

# Coping with climate change.

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

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# **Introduction**

## **Climate change**

Although some reluctance persists,

“[...] Large parts of the Country are suffering from tremendous amounts of snow and near record setting cold. [...] Wouldn’t be bad to have a little of that good old fashioned Global Warming right now!”

— U.S. President, Jan 20, 2019.

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 puts 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 modification 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.

### **Body mass a life-history trait**

We know that body mass is strongly related to both temperature acclimatation (Kurz 2008; i.e., thermoregulation, Riesenfeld 1981) and food abundance (Acquarone et al. 2002). Therefore, we need to study body mass in that context of climate and ecological changes. To study such changes, we rely on Life-History Theory. This framework is used to study how ressources are allocated to specific traits to cope with environment while maximising individual fitness. The theory rely on the fact that ressources are limited and trade-off must be maid between different traits to achieve the best life-history strategy (Bell 1980; Roff 1992; Stearns 1992)

Life history traits (LHTs) are phenotypic characteristics that directly impact an individual's survival and reproduction success, thereby determining its overall fitness (Roff 1992). The concept of life history theory relies on the hypothesis that organisms have limited resources and thus must make trade-offs when strategically allocating the different resources between competing functions such as growth, maintenance, and reproduction (Roff 1992; Stearns 1992).

Various traits can be considered as LHTs, as they represent the outcome of this resource allocation process. Among these, body mass plays a crucial role in many species. Individuals

with greater body mass will have more energetic reserves, making them more resilient to environmental pressures, as they will be able to buffer against seasonal food scarcity (Heldstab 2017). More generally, body fat can be considered as a buffer against harsh environment (Denryter et al. 2022). Extending this reasoning at a wider time scale, we could expect these bigger individuals to be able to buffer poor years in terms of resources, and so increasing their resilience to environmental variability (Einium and Fleming 2004).

Additionally, individuals with greater energy reserves have a better capacity to reproduce (Festa-Bianchet et al. 1998). Body mass would also be an “honest signal” of an individual capacity to accumulate resources and its quality as a reproducer (**REF**). Overall, a bigger body mass would lead to a better reproductive success.

However, a too large body mass can become a handicap. Even though some handicaps have been theorized to be an asset in sexual selection (Zahavi 1997), beyond a certain threshold, too large individuals will be counter-selected as it could induce a cost in individual performance (e.g., capacity to run from predators, Jebb et al. 2021).

Overall, body mass can be considered a key LHT influencing directly both survival and reproduction in many species, but a balance must be reached between performances and costs, and with investment in other traits (Stearns 1992).

### **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 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 [e.g., Beavers, *Castor canadensis*; Smith et al. (1991); Jenkins and Busher (1979)]; storing energy as fat during the good season [e.g. bighorn sheep, *Ovis canadensis*; Stephenson et al. (2020); Denryter et al. (2022)]; 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 favorable season. Beyond hibernators, two main strategies exists, 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 much 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 (Dufresne 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 (Dufresne 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. But, we need to understand what is driving this and how this change is happening.

### **Phenotypic plasticity vs evolution**

When an environment changes, inhabiting populations will have several solutions to avoid disappearance. They can disperse to another, more favorable, environment (Gienapp and Brommer 2014); they can modify their environment to correspond to specific needs (**REF**); 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 is a long-term solution, 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 it's 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 individuals in the population 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 an 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 behavioral 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 theses complex models [REFs]. Again, using long-term datasets brings a lot of expectation to address such limitations (Teplitsky et al. 2014).

### **Individual variation in their plasticity**

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 to estimate 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 individuals. 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.

## **Species and study**

Since 1962, a wild population of Yellow-Bellied Marmots (*Marmota flaviventer*) 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.

