernation period is getting shorter, meaning less time for individuals to lose mass. With these new conditions, individuals are getting heavier.

However, the study by Ozgul et al. (2010) used a flawed approach, not estimating genetic variance properly. With now almost 15 additional years of data, we reanalyzed the body mass data using animal models to properly assess the genetic change in body mass over time using body mass from 199 adult females between 1965 and 2022 (657 observations). Our results show a large genetic basis of body mass with a heritability of 0.56, and an increase at the genetic level of ~400 g over the study period, indicating that roughly two third of the observed body mass increase is in fact due to genetic changes (Biro et al., Manuscript in progress, Figure 3b). With these results, it is reasonable to conclude that plasticity is not

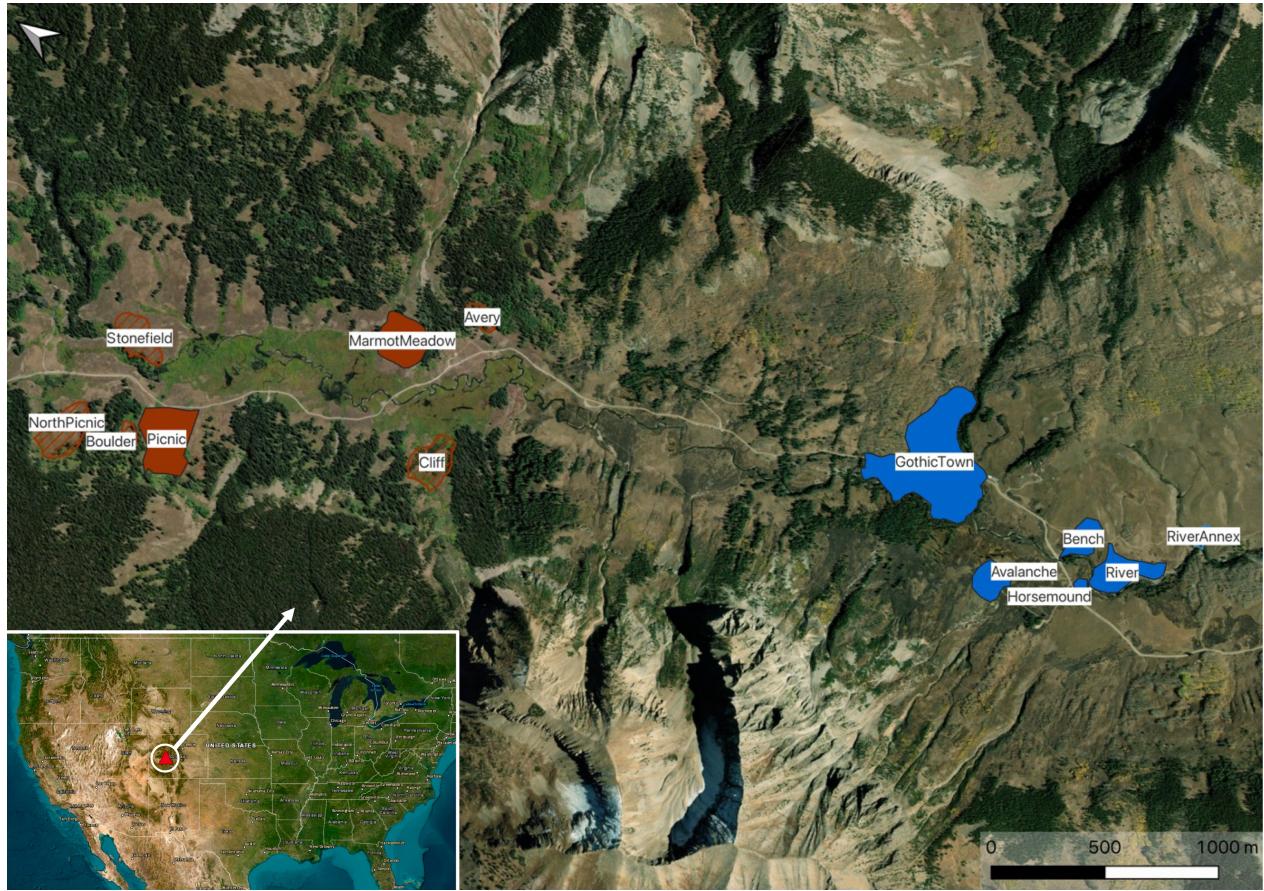


Figure 2: Red colonies represent the “up” valley, blue ones represent the “down” valleys. Plain background polygons represent the seven main colonies. The map was created with QGIS software (QGIS Development Team 2024) and the base map comes from ESRI (“GIS Mapping Software, Location Intelligence & Spatial Analytics | Esri” n.d.).

the only process causing this phenotypic shift, but that evolution also plays a crucial role here.

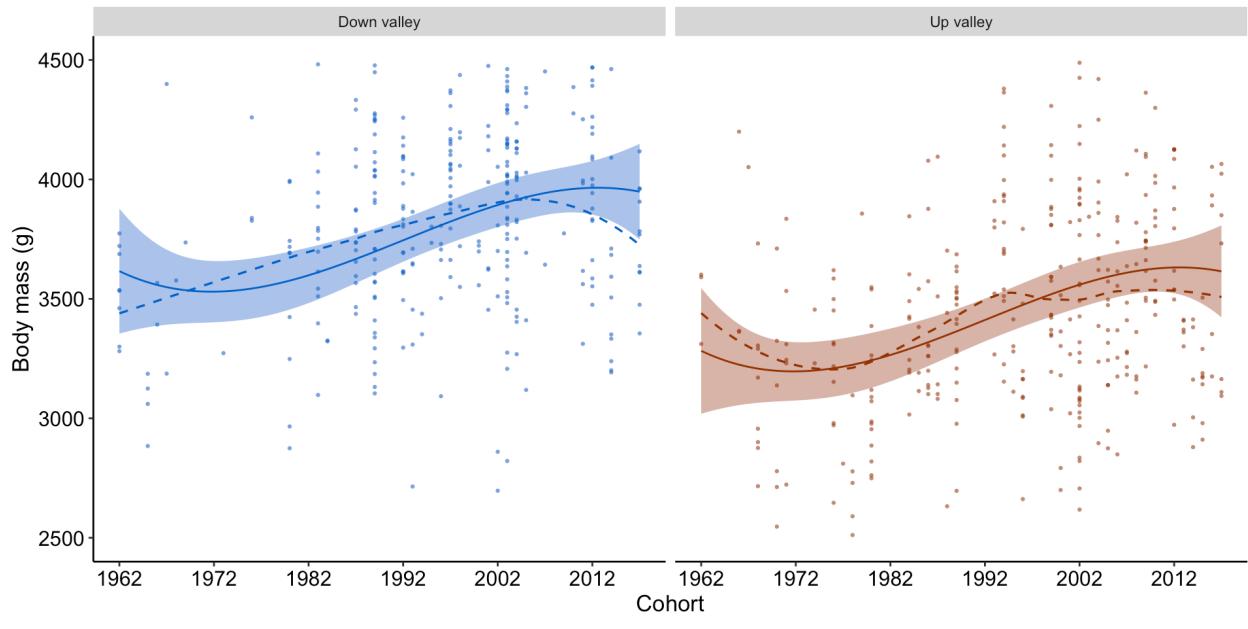
Furthermore, although the lengthening of the active season is indeed a good potential explanation for the body mass increase through phenotypic plasticity, it doesn't match with the observed evolutionary pattern. Indeed, the observed increasingly milder conditions in parallel to this change in body mass should decrease selection on body mass, as it lower the survival pressure through hibernation. The observed body mass increase here should be expected with an increasing pressure over winter survival. It is clear that the lengthening active season and global milder condition are not the only drivers of body mass changes, since we observed both plasticity and microevolution.

Considering the importance of body mass for yellow-bellied marmots, it is crucial to understand how this trait and this population is responding to climate change, both for conservation purposes and better comprehension of the links between phenotype and environment. There is a pressing need to explore which environmental factors may have triggered this shift, the mechanisms behind this increase, and the potential implications for the population's future to better understand how can natural population cope with climate change.

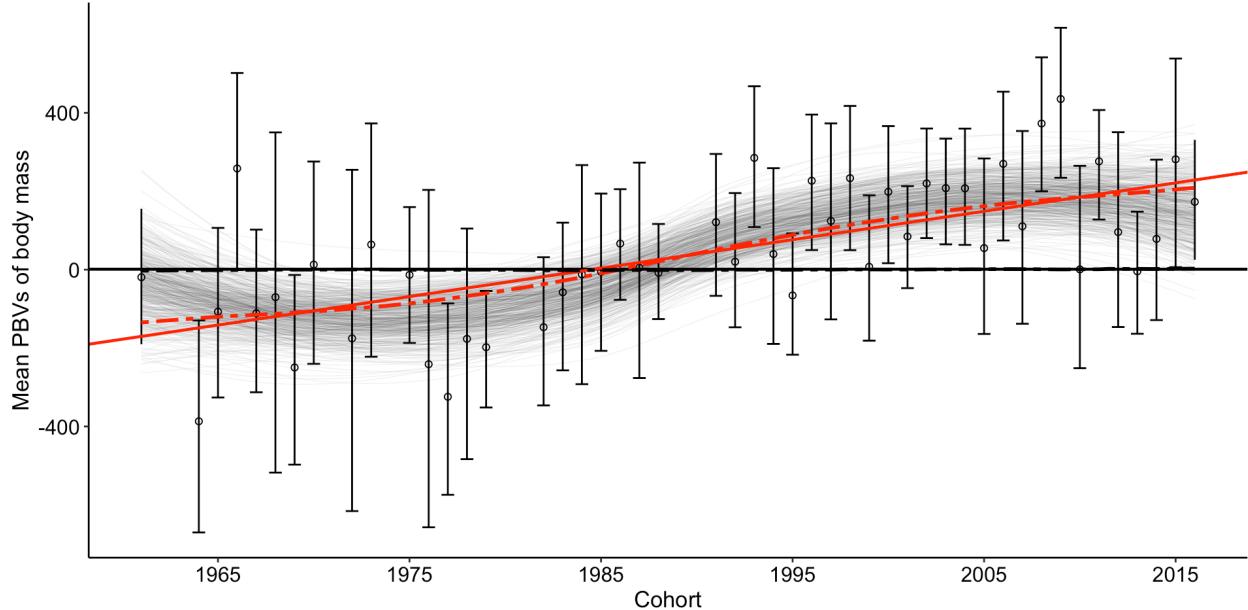
## **Data collection**

Each year between May and September since 1962, marmots are regularly trapped (between 1 and 20 times per individual, with an average of 4.5) using baited Tomahawk live traps (81 \* 25 \* 30 cm) situated near burrow entrances. If the individual is captured for the first time, it is identified by placing a unique pair of numbered ear tag, and with a nontoxic black Nyzanol dye fur mark for distant identification during behavioural observations. Over 95% of individuals are captured during their first 2 summers of life (as juvenile or one-year-old) and thus have known year of birth and age. Marmot age classes can be defined as juveniles, first year of life, yearlings as one-year-old, subadults as two and three years old, and adults over 3 years old (Jebb et al. 2021). It should be noted that subadults can reproduce but have not finished their skeletal growth.

Body mass is a highly plastic trait, particularly for marmots, as it experiences considerable fluctuations throughout the active season. It is, for obvious reasons, impossible to record all individual body mass at the same time. Therefore, it is necessary to estimate it for each individual at the same time of the year. Using repeated measures for each individual throughout each active season, a linear mixed model was fitted and its Best Linear Unbiased Predictors were used to extract each individual's body mass at the beginning and end of each



(a) Phenotypic change



(b) Genetic change

Figure 3: Adult females' mean cohort's body mass. (a) At phenotypic level, trend lines ( $\pm$  SE) represent LMM predictions and points shows raw data. (b) At genetic level, median trends of the observations (red line) and under a null scenario (black line) are represented, according to linear models, points, and error bars represent the median and 95% credibility interval of the posterior mean predicted breeding values for each cohort.

years' active seasons, so June 1<sup>st</sup> and August 15<sup>th</sup> (Jebb et al. 2021; details in Ozgul et al. 2010). Over 61 years of observations (1962 - 2022), we have 7,586 body mass estimations for 4,656 individuals.

