Coping with climate change.

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

Comprehensive exam proposal

by

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Introduction

Climate change

The impacts of climate change on natural environments are well-documented and can, obviously, no longer be ignored (Intergovernmental Panel On Climate Change (Ipcc) 2023). Broadly speaking, climate change is melting ice caps, rising sea levels, increasing temperatures, more frequent extreme weather events, and greater environmental variability and unpredeactability.

Main characteristics of this global change, usually documented, includes:

- **Raising T°**: Explain + study case (!!!)

- **Changing season lengths**: Explain + study case (try to find something at RMBL !!!)

- **Environmental variability and unpredictibility**: Explain + study case (!!!)

- **More frequent and severe droughts**: Explain + study case (!!!)

- **Incresing frequency and severity of extreme weather events**: Explain + study case (!!!)

Climate change do impact human society. This impact is, for example, well represented in Ottawa, looking at the temperature, snowing, raining trends over the last century, we have some pretty disturbing numbers (Walsh and Patterson 2022), and future projections are not much more reassuring (Zhai et al. 2019). An example of concrete consequences of these changes in Ottawa is the management of the Rideau canal ice skating rink. As you probably know if you live here, in later years the oppening of the world's longest ice staking risk has been more and more uncertain, and its future is unfortunately but, fatally, questionable.

But most of all, climate change seriously impacts the vast majority of Earth's ecosystems, as shown by countless studies [Intergovernmental Panel On Climate Change (Ipcc) (2023); !!! *Study cases*]. It is crucial to improve our comprehension of how natural population react to this rapid and unpredictable changes in order to conduct efficient conservation policies.

Body mass as a Life-History Traits (LHT)

Life history traits (LHT) are phenotypic characteristics that impact directly an individual's survival and reproduction representing its selective value, or "**fitness**" (Roff 1992). The concept of life history theory relies on the fact that organisms have limited ressources and must allocate them strategically between competing funtions such as growth, maintenance, and reproduction (Roff 1992, !!!). Various traits can be considered as LHT, as they represent the outcome of this resources allocation process. Among various LHTs, body mass plays a crucial role in many species. Individuals with greater body mass typically have greater energetic resources, making them more resilient to environmental pressures by giving them a greater capacity to buffer poor years in terms of resources (!!!). Additionally, individuals with greater energy reserves have a better capacity to reproduce and are often more attractive to potential mates, leading to higher reproductive sucess, in this context, body mass is considered to be an "honest signal" of the individual capacity to accumalte resources and its quality as a reproducer (!!!). Therefore body mass can be considered a key LHT that directly influnces both survival and reproduction in many species.

However, as said before, energy quantity are limited and cannot be invested only in body mass. Moreover, a too large body mass can become a handicap (Jebb et al. 2021), and even though some handicaps has been theorized to be an asset in sexual selection (Zahavi 1997), beyond a certain threshold, individual with a too large body mass will be counter-selected against smaller ones.

Hence, as predicted in Life History Theory, trade-off must be maid between available energy and individual's performances to find the optimal body mass.

Link with hibernation

The importance of body mass as a LHT is particularly true for a specific group of species: **Hibernating species**. To survive unfavorable season (winter) some species disperse to milder environment, other cope with it and find ways to survive through. Some species survive through unfavorable seasons by entering a specific state of torpor, called "hibernation", where individuals lower their metabolism to the survival minimum required level. More specifically, "Fat-storing" hibernators (in opposition to "Food-storing hibernators") will sustain on their energetic ressources stocked in their white adipose tissue through the winter, then emerge at the start of the favourable season (Spring/Summer) (Carey et al. 2003; Geiser 2013; Nedergaard and Cannon 1990). A commonly prerequired adaptation for that kind of behaviour is therefore the capacity to stock important quantities of reserve (i.e., large body mass) in order to have enough energy to survive without foraging for a full season. Furthermore, this energy gathering must be done in a short amont of time, hibernating species are usually active only for a small part of the year, during which they must forage as efficiently as possible to gain enough mass to survive through next hibernating season, some fat-storing hibernators nearly double their weight during the active season (Armitage 2014; Carey et al. 2003). Hence, not only a prerequired adaptation is an important body mass, but also a sufficiently efficient metabolism to gain weight quickly, which 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, which means that before entering into hibernation, individuals much reach a threshold 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' biodemography.