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 matriline 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. 1; 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 (Birot, Blumstein & Martin, Manuscript in progress, Fig 2a). 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

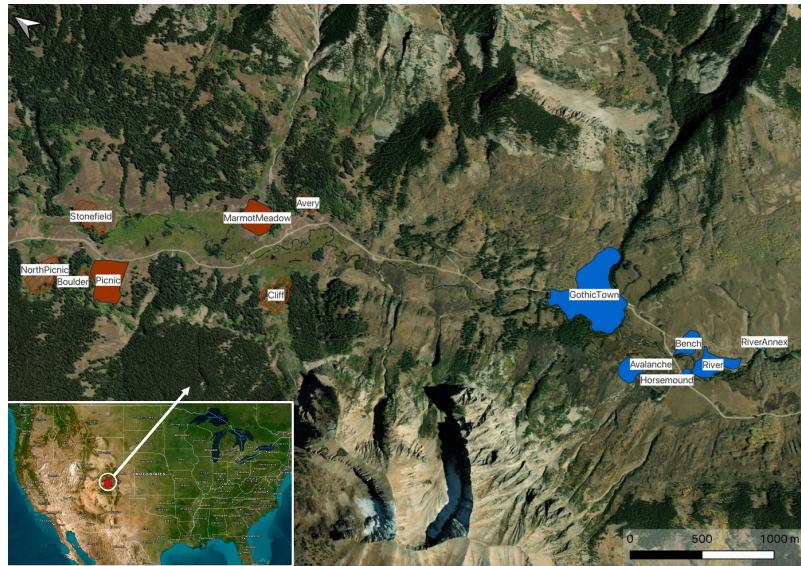


Figure 1: Red colonies represent the “up” valley, blue ones represent the “down” valleys. Plain background polygons represent the seven main colonies. The map was created with QGIS software (QGIS Development Team 2024) and the base map comes from ESRI (“GIS Mapping Software, Location Intelligence & Spatial Analytics | Esri” n.d.).

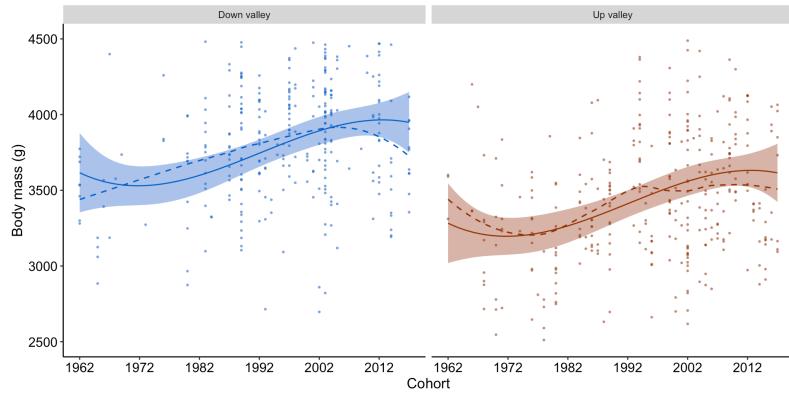
change in body mass over time using body mass from 199 adult females between 1965 and 2022 (657 observations). Our results show a large genetic basis of body mass with a heritability of 0.56, and an increase at the genetic level of ~400 g over the study period, indicating that roughly two third of the observed body mass increase is in fact due to genetic changes (Birot et al., Manuscript in progress, Figure 2b). With these results, it is reasonable to conclude that plasticity is not 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.

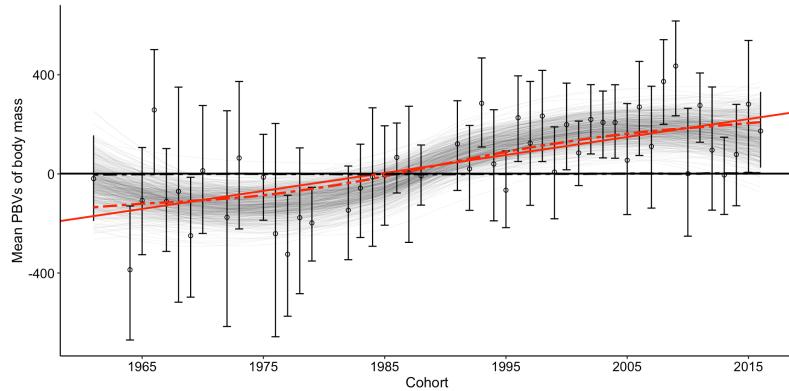
Considering the importance of body mass for yellow-bellied marmots, it is crucial to understand how this trait and this population is responding to climate change, both for conservation purposes and better comprehension of the links between phenotype and environment. There is a pressing need to explore 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

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 Towahawk 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



(a) Phenotypic change



(b) Genetic change

Figure 2: 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.

pair of numbered ear tag, and with a nontoxic black Nyzanol dye fur mark for distant identification during behavioral 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.