Parental links between individuals are known for most individuals in the population (maternal links known for 3,435 individuals and paternal links for 1,943 individuals to this date), allowing the reconstruction of a highly detailed pedigree. Before 2002, maternal links were estimated via behavioural observations. Since 2002, genetic parentage assignment is used to confirm the maternal links and determine the paternal links (details in Blumstein et al. 2010; Olson et al. 2012).

Behavioural observations and experiments [running speed and Flight Initiation Distance; Ydenberg and Dill (1986)] are conducted all along the season. Upon each capture, individuals are sexed, weighted (initially with a spring scale ( $\pm$  50 g) and now with a digital balance ( $\pm$  10 g)) measured and DNA samples are taken. More descriptions can be found in Armitage (2014).

As our study site has been an important scientific station for more than a century, we have various and exhaustive data. By combining multiple sources, such as Billy Barr (a RMBL resident), the National Oceanic and Atmospheric Administration (NOAA), the United States Geological Survey (USGS), the United States Department of Agriculture (USDA) and the Oregon State University's PRISM Climate group, Prather et al. (2023) provides us with exhaustive data. We have weather data (e.g., monthly temperatures, snowing, precipitations, season lengths) at our study site from 1975 to 2022.

Data are stored in the R package "ybamaRmot" (Martin and Blumstein 2024), analysis will be performed in R (R Core Team 2023), Animal models will be performed using R package asreml (Butler et al. n.d.), lme4breeding (Covarrubias-Pazaran 2024) and MCMCglmm (Hadfield 2010), DHGLMs and other complex models using a bayesian approach will be done with brms (Bürkner 2021) or stan directly (Carpenter et al. 2017; Stan Development Team et al. 2020), figures will be made with "ggplot2" (Wickham 2016).

## **Research objectives**

The body mass increased by approximately 20% in Yellow-Bellied marmots over the past 50 years. Contrary to previous studies, I have shown during my MSc work that a large part of the change in body mass is in fact due to microevolution, meaning that we need to rethink the evolutionary scenario explaining this phenotypic change Figure 4.

First, I need to provide a clear explanation of what has precisely changed in the body mass in this population. We already have studied the body mass at the end of the active season for the adult female. However, to properly study this case, we need to understand the structure of this phenotypic change. Hence, I will study the body mass at both the beginning and the end of the active season, for each age class, at both phenotypic and genetic scales.

Even though our results indicate a strong genetic variation in body mass, it doesn't explain the entire phenotypic change. Phenotypic plasticity also plays a role here, and to fully understand the population's reaction to climate change, we need better methods to detect and study  $I * E$ . Therefore, I am going to develop a framework to use DHGLMs to detect  $I * E$  in natural conditions.

Then, I want to understand the causes of this change. After having study the body mass at the beginning and end of the active season, I will be able to test the effect of active, hibernation seasons and season length on body mass increase (during active season) and loss (during hibernation).

Finally, after having studying the structure and cause of this phenotypic change, we need to understand its consequences. I will investigate potential behavioural changes, and the balance between body condition and experience in individual behaviour. Understanding the link between these factor is crucial to predict potential impacts on potential dynamic in the future.

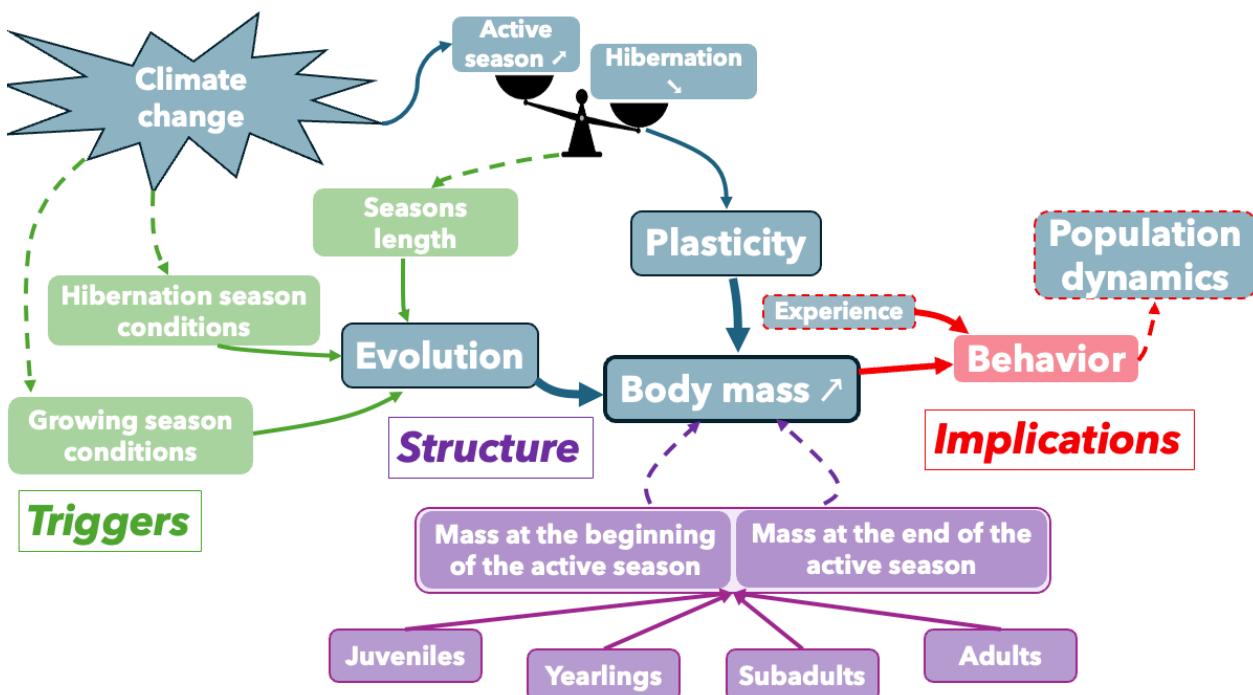


Figure 4: Research objectives illustrative framework.

## Chapter 1 - Structure of the body mass increase.

The first thing needed, is to analyze deeply the structure of change in body mass in our population. We know that body mass at the end of the active season (estimated on August 15<sup>th</sup>) has increased for adult females at both phenotypic and genetic scale (Biro, Blumstein & Martin, Manuscript in progress). However, we still don't know what is happening with the body mass at the beginning of the active season (estimated on June 1<sup>st</sup>), nor for the other age classes. It is crucial to consider that selective pressure, and so evolutionary response, could be different over age classes. We need to consider the “missing fraction” in order to conduct a comprehensive study of the selection acting on marmots body mass (Grafen 1988; Hadfield 2008; Jebb et al. 2021; Mittell and Morrissey 2024).

For instance, body mass in juveniles in our population was predicted to stay stable as it favours a higher running speed, allowing juveniles to escape predators more efficiently and so spending more time foraging. On the contrary, selection was expected for a larger body mass on adults, which rely on social vigilance to avoid predators. This expected stabilizing selection on juvenile body mass was the main explanation for a stable body mass in adults marmots (Jebb et al. 2021). However, with our new results on adult females, we now need to study potential body mass changes and evolution for each age class.

Additionally, we have studied body mass at the end of the active season (August 15<sup>th</sup>), but we also have data at the emergence from hibernation (June 1<sup>st</sup>). We need to analyze potential changes, at both phenotypic and genetic scale, at emergence to better understand our population response to climate change.

A preliminary analysis looking at the body mass in juvenile cohorts over the study period for both males and females reveals interesting details (Figure 5). We see that though the mass at birth is indeed relatively stable (or even slightly decreasing), the mass at the end of the individuals first active season shows a similar pattern found in adult females (i.e., cubic effect, Figure 3), although the decrease at the end of the period seems much more pronounced here. Indeed, the body mass at the end of our juveniles' first foraging season has increased from 1,130.64 g in 1979 to 1,363.03 g in 2001 (*Estimations from local regression on raw data*). These changes represent a body mass increase of 21% in 22 years (22 cohorts), meaning that between the late 1970s and early 2000s, each cohort was almost 1% heavier than the last one at the end of their first foraging season (Figure 5).

Therefore, I will analyze the changes in body mass over the study period for all age classes at the beginning and end of the active season at both phenotypic and genetic level.

To do so, I will use our extensive data set in which we have body mass estimations on June 1<sup>st</sup> and August 15<sup>th</sup> for 1,119 juveniles over 49 years (between 1965 and 2017); 552 yearlings over 52 years (between 1965 and 2018 & born between 1964 and 2017); 257 subadults over 49 years (between 1965 and 2019 & born between 1963 and 2017); and for 199 adults with 657 observations over 57 years (between 1965 and 2022 & born between 1962 and 2017), giving a total of 1,211 different individuals, with parental links known for most of them.

At first, I will look at the variation at a phenotypic scale over time cohorts (individuals year of birth) multivariate linear models to account for correlations between age class.

$$\left( \begin{array}{l} \text{Body mass June}_{Juveniles} \\ \text{Body mass June}_{Yearlings} \\ \text{Body mass June}_{Subadults} \\ \text{Body mass June}_{Adults} \end{array} \right) \sim \begin{array}{l} \textbf{Fixed} = Valley + Age \\ \textbf{Random} = Animal + UID + Measurement year \end{array} \quad (1)$$

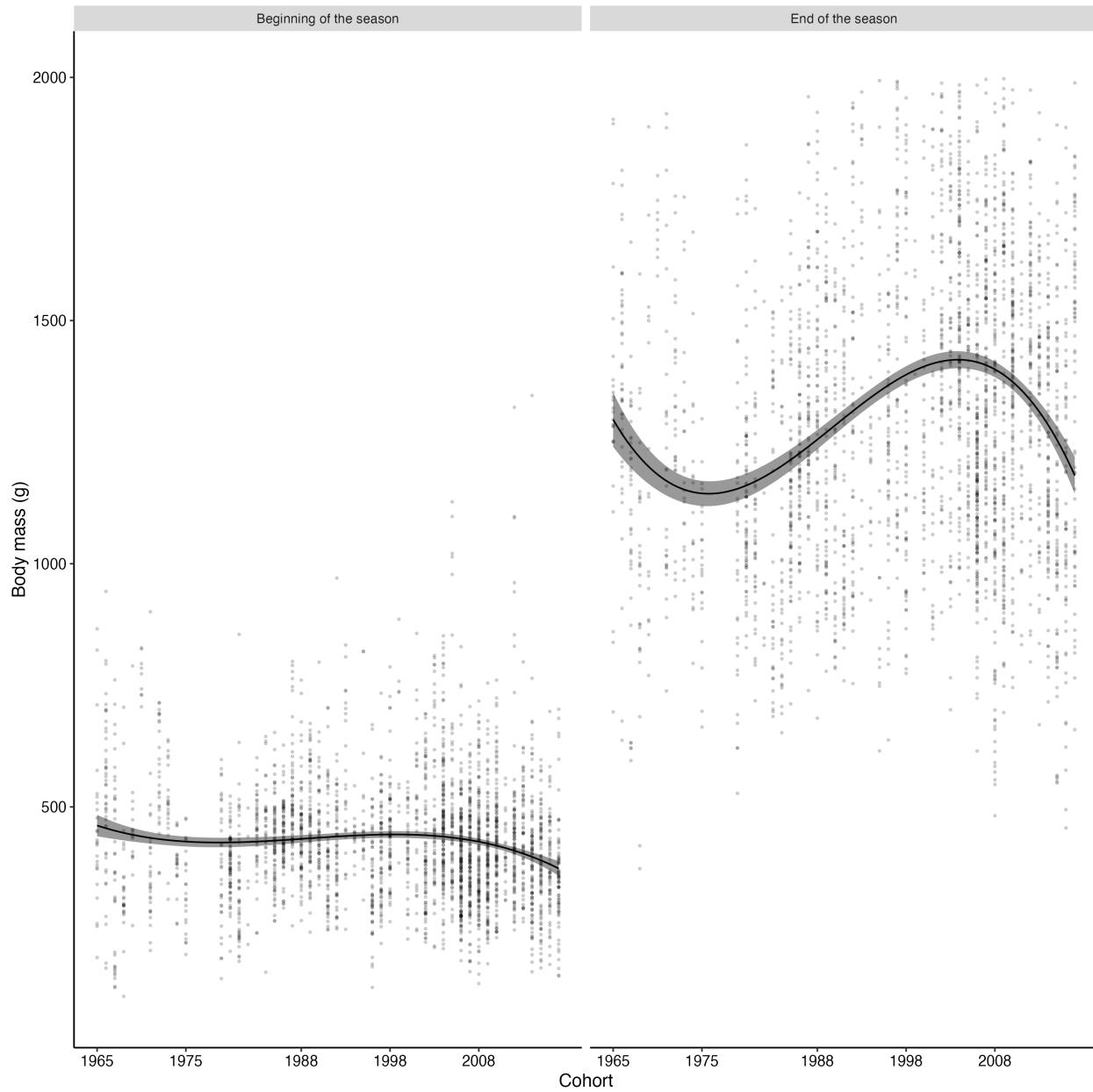


Figure 5: Body mass trend over time cohort for female juveniles compared between the beginning (birth weight) and end of their first active season (mass on August 15th).