Parental links between individuals are known for most individuals in the population (4,652 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).

Behavioral 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).

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 was used to extract each individual's body mass on August 15 each year (Jebb et al. 2021; details in Ozgul et al. 2010).

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 micro-evolution meaning that we need to rethink the evolutionary scenario explaining this phenotypic change Figure 3.

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 studied 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 studied the structure and cause of this phenotypic change, we need to understand its consequences. I will investigate potential behavioral changes, and the balance between body condition and experience in individual behavior. Understanding the link between these factors is crucial to predict potential impacts on potential dynamics in the future.

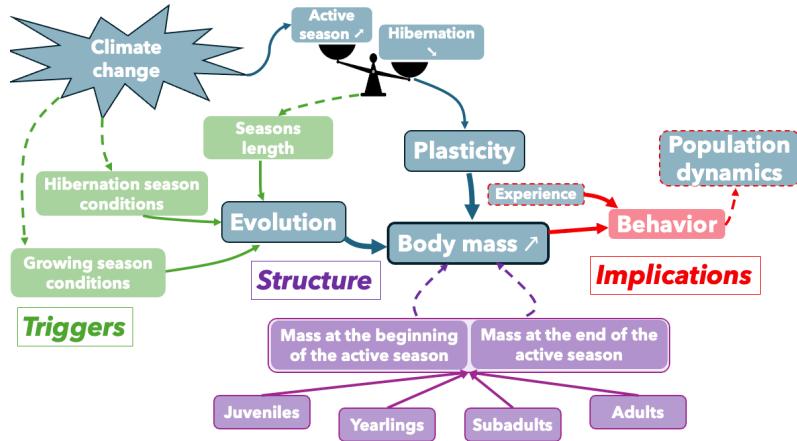


Figure 3: Research objectives illustrative framework.

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

The first thing needed, is to analyse 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 "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 juvenile 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 analyse 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 4). 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 2), 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 4).

Therefore, I will analyse 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.

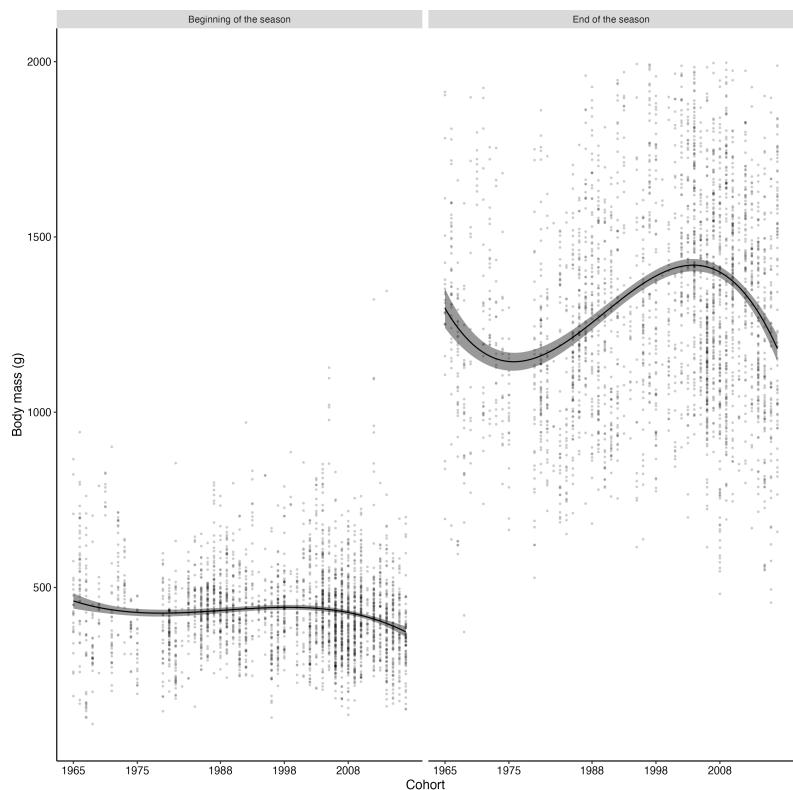


Figure 4: Body mass trend over time cohort for females juveniles compared between the beginning (birth weight) and end of their first active season (mass on August 15th).