Then, In order to conduct a comprehensive study of the selection acting body mass, I will use multivariate animal models to estimate genetic covariation between each age classes for the body mass at emergence, (Equation 1)

$$\left( \begin{array}{l} \text{Body mass August}_{Juveniles} \\ \text{Body mass August}_{Yearlings} \\ \text{Body mass August}_{Subadults} \\ \text{Body mass August}_{Adults} \end{array} \right) \sim \begin{array}{l} \textbf{Fixed} = \text{Valley} + \text{Age} \\ \textbf{Random} = \text{Animal} + \text{UID} + \text{Measurement year} \end{array} \quad (2)$$

And before emergence (Equation 2). These models will allow me to estimate the genetic value of the body mass over time cohort and over the different valleys, while taking into account the environment and within year variability.

## Chapter 2 - Detecting individual variation in plasticity with DHGLMs.

Detecting individual variation in plasticity is challenging due to the unknown aspect of the environmental variables organism are responding to (Nussey et al. 2007; Ramakers et al. 2023). Although some good methods exist today, a lot of biases coming from environmental proxies still limit these methods today. DHGLMs are a promising avenue to help the study of  $I * E$  in natural populations, but an investigation to reveal its potential and limit is needed.

When fitting a DHGLM on a focal phenotypic trait with multiple observations for each individual, in absence of  $I * E$  (i.e., each individual will exhibit the same phenotypic response, Figure 6 a) we expect to see no among-individual variance in the residual variance ( $V_{V_e} = 0$ , Figure 6 c).

However, if there's individual variation in their plastic response ( $I * E$ ) for the focal phenotypic trait (Figure 6 b) and it is not modelled with a reaction norm then within a DHGLM the variation in residual variance won't be the same for each individual, hence  $V_{V_e}$  will be different from 0 (Figure 6 d).

Although detecting  $V_{V_e}$  significantly different from 0 isn't a proof of  $I * E$  in itself, as the variation could be due to other processes, it is a necessary condition of  $I * E$  (except under very unlikely conditions Figure 7 a & b). Finding  $V_{V_e} > 0$  would thus suggest that investigating  $I * E$  and looking for the unknown  $E$  is a worthwhile investigation.

Finally, it is worth noting a potential limitation with this method that must be taken into account before performing such analysis to avoid biases. This method can only work with a balanced setup. By that, understand individuals' phenotypic responses sampled on the same range of dependant variables values. Indeed, if the sampling range isn't the same for individuals, then the range of phenotypic values exhibited by them will be different, whether there is  $I * E$  or not (Figure 7 c). In such a scenario, we would also have significant variance in the residual variance even if there is no actual effects (Figure 7 d). However, adding the environment as a fixed effect in the model should remove this bias.

Based on that, I will simulate phenotypic and environmental values for populations with and without  $I * E$ , with balanced and unbalanced environmental conditions. On these simulated populations, I will fit DHGLMs models, in a Bayesian framework using R package, brms (Bürkner 2021), using stan software (Carpenter et al. 2017; Stan Development Team et al. 2020). I will also investigate the potential use of TMB (Kristensen et al. 2016) which allows

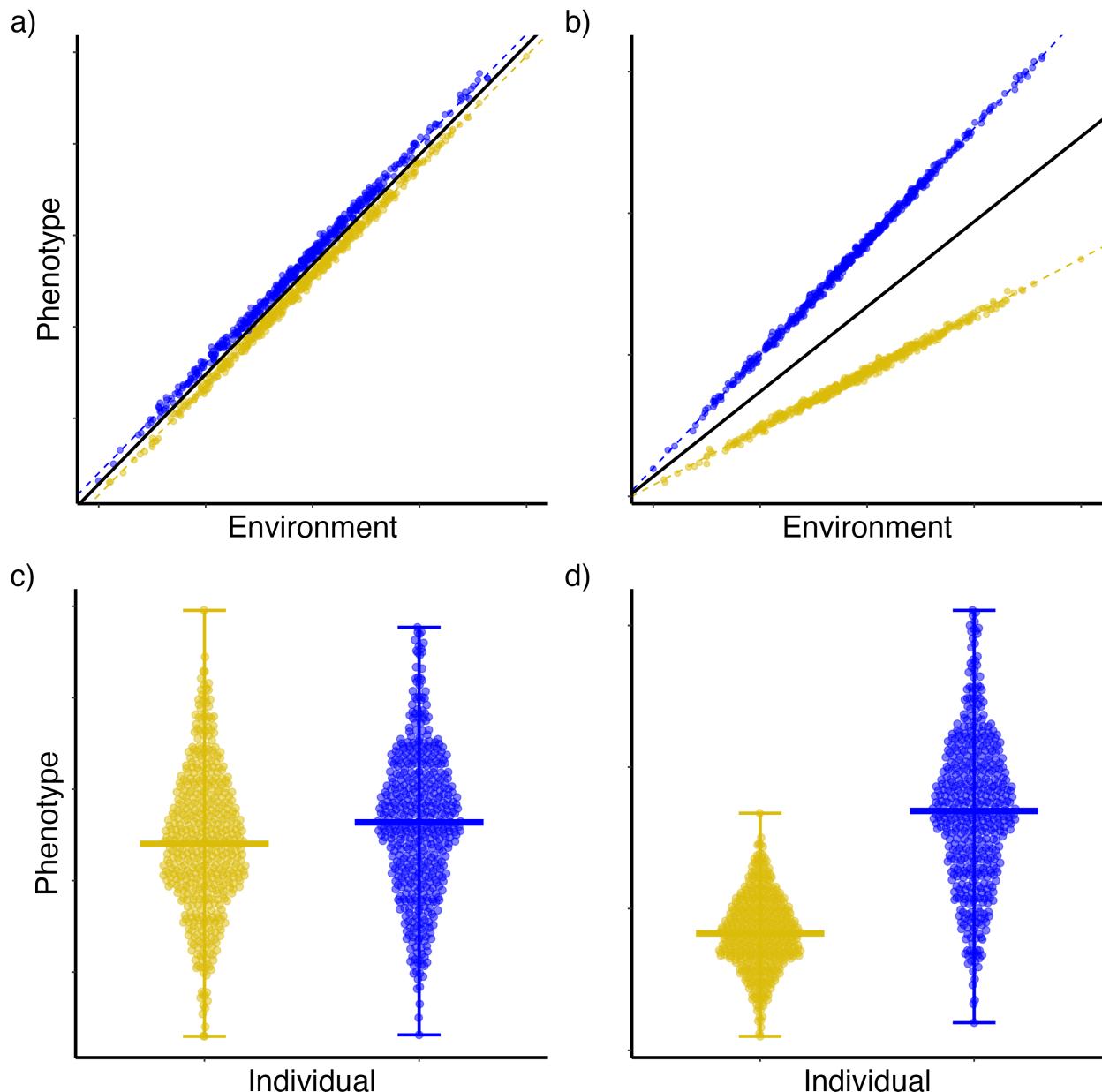


Figure 6: Reaction norms (a,b) and phenotypic variance (c,d) for two individuals (blue and yellow) for a trait without (a,c) and with (b,d) individual variations in plasticity. In the absence of  $I^*E$ , both individual express the same range of phenotypic values. However, with  $I^*E$ , individuals express different range of values.

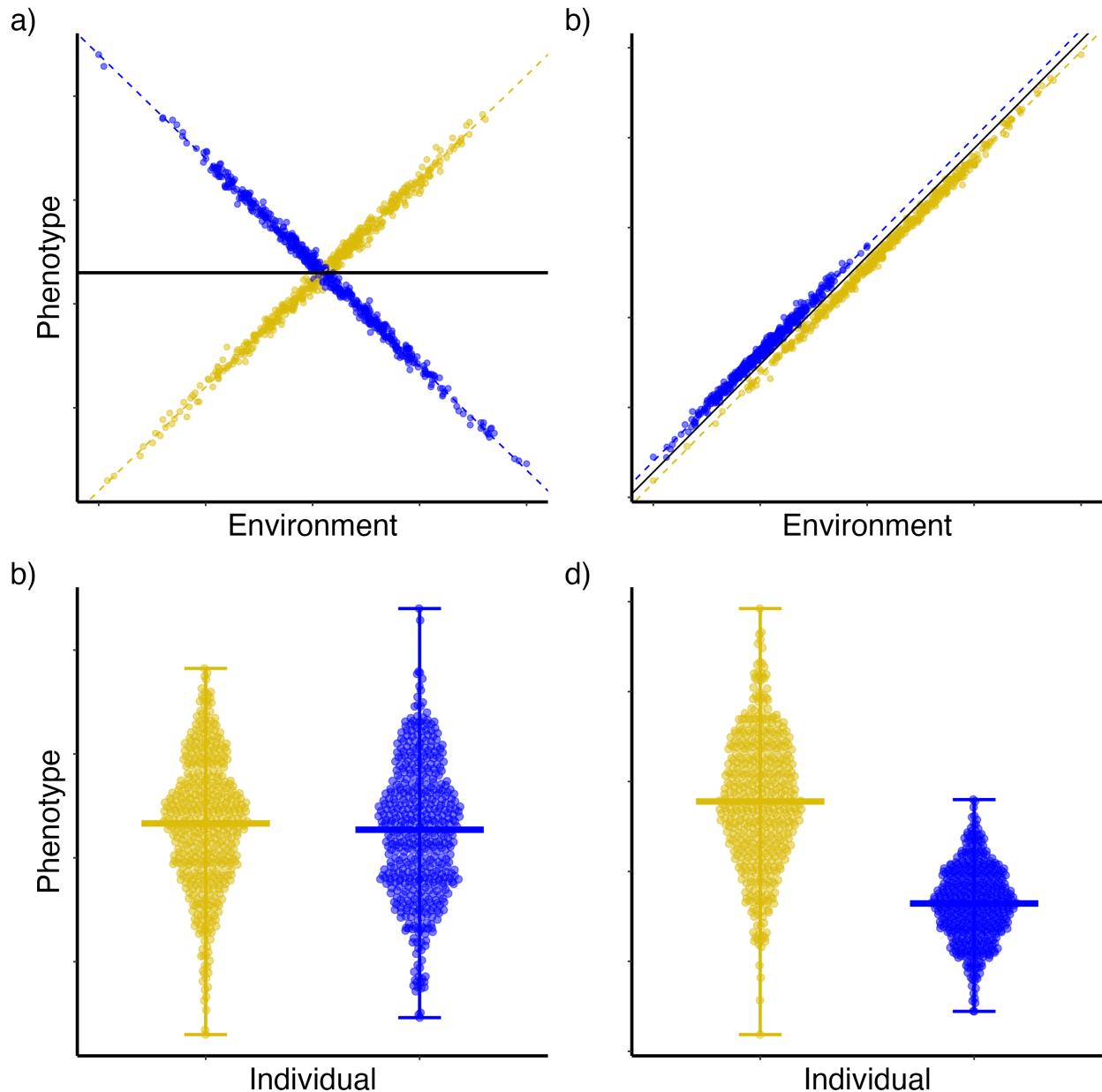
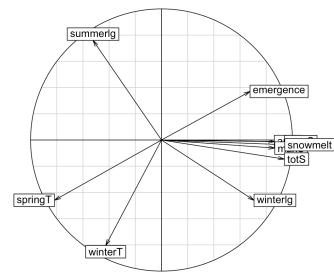


Figure 7: Reaction norms for two individuals (blue and yellow) for a trait a) with individuals expressing exact opposite plastic responses. We can see that b) they express the same range despite the  $I * E$ . Another case, c) without  $I * E$  (i.e., same slope between individuals) but in an unbalanced design, d) We would have different range of expressed phenotype.

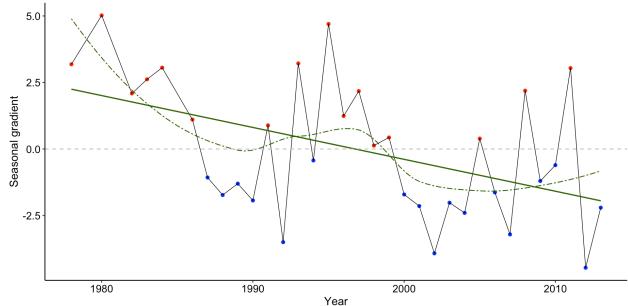
to fit DHGLMs using a frequentist approach which is much faster especially in a simulation setup, but it relies on a different coding language (mix of R and C). Then I will then apply this method on our Yellow-Bellied Marmots population to illustrate it with a real condition example.

## Chapter 3 - Identifying predictors of increased body mass.

If we look at the climate harshness variation at our study site in the last 50 years, as expected with climate change, we see a clear tendency to warmer and milder years through time (Figure 8).



(a) PCA correlation circle



(b) Temporal variation

Figure 8: Climatic variation at RMBL from 1975 to 2013. I conducted a Principal Component Analysis (PCA) using “ade4” package (Dray et al. 2023) over 10 weather variables. (a) We interpret the first axis as a “seasonal gradient” with high values being associated with years of long and cold winter, and low values associated to milder years, with longer active seasons. (b) After extracting seasonal gradient for each year from 1975 to 2013, we can explore the temporal tendency of climatic conditions at study site (Biro et al., manuscript in progress).

At first sight, evolution toward a bigger body mass in marmots seems expected. Indeed, bigger body mass is associated with better fitness as it increases probability of survival over hibernation (Jebb et al. 2021; Ozgul et al. 2010). The main selective pressure being then hibernation. However, here, we have selection for bigger body mass, in a period where the selective pressure from hibernation is decreasing due to climate change (Figure 9). Hence, we face some sort of paradox, where evolution seems to occur when selective pressure is expected to decrease.

Changing season length is a good explanation for the body mass increase through plasticity, individuals having more time to forage. But, this paradox justifies further research to identify the selective pressures driving the observed body mass evolution.

The first step is going to be to gather environmental data. I will be able to extract and estimate hibernation and active season length, seasonal conditions (average snowpacks, average temperatures and precipitation), food availability, and drought frequency and severity over the last 50 years.

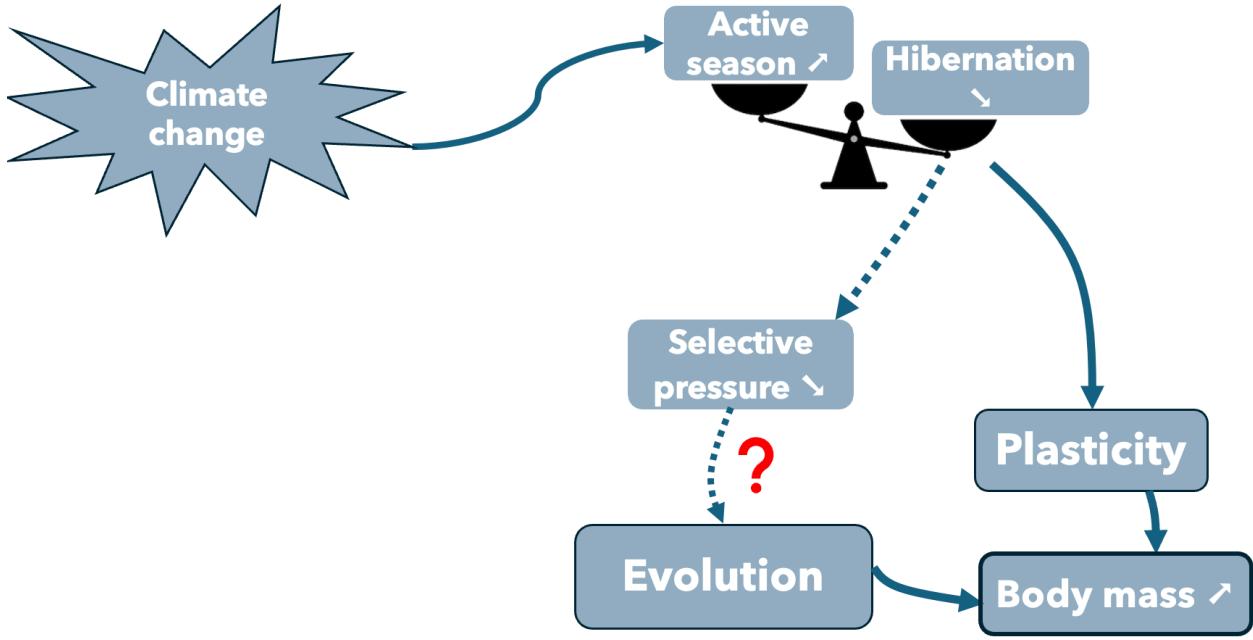


Figure 9: Evolutive paradox behind body mass increase.

Then from the body mass at the beginning and the end of the active season, I will also be able to estimate the body mass gained in an active season (mass in August minus mass in June), but also the mass loss during hibernation (mass in June minus mass in August in previous year).

$$\begin{aligned}
 \text{Fixed} &= \text{Seasonal conditions} + \text{Age} + \text{Drought} \\
 &\quad + \text{Food} + \text{Season lengths} \\
 \binom{\text{Body mass gain}}{\text{Body mass loss}} &\sim \\
 \text{Random} &= \text{Animal} + \text{UID} + \text{Measurement year}
 \end{aligned} \tag{3}$$

I will then begin by examine temporal trend for both environmental and body mass data. I will also estimate the genetic variance covariance between mass gain and mass loss using bivariate animal models. And finally, I am going to test the effect of the different environmental data, while controlling for individuals' age (Equation 3).

## Chapter 4 - Balance between body condition and experience as predictors of marmots' behavior.

In the context of the extended pace of life syndrome framework (Dammhahn et al. 2018; Réale et al. 2010), we expect to see correlation between body mass and individuals' behaviour (e.g., bigger individuals would be expected to be bolder).

But we also expect that behaviour and personality will be impacted by life experience and change through an individual's life (Stamps and Groothuis 2010).

In our population, for example, the proportion of time "stand looking" seems to be more impacted by body mass during the two first years of life than it is for adults (Figure 10).

Although the impact of body mass, with bigger individuals spending more time looking is easily explainable as heavier individuals are slower and thus must stay more vigilant to avoid predation, this age effect is interesting to note and advocate for the hypothesis that with age, experience could prevail on physical condition to dictate behaviour, with older individuals more careful than juveniles, as already suggested by Jebb et al. (2021).

$$\begin{aligned} \text{Fixed} &= \text{Cohort} \\ \text{Boldness} &\sim \quad (4) \\ \text{Random} &= \text{Animal} + \text{UID} + \text{Measurement year}_{\text{Factor}} \end{aligned}$$

We have repeated observations for a lot of individuals over various variables from observations from 2-min focal field observations and flight-initiation distance experiments. I am going to use that to conduct PCAs to determine individual values for various personality traits such as boldness (Réale et al. 2007) and estimate its repeatability (using mixed models) and heritability (using animal models, Equation 4).

$$\begin{pmatrix} \text{Boldness} \\ \text{Body mass} \end{pmatrix} \sim \begin{aligned} \text{Fixed} &= \text{Cohort} \\ \text{Random} &= \text{Animal} + \text{UID} + \text{Measurement year}_{\text{Factor}} \end{aligned} \quad (5)$$

Then, I will estimate the genetic correlation between those personality traits and body mass over cohorts using a bivariate animal model (Equation 5).

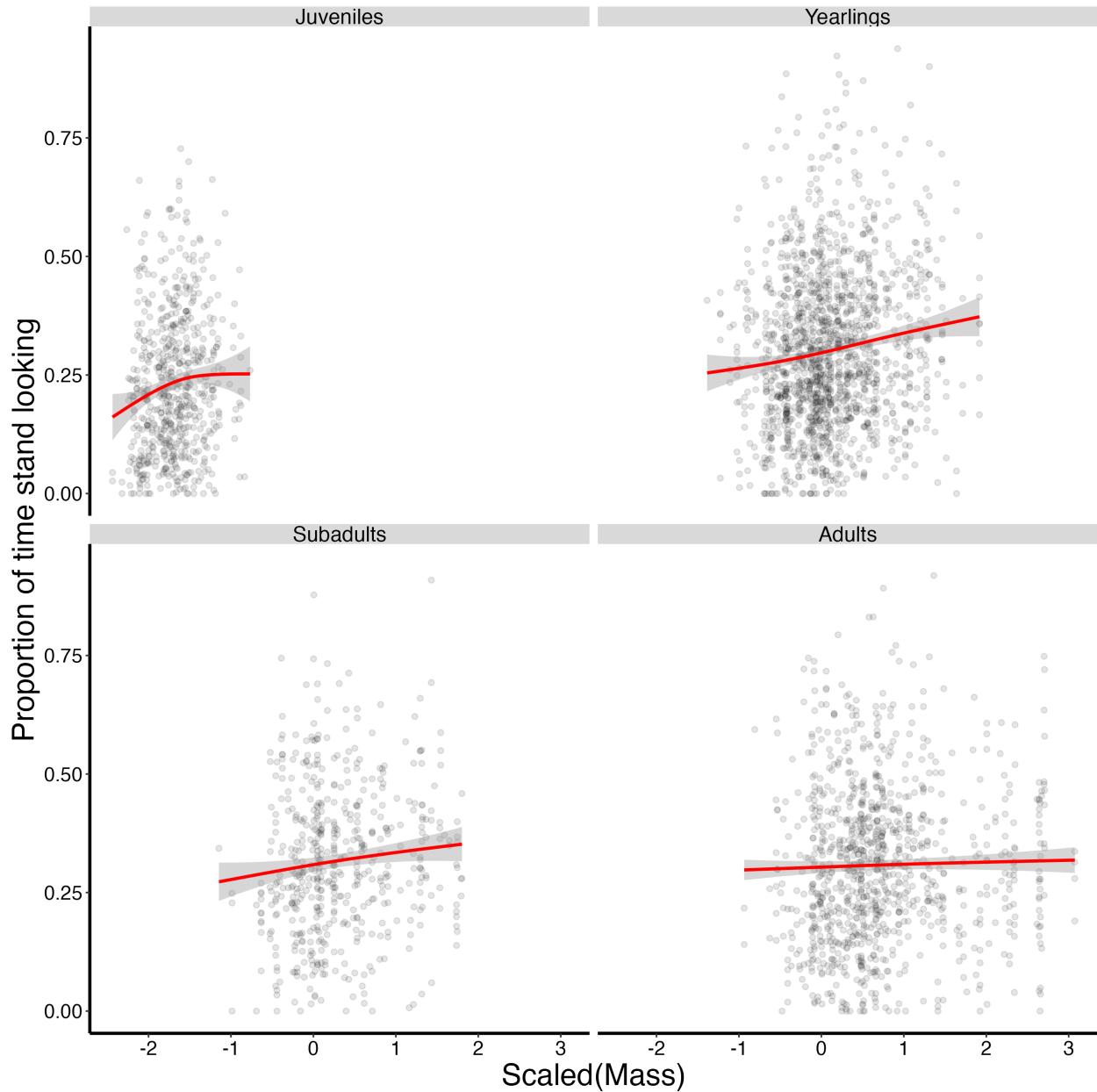


Figure 10: Proportion of time spent stand looking (within two-minute focal observations) as a function of scaled mass on August 15th across age classes: Juveniles (0-1 year), Yearlings (1-2 years), Subadults (2-3 years), and Adults (3+ years). Red lines represent local regressions, and points represent raw data.