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

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)

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

And before emergence (Equation 2). These models will allow me to estimate the genetic value of the body mass over the 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 exists 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 individuals, an absence of  $I * E$  (i.e., each individual's phenotypic response will be the same, Figure 5 a) should show and absence of among-individual variance in the residual variance ( $V_{V_e} = 0$ ) as each individual will exhibit the same range of phenotypic values (Fig. 5 c), so .

However, if there's individual variation in their plastic response ( $I * E$ ) for the focal phenotypic trait (Figure 5 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 5 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 6 a & b). Finding  $V_{V_e} > 0$  would thus suggest that investigating  $I * E$  and looking for the enknown 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 6 c). In such a scenario, we would also have significant variance in the residual variance even if there is no actual effects

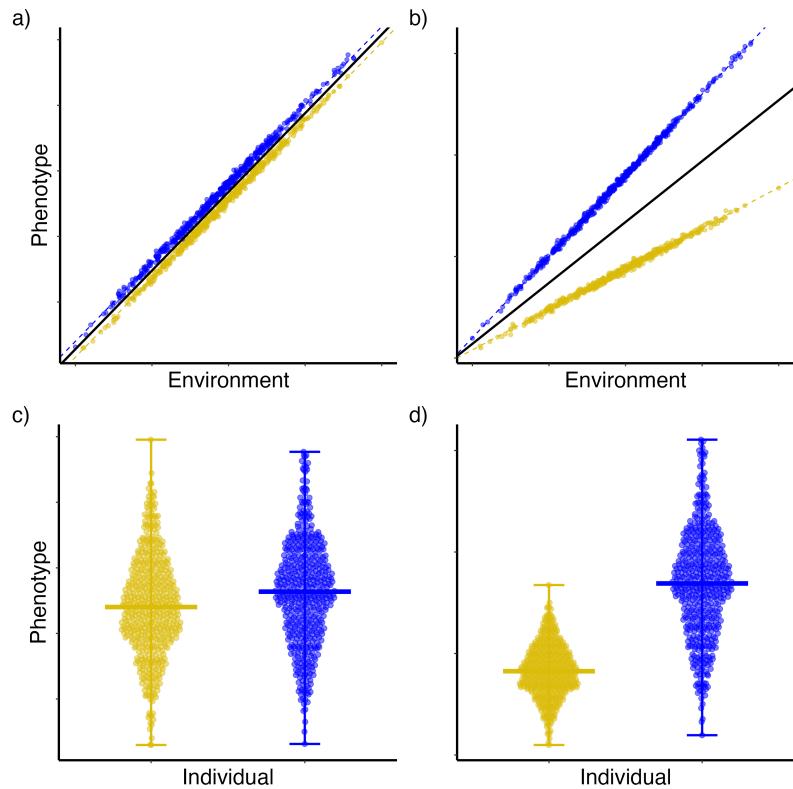


Figure 5: Reaction norms (a,b) and phenotypic variance (c,d) for two individuals (blue and yellow) for a trait without (a,c) and with (b,d) individual variations in plasticity. In the absence of  $I^*E$ , both individual express the same range of phenotypic values. However, with  $I^*E$ , individuals express different range of values.

(Figure 6 d). However, adding the environment as a fixed effect in the model should remove this bias.