$$\begin{aligned}
 \textbf{Fixed} &= \textit{Body mass} * \textit{Age} + \textit{Cohort} \\
 \textit{Boldness} &\sim \\
 \textbf{Random} &= \textit{UID} + \textit{Measurement year}_{Factor}
 \end{aligned} \tag{6}$$

Finally, I will test the effect of the interaction between body mass and individual age while accounting for time cohort variation and controlling for individual and measurement year effects, using LMM (Equation 6).

In addition to that, our marmot population seems to be in a demographic expansion since the 2000s (Ozgul et al. 2010). Furthermore, it is known that both body mass (Ozgul et al. 2010), but also behaviour (Réale et al. 2007; Wolf and Weissing 2012) can impact population dynamics. It is therefore crucial to study the relation between body mass, behaviour, and population dynamics to better understand, and predict, future implications of this body mass increase for our population in a context of climate change.

## **Significance and impacts**

This project provide a rare opportunity to study a remarkable response to climate change at both phenotypic and genetic levels. The observed body mass increase in Yellow-Bellied Marmots -representing a substantial 20% rise in adult females occurred at a notable speed, seemingly, three decades, between the 1970s and the early 2000s.

Using one of the most extensive and detailed long-term datasets on a natural population, this research enables an unparalleled exploration of wild populations' response to climate change. This research allows for powerful analyses, typically unfeasible in natural systems.

By investigating how the body mass has changed (i.e., basis constitution or growing capacity), developing new methods to detect individual variation in plasticity, and identifying predictors of this shift, this research will contribute crucial knowledge about the complex interplay between genotype, phenotype, and environment. Furthermore, exploring the balance between body condition and life experience as predictors of individual behaviour will improve our understanding of adaptive strategies in wild population.

By studying how natural population respond to rapidly changing environmental conditions, this project aims to give critical insights for conservations strategies and predictions. Understanding the causes and consequences of phenotypic response to climate change is essential for predicting future viability of natural populations.

We hope that findings from this research will help inform conservation policymakers by improving projections of species' adaptive capacity and resilience to climate change, offering guidance for managing biodiversity in a rapidly changing world.

## Potential side projects

1. Buffer environmental instability by increasing your body mass: an application of conservative bet-hedging in a hibernant rodent.

When producing offspring, bet-hedging strategy correspond to “bet” on the best fitness for the long term, at the expense of immediate fitness, in order to cope with an unpredictable environment (Childs et al. 2010; Philippi and Seger 1989; Starrfelt and Kokko 2012).

Bet-hedging strategy can be of two types, either diversified bet-hedging (usually explained with the adage “don’t put all your eggs in the same basket”), corresponding to increasing phenotypic variance in offspring, increasing the chance that at least some of them will be adapted to the condition they will face, and therefore assuring gene transmission to next generations (Cohen 1966; Rajon et al. 2014); or conservative bet-hedging (explained by the adage “one bird in the hand is worth two in the bush”), corresponding to lower fitness (i.e., number of offsprings) variation, which can be costly in years with good conditions as the fitness isn’t maximized, but more secured in poor years, as the fitness is less variable (Einium and Fleming 2004; Philippi and Seger 1989).

With climate change, environment are less predictable than ever. To cope with that unpredictability, conservative bet-hedging is expected to be a relevant adaptive strategy (Einium and Fleming 2004).

Applied to body mass, conservative bet-hedging would correspond to the production of less but bigger offspring, and a reduced variance in the offspring phenotype. The costs on immediate fitness for the parent is that in a good year, more offspring could have been produced, assuring more gene transmission. However, in poor years, the chances that offspring will survive is greater (Philippi and Seger 1989).

For the marmots, bigger individuals would have more chance to survive over hibernation and therefore participate in the next breeding season. With environment becoming less and less predictable, especially at high altitude (Inouye and Wielgolaski 2003), conservative bet-hedging can be seen as an insurance. With that strategy, fitness will be less variable as it is less impacted by the quality of the year in terms of resources, bigger individuals being able to buffer poor years. This decreasing fitness variability over time is predicted to be favoured by selection (Cohen 1966; Einum and Fleming 2004).

Using our environmental records at RMBL, I will define each year of study as either “good”, “mid” or “poor” in terms of resources and environmental conditions. Given that the mean

number of offsprings per year, per female in our population are of, let's say, [3] in the up valley and [5] in down valley , I will simulate two populations with the same means but different variance.

The first one, "savage", will be highly environmentally dependant, in a "poor" year, each female will produce 1 offspring in the up valley and 3 in down; in "good" years: 5 and 7; and "mid" years: 3 and 5. In the other one, "conservative", during "poor" years each female will produce 2 offsprings in the up valley and 4 in the down valley; in "good" years it will be 4 and 6; and "mid" years: 3 and 5.

With that model, I will be able to simulate what would have been populations dynamics during our study period. At first, I will compare fitness geometric mean (Philippi and Seger 1989) over the period for the two populations. This will allow me to check which strategy would be the best in our habitat.

Then, using our models predictions, I will be able to see from which strategy, our actual population is the closest.

Although conservative bet-hedging for fewer but bigger offspring has been predicted to be a good strategy to cope with unpredictable environment, if it becomes too variable, simulations shows that diversified bet-hedging becomes a better option (Einium and Fleming 2004). Indeed, the population can mismatch with its environment (Stenseth and Mysterud 2002; Visser and Both 2005). Then, if phenotypic variation has decreased too much, the population looses its adaption capacity and finds itself in an "evolutionary trap" (Robertson et al. 2013; Schlaepfer et al. 2002).

We have here a good opportunity to use one of the longest monitoring in the world to see how populations actually react in real conditions.

2. Identify key patches for metapopulation persistence using Social Network Analysis methods. (*Continuation of a project previously started at NTNU with Dr. Yimen Araya-Ajoy*)

A metapopulation is defined as a set of subpopulations distributed across various patches, more or less interconnected. Links between subpopulations (i.e., migration fluxes) in a metapopulations is crucial for its survival over time, as it maintains genetic diversity (). If a subpopulation finds itself isolated from the rest of the network, lack of genetic diversity putting it at risk of extinction ()�.

To various extent, a metapopulation can be viewed as a population-scale network (i.e., a set of patches connected by edges of varying intensity, Krause et al. 2015). Therefore, Social Network Analysis can offer a valuable approach to study metapopulation dynamics by identifying key patches contributing to network connectivity and resilience (Farine and Whitehead 2015).

Using data from a long-term study on a wild house sparrow metapopulation inhabiting an archipelago in the district Helgeland, northern Norway, I conducted preliminary analysis to test these analyses. Initial findings (e.g., non-random structural patterns and hierarchical order in island selection for emigration, independent of geographic distance) provides encouraging insight about migratory behaviour within metapopulation.

Focus on understanding the migration dynamics and identifying critical patches in metapopulation can offer insight for policymakers. We hope to develop new methods allowing to take effective measures, applicable more efficiently with less need of extensive data. This would help to preserve metapopulation, safeguarding genetic diversity, connectivity, and better understanding their resilience capacity in context of changing environment. I am planing to test the efficiency of different tools already develops for SNA, applied to metapopulation dynamics, and try to develop new ones from simulations.

# Expected Products

**Introduction** (*French MSc second year project*)

1. *Just plasticity, are you sure?* Evidence for a strong increase in Yellow-bellied Marmot's body mass predicted breeding values in the last half century. A Birot, D Blumstein and JGA Martin *Prepared for Evolution*

## Thesis

2. Towards more comprehensive studies of phenotypic changes: Addressing the missing fraction problem in Yellow-bellied Marmots' body mass. A Birot, D Blumstein and JGA Martin. Targeted journal: *Evolution*
3. Break free from bad environmental proxies when studying I \* E, the DHGLMs solution. A Birot, N Dochtermann and JGA Martin. Targeted journal: *Journal of Evolutionary Biology*
4. Which part of climate change drives body mass evolution? A Birot, D Blumstein and JGA Martin. Targeted journal: *The American Naturalist*
5. From Mass to Manner: How Body Mass and Age Shape Behaviour in Yellow-Bellied Marmots. A Birot, D Blumstein and JGA Martin. Targeted journal: *Oikos*

## Side projects

6. Buffer environmental instability by increasing your body mass: an application of conservative bet-hedging in a hibernant rodent. A Birot, D Blumstein and JGA Martin. Targeted journal: *Journal of Evolutionary Biology; Oikos*
7. Identify key patches for metapopulation persistence using Social Network Analysis methods. A Birot, B-E Sæther, H Jensen, J Wright, (JGA Martin), Y Araya-Ajoy. Targeted journal: *Functional ecology; Journal of Animal Ecology*