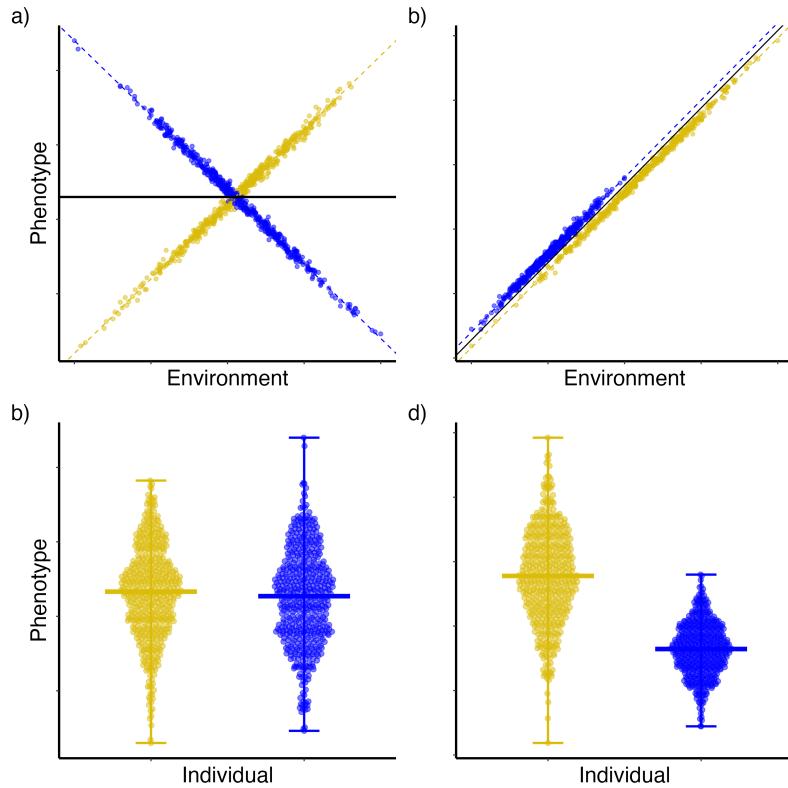


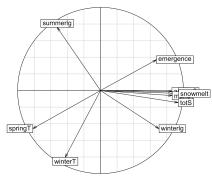
Figure 6: Reaction norms for two individuals (blue and yellow) for a trait a) with individuals expressing exact opposite plastic responses. We can see that b) they express the same range despite the  $I * E$ . Another case, c) without  $I * E$  (i.e., same slope between individuals) but in an unbalanced design, d) We would have different range of expressed phenotype

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 (Kris-

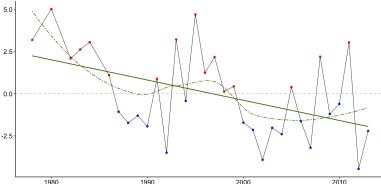
tensen et al. 2016) which allows to fit DHGLMs using a frequentist approach which is much faster especially in a simulation setup but it relies on a different coding language (mix of R and C). Then I will then apply this method on our Yellow-Bellied Marmots population to illustrate it with a real condition 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 7).



(a) PCA correlation circle



(b) Temporal variation

Figure 7: 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 years from 1975 to 2013, we can explore the temporal tendency of climatic conditions at study site (Birot 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 8). Hence, we face some sort of paradoxe, 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 for-

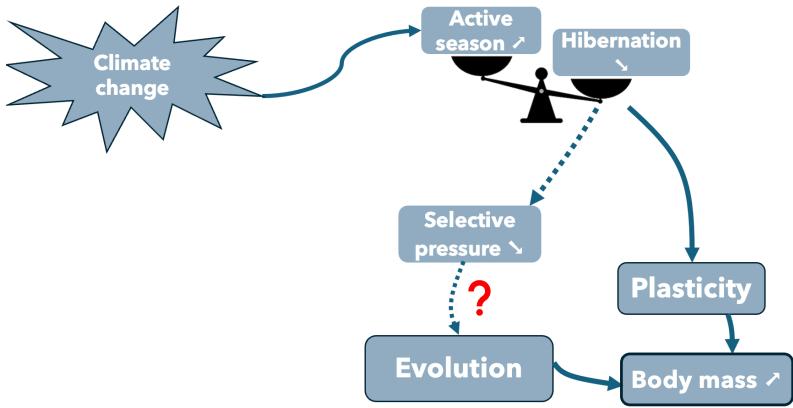


Figure 8: Evolutive paradoxe behind body mass increase.

age. But, this paradoxe justify further research to identify the selective pressures driving the observed body mass evolution.

The first step is gonna 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.

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).

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

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' behavior (e.g., bigger individuals would be expected to be bolder).

But we also expect that behavior 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 9).

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 behavior, with older individuals more careful than juveniles, as already suggested by Jebb et al. (2021).

We have repeated observations for a lot of individual 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 personal traits such as boldness (Réale et al. 2007) and estimate its repeatability (using mixed models) and heritability (using animal models). Then I will use these data to test the effect of body mass.

$$\text{Fixed} = \text{Body mass} + \text{Age} + \text{Cohort}$$

*Boldness* ~

$$\text{Random} = \text{Animal} + \text{UID} + \text{Measurement year}$$

(4)

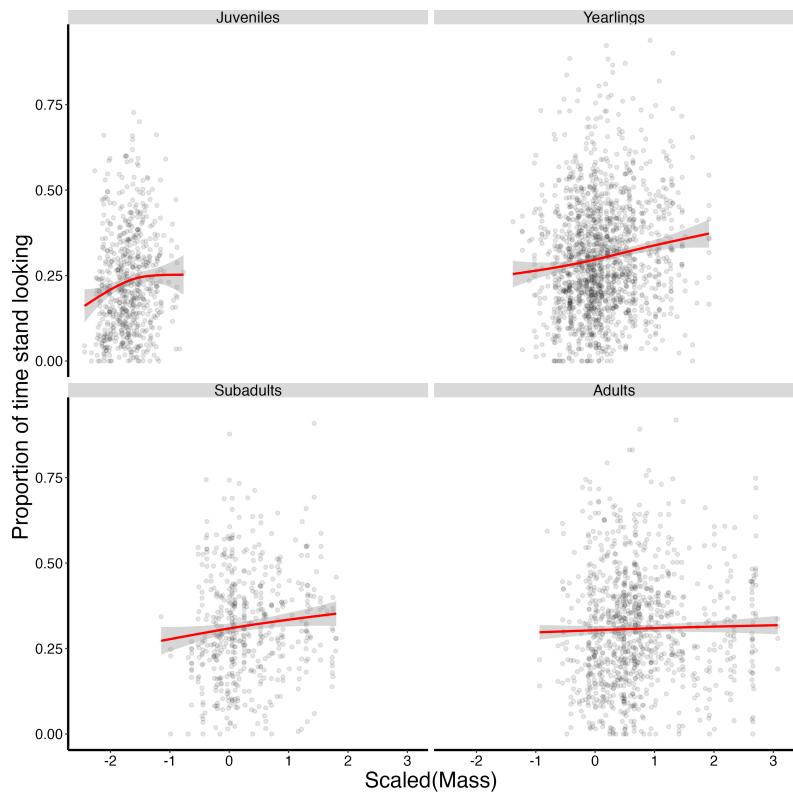


Figure 9: Proportion of time spent stand looking (within two-minute focal observations) as a function of scaled mass on August 15th across age classes: Juveniles (0-1 year), Yearlings (1-2 years), Subadults (2-3 years), and Adults (3+ years). Red lines represent local regressions, and points represent raw data.

I will test if body mass, and age impact behavior, and if the impact of body mass on behavior is different depending on the individual's age (Equation 4).

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 behavior (Réale et al. 2007; Wolf and Weissing 2012) can impact population dynamics. It is therefore crucial to study the relation between body mass, behavior 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 subststantial 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), developping 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 balance between body condition and life experience as predictors of individual behavior 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 producind 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 you 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 conditon 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 unpredicatbility, 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 offpsring phenotype. The costs on immeidate 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 to the next breeding season. With environment becoming less and less pre-dictible, 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 favored by selection (Cohen 1966; Eenum and Fleming 2004).

Using our environmental records at RMBL, I will define each years 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 is of [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 dependent, 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 (Eenum 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 loses 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 (**REF**). If a subpopulation finds itself isolated from the rest of the network, lack of genetic diversity putting it at risk of extinction (**REF**).