# Timeline

| PhD - First year                              |  | Fall 2024                           |          |     |     | Winter 2025 |     |     |     | Spring-Summer 2025 |     |     |     |
|---|--|-------------------------------------|----------|-----|-----|-------------|-----|-----|-----|--------------------|-----|-----|-----|
|   |  | Sep                                 | Oct      | Nov | Dec | Jan         | Feb | Mar | Apr | May                | Jun | Jul | Aug |
| <b>Task</b>                                   |  |                                     |          |     |     |             |     |     |     |                    |     |     |     |
| <b>Professional</b>                           |  |                                     |          |     |     |             |     |     |     |                    |     |     |     |
| TA (Biostats)                                 |  |                                     |          |     |     |             |     |     |     |                    |     |     |     |
| Grants & scholarships application             |  |                                     |          |     |     |             |     |     |     |                    |     |     |     |
| Conference & Networking                       |  |                                     |          |     |     |             |     |     |     |                    |     |     |     |
| <b>Program</b>                                |  |                                     |          |     |     |             |     |     |     |                    |     |     |     |
| Proposal - Submission                         |  |                                     |          |     |     |             |     |     |     |                    |     |     |     |
| Comprehensive exam                            |  |                                     |          |     |     |             |     |     |     |                    |     |     |     |
| TAC meeting                                   |  |                                     |          |     |     |             |     |     |     |                    |     |     |     |
| <b>Research</b>                               |  |                                     |          |     |     |             |     |     |     |                    |     |     |     |
| Proposal - Literature review                  |  |                                     |          |     |     |             |     |     |     |                    |     |     |     |
| Proposal - Writing (Thesis introduction)      |  |                                     |          |     |     |             |     |     |     |                    |     |     |     |
| MSc Project (Paper 1) - Finish analysis       |  |                                     |          |     |     |             |     |     |     |                    |     |     |     |
| MSc Project (Paper 1) - Writing               |  |                                     |          |     |     |             |     |     |     |                    |     |     |     |
| MSc Project (Paper 1) - Manuscript submission |  |                                     |          |     |     |             |     |     |     |                    |     |     |     |
| Field season                                  |  |                                     |          |     |     |             |     |     |     |                    |     |     |     |
|   |  | Working on it                       |          |     |     |             |     |     |     |                    |     |     |     |
|   |  | <input checked="" type="checkbox"/> | Deadline |     |     |             |     |     |     |                    |     |     |     |
| PhD - Second year                             |  | Fall 2025                           |          |     |     | Winter 2026 |     |     |     | Spring-Summer 2026 |     |     |     |
|   |  | Sep                                 | Oct      | Nov | Dec | Jan         | Feb | Mar | Apr | May                | Jun | Jul | Aug |
| <b>Task</b>                                   |  |                                     |          |     |     |             |     |     |     |                    |     |     |     |
| <b>Professional</b>                           |  |                                     |          |     |     |             |     |     |     |                    |     |     |     |
| TA (TBD)                                      |  |                                     |          |     |     |             |     |     |     |                    |     |     |     |
| TA (TBD)                                      |  |                                     |          |     |     |             |     |     |     |                    |     |     |     |
| Grants & scholarships application             |  |                                     |          |     |     |             |     |     |     |                    |     |     |     |
| Conference & Networking                       |  |                                     |          |     |     |             |     |     |     |                    |     |     |     |
| Honors student supervision                    |  |                                     |          |     |     |             |     |     |     |                    |     |     |     |
| <b>Program</b>                                |  |                                     |          |     |     |             |     |     |     |                    |     |     |     |
| Class (TBD)                                   |  |                                     |          |     |     |             |     |     |     |                    |     |     |     |
| TAC meeting                                   |  |                                     |          |     |     |             |     |     |     |                    |     |     |     |
| <b>Research</b>                               |  |                                     |          |     |     |             |     |     |     |                    |     |     |     |
| Chapter 1 (Paper 2) - Analysis                |  |                                     |          |     |     |             |     |     |     |                    |     |     |     |
| Chapter 1 (Paper 2) - Writing                 |  |                                     |          |     |     |             |     |     |     |                    |     |     |     |
| Chapter 1 (Paper 2) - Manuscript submission   |  |                                     |          |     |     |             |     |     |     |                    |     |     |     |
| Chapter 2 (Paper 3) - Analysis                |  |                                     |          |     |     |             |     |     |     |                    |     |     |     |
| Field season                                  |  |                                     |          |     |     |             |     |     |     |                    |     |     |     |
|   |  | Working on it                       |          |     |     |             |     |     |     |                    |     |     |     |
|   |  | <input checked="" type="checkbox"/> | Deadline |     |     |             |     |     |     |                    |     |     |     |

Figure 11: Proposed timeline for the first and second year.

| PhD - Third year                            |   | Fall 2026                                    |     |     |     | Winter 2027 |     |     |     | Spring-Summer 2027 |     |     |     |
|---|---|--|-----|-----|-----|-------------|-----|-----|-----|--------------------|-----|-----|-----|
|   |   | Sep  | Oct | Nov | Dec | Jan         | Feb | Mar | Apr | May                | Jun | Jul | Aug |
| <b>Task</b>                                 |   |  |     |     |     |             |     |     |     |                    |     |     |     |
| <b>Professional</b>                         |   |  |     |     |     |             |     |     |     |                    |     |     |     |
| TA (TBD)                                    |   |  |     |     |     |             |     |     |     |                    |     |     |     |
| TA (TBD)                                    |   |  |     |     |     |             |     |     |     |                    |     |     |     |
| Grants & scholarships application           |   |  |     |     |     |             |     |     |     |                    |     |     |     |
| Conference & Networking                     |   |  |     |     |     |             |     |     |     |                    |     |     |     |
| Honors student supervision                  |   |  |     |     |     |             |     |     |     |                    |     |     |     |
| <b>Program</b>                              |   |  |     |     |     |             |     |     |     |                    |     |     |     |
| TAC meeting                                 |   |  |     |     |     |             |     |     | ✓   |                    |     |     |     |
| <b>Research</b>                             |   |  |     |     |     |             |     |     |     |                    |     |     |     |
| Chapter 2 (Paper 3) - Analysis              |   |  |     |     |     |             |     |     |     |                    |     |     |     |
| Chapter 2 (Paper 3) - Writing               |   |  |     |     |     |             |     |     |     |                    |     |     |     |
| Chapter 2 (Paper 3) - Manuscript submission |   |  |     |     | ✓   |             |     |     |     |                    |     |     |     |
| Chapter 3 (Paper 4) - Analysis              |   |  |     |     |     |             |     |     |     |                    |     |     |     |
| Chapter 3 (Paper 4) - Writing               |   |  |     |     |     |             |     |     |     |                    |     |     |     |
| Field season                                |   |  |     |     |     |             |     |     |     |                    |     |     |     |
|   |   | Working on it                                |     |     |     |             |     |     |     |                    |     |     |     |
|   |   | <input checked="" type="checkbox"/> Deadline |     |     |     |             |     |     |     |                    |     |     |     |
| PhD - Fourth year                           |   | Fall 2027                                    |     |     |     | Winter 2028 |     |     |     | Spring-Summer 2028 |     |     |     |
|   |   | Sep  | Oct | Nov | Dec | Jan         | Feb | Mar | Apr | May                | Jun | Jul | Aug |
| <b>Task</b>                                 |   |  |     |     |     |             |     |     |     |                    |     |     |     |
| <b>Professional</b>                         |   |  |     |     |     |             |     |     |     |                    |     |     |     |
| TA (TBD)                                    |   |  |     |     |     |             |     |     |     |                    |     |     |     |
| TA (TBD)                                    |   |  |     |     |     |             |     |     |     |                    |     |     |     |
| Grants & scholarships application           |   |  |     |     |     |             |     |     |     |                    |     |     |     |
| Conference & Networking                     |   |  |     |     |     |             |     |     |     |                    |     |     |     |
| <b>Program</b>                              |   |  |     |     |     |             |     |     |     |                    |     |     |     |
| Thesis submission                           |   |  |     |     |     |             |     |     | ✓   |                    |     |     |     |
| TAC meeting                                 |   |  |     |     |     |             |     |     |     |                    |     | ✓   |     |
| Thesis defence                              |   |  |     |     |     |             |     |     |     |                    |     |     | ✓   |
| <b>Research</b>                             |   |  |     |     |     |             |     |     |     |                    |     |     |     |
| Chapter 3 (Paper 4) - Manuscript submission | ✓ |  |     |     |     |             |     |     |     |                    |     |     |     |
| Chapter 4 (Paper 5) - Analysis              |   |  |     |     |     |             |     |     |     |                    |     |     |     |
| Chapter 4 (Paper 5) - Writing               |   |  |     |     |     |             |     |     |     |                    |     |     |     |
| Chapter 4 (Paper 5) - Manuscript submission |   |  |     |     |     |             |     |     |     | ✓                  |     |     |     |
| Thesis writing (General discussion)         |   |  |     |     |     |             |     |     |     |                    |     |     |     |
|   |   | Working on it                                |     |     |     |             |     |     |     |                    |     |     |     |
|   |   | <input checked="" type="checkbox"/> Deadline |     |     |     |             |     |     |     |                    |     |     |     |

Figure 12: Proposed timeline for the third and fourth year.

## References

- Acquarone, C., Cucco, M., Cauli, S. L., and Malacarne, G. (2002), “Effects of food abundance and predictability on body condition and health parameters: Experimental tests with the Hooded Crow,” *Ibis*, 144. [https://doi.org/10.1046/j.1474-919X.2002.t01-2-00094\\_1.x](https://doi.org/10.1046/j.1474-919X.2002.t01-2-00094_1.x).
- Alerstam, T., and Christie, D. A. (2004), *Bird migration*, Cambridge University Press.
- Armitage, K. B. (1965), “Vernal behaviour of the yellow-bellied marmot (*Marmota flaviventris*),” *Animal Behaviour*, 13, 59–68. [https://doi.org/10.1016/0003-3472\(65\)90072-2](https://doi.org/10.1016/0003-3472(65)90072-2).
- Armitage, K. B. (2014), *Marmot Biology: Sociality, Individual Fitness, and Population Dynamics*, Cambridge University Press. <https://doi.org/10.1017/CBO9781107284272>.
- Arnold, S. J., Pfrender, M. E., and Jones, A. G. (2001), “The adaptive landscape as a conceptual bridge between micro- and macroevolution,” in *Microevolution Rate, Pattern, Process*, eds. A. P. Hendry and M. T. Kinnison, Dordrecht: Springer Netherlands, pp. 9–32. [https://doi.org/10.1007/978-94-010-0585-2\\_2](https://doi.org/10.1007/978-94-010-0585-2_2).
- Bell, G. (1980), “The Costs of Reproduction and Their Consequences,” *The American Naturalist*, 116, 45–76. <https://doi.org/10.1086/283611>.
- Bergmann (1847), “About the relationships between heat conservation and body size of animals,” *Goett Stud*, 1, 595–708.
- Bieber, C., Lebl, K., Stalder, G., Geiser, F., and Ruf, T. (2014), “Body mass dependent use of hibernation: Why not prolong the active season, if they can?” *Functional Ecology*, (C. Franklin, ed.), 28, 167–177. <https://doi.org/10.1111/1365-2435.12173>.
- Biro, P. A., and Stamps, J. A. (2008), “Are animal personality traits linked to life-history productivity?” *Trends in Ecology & Evolution*, 23, 361–368. <https://doi.org/10.1016/j.tree.2008.04.003>.
- Blums, P., Nichols, J. D., Hines, J. E., Lindberg, M. S., and Mednis, A. (2005), “Individual quality, survival variation and patterns of phenotypic selection on body condition and timing of nesting in birds,” *Oecologia*, 143, 365–376. <https://doi.org/10.1007/s00442-004-1794-x>.
- Blumstein, D. T. (2009), “SOCIAL EFFECTS ON EMERGENCE FROM HIBERNATION IN YELLOW-BELLIED MARMOTS.”
- Blumstein, D. T., Im, S., Nicodemus, A., and Zugmeyer, C. (2004), “Yellow-bellied Marmots (*Marmota flaviventris*) Hibernate Socially,” *Journal of Mammalogy*, 85, 25–29. [https://doi.org/10.1644/1545-1542\(2004\)085%3C0025:YMMFHS%3E2.0.CO;2](https://doi.org/10.1644/1545-1542(2004)085%3C0025:YMMFHS%3E2.0.CO;2).
- Blumstein, D. T., Lea, A. J., Olson, L. E., and Martin, J. G. A. (2010), “Heritability of anti-predatory traits: Vigilance and locomotor performance in marmots,” *Journal of Evolutionary Biology*, 23, 879–887. <https://doi.org/10.1111/j.1420-9101.2010.01967.x>.

- Bürkner, P.-C. (2021), “Bayesian Item Response Modeling in *R* with **Brms** and *Stan*,” *Journal of Statistical Software*, 100. <https://doi.org/10.18637/jss.v100.i05>.
- Butler, D. G., Cullis, B. R., Gilmour, A. R., Gogel, B. J., and Thompson, R. (n.d.). “ASReml estimates variance components under a general linear.”
- Carey, H. V., Andrews, M. T., and Martin, S. L. (2003), “Mammalian Hibernation: Cellular and Molecular Responses to Depressed Metabolism and Low Temperature,” *Physiological Reviews*, 83, 1153–1181. <https://doi.org/10.1152/physrev.00008.2003>.
- Carpenter, B., Gelman, A., Hoffman, M. D., Lee, D., Goodrich, B., Betancourt, M., Brubaker, M., Guo, J., Li, P., and Riddell, A. (2017), “Stan: A Probabilistic Programming Language,” *Journal of Statistical Software*, 76. <https://doi.org/10.18637/jss.v076.i01>.
- Charmantier, A., Garant, D., and Kruuk, L. E. B. (2014), *Quantitative genetics in the wild*, Oxford University Press. <https://doi.org/10.1093/acprof:oso/9780199674237.001.0001>.
- Childs, D. Z., Metcalf, C. J. E., and Rees, M. (2010), “Evolutionary bet-hedging in the real world: Empirical evidence and challenges revealed by plants,” *Proceedings of the Royal Society B: Biological Sciences*, 277, 3055–3064. <https://doi.org/10.1098/rspb.2010.0707>.
- Cohen, D. (1966), “Optimizing reproduction in a randomly varying environment,” *Journal of Theoretical Biology*, 12, 119–129. [https://doi.org/10.1016/0022-5193\(66\)90188-3](https://doi.org/10.1016/0022-5193(66)90188-3).
- Covarrubias-Pazaran, G. (2024), “Lme4breeding: Enabling genetic evaluation in the era of genomic data,” *bioRxiv : the preprint server for biology*, Cold Spring Harbor Laboratory, 2024–05.
- Crocker, D. E., Houser, D. S., and Webb, P. M. (2012), “Impact of Body Reserves on Energy Expenditure, Water Flux, and Mating Success in Breeding Male Northern Elephant Seals,” *Physiological and Biochemical Zoology*, 85, 11–20. <https://doi.org/10.1086/663634>.
- Dammhahn, M., Dingemanse, N. J., Niemelä, P. T., and 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, s00265-018-2473-y. <https://doi.org/10.1007/s00265-018-2473-y>.
- Darveau, C.-A., Suarez, R. K., Andrews, R. D., and Hochachka, P. W. (2002), “Allometric cascade as a unifying principle of body mass effects on metabolism,” *Nature*, 417, 166–170. <https://doi.org/10.1038/417166a>.
- Daufresne, M., Lengfellner, K., and Sommer, U. (2009), “Global warming benefits the small in aquatic ecosystems,” *Proceedings of the National Academy of Sciences*, 106, 12788–12793. <https://doi.org/10.1073/pnas.0902080106>.
- Denryter, K., Conner, M. M., Stephenson, T. R., German, D. W., and Monteith, K. L. (2022), “Survival of the fattest: How body fat and migration influence survival in highly seasonal environments,” *Functional Ecology*, 36, 2569–2579. <https://doi.org/10.1111/1365-2435>.

14151.

- DeWitt, T. J., Sih, A., and Wilson, D. S. (1998), “Costs and limits of phenotypic plasticity,” *Trends in Ecology & Evolution*, 13, 77–81. [https://doi.org/10.1016/S0169-5347\(97\)01274-3](https://doi.org/10.1016/S0169-5347(97)01274-3).
- Dray, S., Dufour, A.-B., Thioulouse, J., Jombart, T., Pavoine, S., Lobry, J. R., Ollier, S., Siberchicot, A., and Chessel, D. (2023), *Ade4: Analysis of Ecological Data: Exploratory and Euclidean Methods in Environmental Sciences*.
- Durant, J., Hjermann, D., Ottersen, G., and Stenseth, N. (2007), “Climate and the match or mismatch between predator requirements and resource availability,” *Climate Research*, 33, 271–283. <https://doi.org/10.3354/cr033271>.
- Einum, S., and Fleming, I. A. (2004), “Environmental unpredictability and offspring size: Conservative versus diversified bet-hedging,” *Evolutionary Ecology Research*, Evolutionary Ecology, Ltd., 6, 443–455.
- Farine, D. R., and Whitehead, H. (2015), “Constructing, conducting and interpreting animal social network analysis,” *Journal of Animal Ecology*, (S. Altizer, ed.), 84, 1144–1163. <https://doi.org/10.1111/1365-2656.12418>.
- Festa-Bianchet, M., Gaillard, J.-M., and Jorgenson, J. T. (1998), “Mass- and Density-Dependent Reproductive Success and Reproductive Costs in a Capital Breeder,” *The American Naturalist*.
- Finlay, K., and Wilkinson, G. (1963), “The analysis of adaptation in a plant-breeding programme,” *Australian Journal of Agricultural Research*, 14, 742. <https://doi.org/10.1071/AR9630742>.
- Gardner, J. L., Peters, A., Kearney, M. R., Joseph, L., and Heinsohn, R. (2011), “Declining body size: A third universal response to warming?” *Trends in Ecology & Evolution*, 26, 285–291. <https://doi.org/10.1016/j.tree.2011.03.005>.
- Geiser, F. (2013), “Hibernation,” *Current Biology*, 23, R188–R193. <https://doi.org/10.1016/j.cub.2013.01.062>.
- Gienapp, P., and Brommer, J. E. (2014), “Evolutionary dynamics in response to climate change,” in *Quantitative Genetics in the Wild*, eds. A. Charmantier, D. Garant, and L. E. B. Kruuk, Oxford University PressOxford, pp. 254–274. <https://doi.org/10.1093/acprof:oso/9780199674237.003.0015>.
- Giorgi, F., Hurrell, J. W., Marinucci, M. R., and Beniston, M. (1997), “Elevation Dependency of the Surface Climate Change Signal: A Model Study,” *Journal of Climate*, 10, 288–296. [https://doi.org/10.1175/1520-0442\(1997\)010%3C0288:EDOTSC%3E2.0.CO;2](https://doi.org/10.1175/1520-0442(1997)010%3C0288:EDOTSC%3E2.0.CO;2).
- “GIS Mapping Software, Location Intelligence & Spatial Analytics | Esri” (n.d.). <https://www.esri.com/en-us/home>.

- Gould, S. J., and Lewontin, R. C. (1979), “The spandrels of San Marco and the Panglossian paradigm: A critique of the adaptationist programme,” *Proceedings of the Royal Society of London. Series B. Biological Sciences*, 205, 581–598. <https://doi.org/10.1098/rspb.1979.0086>.
- Grabbherr, G., Gottfried, M., and Pauli, H. (2010), “Climate Change Impacts in Alpine Environments,” *Geography Compass*, 4, 1133–1153. <https://doi.org/10.1111/j.1749-8198.2010.00356.x>.
- Grafen, A. (1988), “On the uses of data on lifetime reproductive success,” *Reproductive success. Studies of individual variation in contrasting breeding systems*, University of Chicago Press, 454–471.
- Guillemain, M., Elmberg, J., Gauthier-Clerc, M., Massez, G., Hearn, R., Champagnon, J., and Simon, G. (2010), “Wintering French Mallard and Teal Are Heavier and in Better Body Condition than 30 Years Ago: Effects of a Changing Environment?” *AMBIO*, 39, 170–180. <https://doi.org/10.1007/s13280-010-0020-9>.
- Hadfield, J. D. (2008), “Estimating evolutionary parameters when viability selection is operating,” *Proceedings of the Royal Society B: Biological Sciences*, 275, 723–734. <https://doi.org/10.1098/rspb.2007.1013>.
- Hadfield, J. D. (2010), “MCMC Methods for Multi-Response Generalized Linear Mixed Models: The **MCMCglmm** R Package,” *Journal of Statistical Software*, 33. <https://doi.org/10.18637/jss.v033.i02>.
- Haramis, G. M., Nichols, J. D., Pollock, K. H., and Hines, J. E. (1986), “The Relationship Between Body Mass and Survival of Wintering Canvasbacks,” *The Auk*, 103, 506–514. <https://doi.org/10.1093/auk/103.3.506>.
- Heldstab, S. A. (2017), “How do mammals buffer environmental seasonality? The role of brain size, body fat and allomaternal care in dealing with energy shortage,” PhD thesis, University of Zurich. <https://doi.org/10.5167/UZH-144968>.
- Inouye, D. W., and Wielgolaski, F. E. (2003), “High Altitude Climates,” in *Phenology: An integrative Environmental Science*, pp. 195–214.
- Intergovernmental Panel On Climate Change (Ipcc) (2022), *Climate Change 2022 – Impacts, Adaptation and Vulnerability: Working Group II Contribution to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change*, Cambridge University Press. <https://doi.org/10.1017/9781009325844>.
- Jebb, A. H. M., Blumstein, D. T., Bize, P., and Martin, J. G. A. (2021), “Bigger is not always better: Viability selection on body mass varies across life stages in a hibernating mammal,” *Ecology and Evolution*, 11, 3435–3445. <https://doi.org/10.1002/ece3.7304>.
- Jenkins, S. H., and Busher, P. E. (1979), “Castor canadensis,” *Mammalian Species*, 1–8.

- <https://doi.org/10.2307/3503787>.
- Jones, C. G., Lawton, J. H., and Shachak, M. (1994), “Organisms as Ecosystem Engineers,” *Oikos*, 69, 373. <https://doi.org/10.2307/3545850>.
- Kittel, T., Thornton, P. E., Royle, J. Andrew, and Chase, T. (2002), “Climates of the rocky mountains: Historical and future patterns,” pp. 59–92. <https://doi.org/10.13140/RG.2.1.1683.0487>.
- Krause, J., James, R., Franks, D. W., and Croft, D. P. (eds.) (2015), *Animal social networks*, Oxford ; New York, NY: Oxford University Press.
- Kristensen, K., Nielsen, A., Berg, C. W., Skaug, H., and Bell, B. M. (2016), “TMB : Automatic Differentiation and Laplace Approximation,” *Journal of Statistical Software*, 70. <https://doi.org/10.18637/jss.v070.i05>.
- Kruuk, L. E. B. (2004), “Estimating genetic parameters in natural populations using the ‘animal model’,” *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, 359, 873–890. <https://doi.org/10.1098/rstb.2003.1437>.
- Kruuk, L. E. B., Charmantier, A., and Garant, D. (2014), “The study of quantitative genetics in wild populations,” in *Quantitative Genetics in the Wild*, Oxford University PressOxford, pp. 1–15. <https://doi.org/10.1093/acprof:oso/9780199674237.003.0012>.
- Kurz, A. (2008), “Physiology of Thermoregulation,” *Best Practice & Research Clinical Anaesthesia*, 22, 627–644. <https://doi.org/10.1016/j.bpa.2008.06.004>.
- Lee, Y., and Nelder, J. A. (2006), “Double hierarchical generalized linear models,” *Journal of the Royal Statistical Society Series C: Applied Statistics*.
- Lynch, M., and Walsh, B. (1998), *Genetics and Analysis of Quantitative Traits*, Sinauer.
- Martin, J., and Blumstein, D. (2024), *ybamaRmot: Database of the Marmot Study in the East River Valley, Colorado*.
- Meier, C. M., Karaardıç, H., Aymí, R., Peev, S. G., Witvliet, W., and Liechti, F. (2020), “Population-specific adjustment of the annual cycle in a super-swift trans-Saharan migrant,” *Journal of Avian Biology*, 51, jav.02515. <https://doi.org/10.1111/jav.02515>.
- Milner, J. M., Van Beest, F. M., Solberg, E. J., and Storaas, T. (2013), “Reproductive success and failure: The role of winter body mass in reproductive allocation in Norwegian moose,” *Oecologia*, 172, 995–1005. <https://doi.org/10.1007/s00442-012-2547-x>.
- Mittell, E. A., and Morrissey, M. B. (2024), “The missing fraction problem as an episodes of selection problem,” *Evolution; international journal of organic evolution*, Oxford University Press US, 78, 601–611.
- Monclús, R., Pang, B., and Blumstein, D. T. (2014), “Yellow-bellied marmots do not compensate for a late start: The role of maternal allocation in shaping life-history trajectories,” *Evolutionary Ecology*, 28, 721–733. <https://doi.org/10.1007/s10682-014-9705-z>.