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 offers 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 analysis. Initial findings (e.g., non-random structural patterns and hierarchical order in island selection for emigration, independant from geographic distance) provides encouraging insight about migratory behavior within metapopulation.

Focus on understanding the migration dynamics and identifying critical patches in metapopulation can offer insight for policymakers. We hope to develop new methodes 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 developps 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 you say?*<sup>1</sup> 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

<sup>1</sup> AB Too much?

### 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; Trends in Evolutionary Biology*
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: *Trends in Ecology and Evolution; Proc. R. Soc. B.*
5. From Mass to Manner: How Body Mass and Age Shape Behavior in Yellow-Bellied Marmots.<sup>2</sup> A Birot, D Blumstein and JGA Martin. Targeted journal: *Proc. R. Soc. B.; Oikos*

<sup>2</sup> AB - AI suggestion

### 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: *Functionnal ecology; Journal of Animal Ecology*

# Timeline

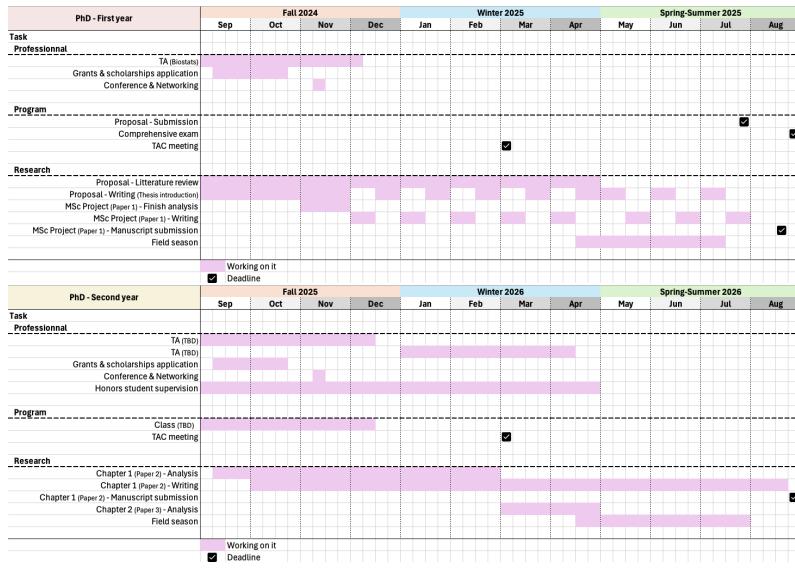


Figure 10: Proposed timeline for the first and second year.

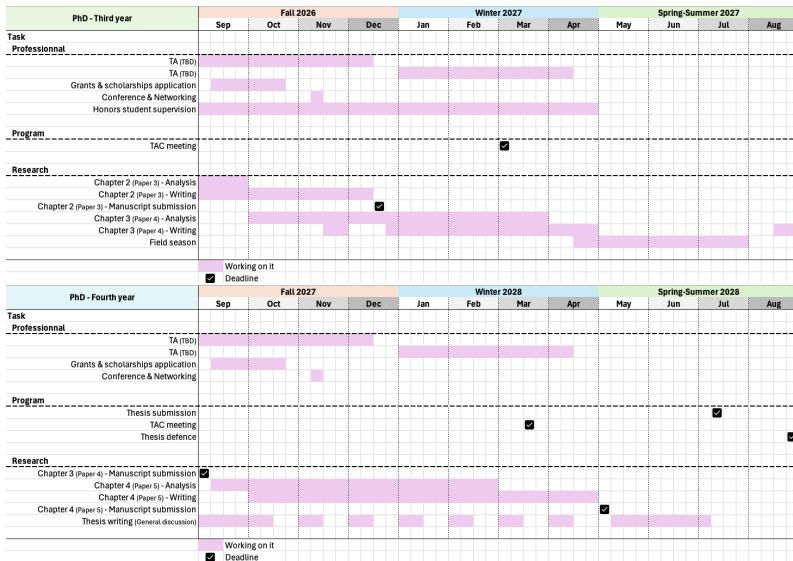


Figure 11: Proposed timeline for the third and fourth year.

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