- Nedergaard, J., and Cannon, B. (1990), “Mammalian hibernation,” *Philosophical Transactions of the Royal Society of London. B, Biological Sciences*, 326, 669–686. <https://doi.org/10.1098/rstb.1990.0038>.
- Nussey, D. H., Wilson, A. J., and Brommer, J. E. (2007), “The evolutionary ecology of individual phenotypic plasticity in wild populations,” *Journal of Evolutionary Biology*, 20, 831–844. <https://doi.org/10.1111/j.1420-9101.2007.01300.x>.
- Ohmura, A. (2012), “Enhanced temperature variability in high-altitude climate change,” *Theoretical and Applied Climatology*, 110, 499–508. <https://doi.org/10.1007/s00704-012-0687-x>.
- Olson, L. E., Blumstein, D. T., Pollinger, J. R., and Wayne, R. K. (2012), “No evidence of inbreeding avoidance despite demonstrated survival costs in a polygynous rodent,” *Molecular Ecology*, 21, 562–571. <https://doi.org/10.1111/j.1365-294X.2011.05389.x>.
- Ozgul, A., Childs, D. Z., Oli, M. K., Armitage, K. B., Blumstein, D. T., Olson, L. E., Tuljapurkar, S., and Coulson, T. (2010), “Coupled dynamics of body mass and population growth in response to environmental change,” *Nature*, 466, 482–485. <https://doi.org/10.1038/nature09210>.
- Philippi, T., and Seger, J. (1989), “Hedging one’s evolutionary bets, revisited,” *Trends in ecology & evolution*, Elsevier Current Trends, 4, 41–44.
- Phillips, P. C., and Arnold, S. J. (1989), “VISUALIZING MULTIVARIATE SELECTION,” *Evolution*, 43, 1209–1222. <https://doi.org/10.1111/j.1558-5646.1989.tb02569.x>.
- Pigliucci, M. (2001), *Phenotypic plasticity: Beyond nature and nurture*, JHU Press.
- Pigliucci, M. (2005), “Evolution of phenotypic plasticity: Where are we going now?” *Trends in Ecology & Evolution*, 20, 481–486. <https://doi.org/10.1016/j.tree.2005.06.001>.
- Prather, R. M., Underwood, N., Dalton, R. M., Barr, B., and Inouye, B. D. (2023), “Climate data from the Rocky Mountain Biological Laboratory (1975–2022),” *Ecology*, 104, e4153. <https://doi.org/10.1002/ecy.4153>.
- QGIS Development Team (2024), “QGIS Geographic Information System,” QGIS Association.
- R Core Team (2023), *R: A language and environment for statistical computing*, Manual, Vienna, Austria: R Foundation for Statistical Computing.
- Rajon, E., Desouhant, E., Chevalier, M., Débias, F., and Menu, F. (2014), “The Evolution of Bet Hedging in Response to Local Ecological Conditions,” *The American Naturalist*, 184, E1–E15. <https://doi.org/10.1086/676506>.
- Ramakers, J. J. C., Reed, T. E., Harris, M. P., and Gienapp, P. (2023), “Probing variation in reaction norms in wild populations: The importance of reliable environmental proxies,” *Oikos*, 2023, e09592. <https://doi.org/10.1111/oik.09592>.

- Réale, D., Garant, D., Humphries, M. M., Bergeron, P., Careau, V., and Montiglio, P.-O. (2010), “Personality and the emergence of the pace-of-life syndrome concept at the population level,” *Philosophical Transactions of the Royal Society B: Biological Sciences*, Royal Society, 365, 4051–4063. <https://doi.org/10.1098/rstb.2010.0208>.
- Réale, D., Reader, S. M., Sol, D., McDougall, P. T., and Dingemanse, N. J. (2007), “Integrating animal temperament within ecology and evolution,” *Biological Reviews*, 82, 291–318. <https://doi.org/10.1111/j.1469-185X.2007.00010.x>.
- Riesenfeld, A. (1981), “The role of body mass in thermoregulation,” *American Journal of Physical Anthropology*, 55, 95–99. <https://doi.org/10.1002/ajpa.1330550113>.
- Robertson, B. A., Rehage, J. S., and Sih, A. (2013), “Ecological novelty and the emergence of evolutionary traps,” *Trends in Ecology & Evolution*, 28, 552–560. <https://doi.org/10.1016/j.tree.2013.04.004>.
- Roff, D. A. (1992), “The evolution of life histories : Theory and analysis.”
- Schlaepfer, M. A., Runge, M. C., and Sherman, P. W. (2002), “Ecological and evolutionary traps,” *Trends in Ecology & Evolution*, 17, 474–480. [https://doi.org/10.1016/S0169-5347\(02\)02580-6](https://doi.org/10.1016/S0169-5347(02)02580-6).
- Sheridan, J. A., and Bickford, D. (2011), “Shrinking body size as an ecological response to climate change,” *Nature Climate Change*, 1, 401–406. <https://doi.org/10.1038/nclimate1259>.
- Siepielski, A. M., Morrissey, M. B., Carlson, S. M., Francis, C. D., Kingsolver, J. G., Whitney, K. D., and Kruuk, L. E. B. (2019), “No evidence that warmer temperatures are associated with selection for smaller body sizes,” *Proceedings of the Royal Society B: Biological Sciences*, 286, 20191332. <https://doi.org/10.1098/rspb.2019.1332>.
- Smith, B. R., and Blumstein, D. T. (2010), “Behavioral types as predictors of survival in Trinidadian guppies (*Poecilia reticulata*),” *Behavioral Ecology*, 21, 919–926. <https://doi.org/10.1093/beheco/arq084>.
- Smith, D. W., Peterson, R. O., Drummer, T. D., and Sheputis, D. S. (1991), “Over-winter activity and body temperature patterns in northern beavers,” *Canadian Journal of Zoology*, 69, 2178–2182. <https://doi.org/10.1139/z91-304>.
- Stamps, J. A. (2007), “Growth-mortality tradeoffs and ‘personality traits’ in animals,” *Ecology Letters*, 10, 355–363. <https://doi.org/10.1111/j.1461-0248.2007.01034.x>.
- Stamps, J., and Groothuis, T. G. G. (2010), “The development of animal personality: Relevance, concepts and perspectives,” *Biological Reviews*, 85, 301–325. <https://doi.org/10.1111/j.1469-185X.2009.00103.x>.
- Stan Development Team, C., and others (2020), “RStan: The R interface to stan,” *R package version 2.21. 2.*

- Starrfelt, J., and Kokko, H. (2012), “Bet-hedging—a triple trade-off between means, variances and correlations,” *Biological Reviews*, 87, 742–755. <https://doi.org/10.1111/j.1469-185X.2012.00225.x>.
- Stearns, S. C. (1992), *The evolution of life histories*, Oxford University Press. <https://doi.org/10.1093/oso/9780198577416.001.0001>.
- Stenseth, N. Chr., and Mysterud, A. (2002), “Climate, changing phenology, and other life history traits: Nonlinearity and match–mismatch to the environment,” *Proceedings of the National Academy of Sciences*, 99, 13379–13381. <https://doi.org/10.1073/pnas.212519399>.
- Stephenson, T. R., German, D. W., Cassirer, E. F., Walsh, D. P., Blum, M. E., Cox, M., Stewart, K. M., and Monteith, K. L. (2020), “Linking population performance to nutritional condition in an alpine ungulate,” *Journal of Mammalogy*, (P. Barboza, ed.), 101, 1244–1256. <https://doi.org/10.1093/jmammal/gyaa091>.
- Teplitsky, C., Robinson, M. R., and Merilä, J. (2014), “Evolutionary potential and constraints in wild populations,” in *Quantitative Genetics in the Wild*, eds. A. Charmantier, D. Garant, and L. E. B. Kruuk, Oxford University PressOxford, pp. 190–208. <https://doi.org/10.1093/acprof:oso/9780199674237.003.0012>.
- Via, S., Gomulkiewicz, R., De Jong, G., Scheiner, S. M., Schlichting, C. D., and Van Tienderen, P. H. (1995), “Adaptive phenotypic plasticity: Consensus and controversy,” *Trends in Ecology & Evolution*, 10, 212–217. [https://doi.org/10.1016/S0169-5347\(00\)89061-8](https://doi.org/10.1016/S0169-5347(00)89061-8).
- Visser, M. E., and Both, C. (2005), “Shifts in phenology due to global climate change: The need for a yardstick,” *Proceedings of the Royal Society B: Biological Sciences*, 272, 2561–2569. <https://doi.org/10.1098/rspb.2005.3356>.
- Walsh, B., and Blows, M. W. (2009), “Abundant Genetic Variation + Strong Selection = Multivariate Genetic Constraints: A Geometric View of Adaptation,” *Annual Review of Ecology, Evolution, and Systematics*, 40, 41–59. <https://doi.org/10.1146/annurev.ecolsys.110308.120232>.
- Walsh, C. R., and Patterson, R. T. (2022), “Precipitation and Temperature Trends and Cycles Derived from Historical 1890–2019 Weather Data for the City of Ottawa, Ontario, Canada,” *Environments*, 9, 35. <https://doi.org/10.3390/environments9030035>.
- Weibel, E. R., Bacigalupe, L. D., Schmitt, B., and Hoppele, H. (2004), “Allometric scaling of maximal metabolic rate in mammals: Muscle aerobic capacity as determinant factor,” *Respiratory Physiology & Neurobiology*, 140, 115–132. <https://doi.org/10.1016/j.resp.2004.01.006>.
- Wickham, H. (2016), *Ggplot2: Elegant Graphics for Data Analysis*, Springer-Verlag New York.

- Williams, C. M., Ragland, G. J., Betini, G., Buckley, L. B., Cheviron, Z. A., Donohue, K., Hereford, J., Humphries, M. M., Lisovski, S., Marshall, K. E., Schmidt, P. S., Sheldon, K. S., Varpe, Ø., and Visser, M. E. (2017), “Understanding Evolutionary Impacts of Seasonality: An Introduction to the Symposium,” *Integrative and Comparative Biology*, 57, 921–933. <https://doi.org/10.1093/icb/icx122>.
- Wilson, A. J., Réale, D., Clements, M. N., Morrissey, M., Postma, E., Walling, C., Kruuk, L., and Nussey, D. (2010), “An ecologist’s guide to the animal model.” *The Journal of animal ecology*, 79 1, 13–26. <https://doi.org/10.1111/j.1365-2656.2009.01639.x>.
- Wolf, M., Van Doorn, G. S., Leimar, O., and Weissing, F. J. (2007), “Life-history trade-offs favour the evolution of animal personalities,” *Nature*, 447, 581–584. <https://doi.org/10.1038/nature05835>.
- Wolf, M., and Weissing, F. J. (2012), “Animal personalities: Consequences for ecology and evolution,” *Trends in Ecology & Evolution*, 27, 452–461. <https://doi.org/10.1016/j.tree.2012.05.001>.
- Ydenberg, R. C., and Dill, L. M. (1986), “The Economics of Fleeing from Predators,” in *Advances in the Study of Behavior*, Elsevier, pp. 229–249. [https://doi.org/10.1016/S0065-3454\(08\)60192-8](https://doi.org/10.1016/S0065-3454(08)60192-8).
- Yom-Tov, Y., Yom-Tov, S., and Jarrell, G. (2008), “Recent increase in body size of the American marten *Martes americana* in Alaska: GLOBAL WARMING AND BODY SIZE OF THE AMERICAN MARTEN,” *Biological Journal of the Linnean Society*, 93, 701–707. <https://doi.org/10.1111/j.1095-8312.2007.00950.x>.
- Zahavi, A. A. (1997), *The handicap principle: A missing piece of darwin’s puzzle*, Oxford University Press. <https://doi.org/10.1093/oso/9780195100358.001.0001>.
- Zhai, Y., Huang, G., Wang, X., Zhou, X., Lu, C., and Li, Z. (2019), “Future projections of temperature changes in Ottawa, Canada through stepwise clustered downscaling of multiple GCMs under RCPs,” *Climate Dynamics*, 52, 3455–3470. <https://doi.org/10.1007/s00382-018-4340-y>.