Meanwhile, Climate change is expected to have significant impact on such LHT. It has been theorized that change 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)

Expected effect of global warming on body mass

As reminded earlier, one of the most significant consequences of climate change is an increase in global temperature (which is why climate change is also commonly reffered to as *global warming*, although this term is often used in climate sceptics rethoric during episodes of intense cold and violent blizzards[1]).

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[1]"[...] 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.

This average temperature increase is suspected to influence phenotypic traits such as body mass or size. However, the direction of the response remains uncertain. Some authors argue that a shrinking body size could be one the universal climate change response (Daufresne et al. 2009). This hypothesis follows Bergmann's rules, which state that smaller body size should be favoured in warmer environment as it raises the surface to volume ratio, thus facilitating heat dissipation (Bergmann, C 1847). Thus, in a warmer environment caused by global warming, a universal evolutionary response could indeed be a shrinking body size to cope with that.

However, as noted by Gardner et al. (2011), a lack of large-scale comparative studies prevent us to demonstrate that this response could be universal, also in 2022 IPCC report state that "Evidence is weak for a consistent reduction in body size across taxonomic groups in terrestrial animals" (Intergovernmental Panel On Climate Change (Ipcc) 2023; Siepielski et al. 2019).

Moreover, several studies at higher latitude 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). At higher latitudes and altitude, climate change is synonym of milder conditions, so individuals have access to a large food supply for a longer time and face less hard conditions during the less favorable season which overall is less energetically demanding. Hence these new, milder, conditions allows individuals to become larger.

Quantitative Genetics (QG) and Animal Models

As we have discussed, climate change is expected to cause long-term environmental changes. Thus, natural population will need to adapt to these new conditions in order to persist. As mentioned earlier these adaptations can involve shift in geographical ranges, phenology, or phenotype (Daufresne et al. 2009; Durant et al. 2007; Gardner et al. 2011; Visser and Both 2005). Therefore, we expect natural population to **evolve**, allowing them to be better suited to new environmental conditions (Darwin 1859).

However, estimating evolutionary signal in natural conditions can be complicated, and an observed phenotypic change is not necessarily due to evolution (i.e., phenotypic plasticity). Fortunately, quantitative genetic provides us a robust and well-established method to adress this by decomposing the total phenotypic variance (V_P) into it's genetic (V_A) and environmental (V_{PE}) components: $V_P = V_A + V_{PE}$ (Lynch and Walsh 1998; Wilson et al. 2010).

A well-known statistical method to compute this from observed phenotype variation is the **Animal Models** (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 (i.e., a "quantitative trait," Kruuk et al. 2014).

An Animal model is a specific kind of mixed model with individual identity as a non-independant random effect, linked to a relatedness matrix between each individual, 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 parameters estimation directly from phenotypic data. Only parental links between individuals need to be known, making this method 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 could be adressed with 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-known challenge when studying evolution in natural context, is to consider that most traits are genetically correlated, causing **traits coevolution** (Gould and Lewontin 1979; Roff 1992).

Indeed a trait cannot evolve independently without impacting other traits. This conception will narrow the range of possibility and reachable outcomes in the adaptive landscape (Arnold et al. 2001; Teplitsky et al. 2014).

When studying the evolution of a specific trait (especially a trait having important phenotypic consequences), failling to account for its genetic correlations with other traits is an oversimplification (Teplitsky et al. 2014).

This misconception can bias not only our understanding of the causes and consequences of phenotypic change, but also when estimates of a trait's evolutionary potential [Teplitsky et al. (2014); !!!].

To trully understand the evolutionary potential of a trait, we need to acount for its non-independance with other gentically correlated traits (Teplitsky et al. 2014).

In this context, we need to consider for the fact that selection will generally act on multiple traits as phenotype is the result of a combination of traits (Phillips and Arnold 1989).

A continuation of this reasoning is the **Pace Of Life Syndrome** (POLS) and it's extension (Dammhahn et al. 2018; Réale et al. 2010) suggesting that life-history strategy, physiological and behavioural traits coevolve in response to the environment.

Hence, if climate change induce phenotypic changes in LHT, it is to expect that other key physiological or behavioural trait will coevolve with it; for example, it has been observed that certain behvioural types will be consistently associated with certain Life-History strategies (Biro and Stamps 2008; Stamps 2007; Wolf et al. 2007).

In that case, the consequences of a phenotypic change in a LHT would be even greater, and again, need to be considered and studied efficiently.

A robust method to study that is **Multivariate Animal model** (i.e., an Animal model with multiple phenotypic trait as dependant variables) which allows us to estimate the genetic covariance between multiple traits (Teplitsky et al. 2014).

However such models are heavily data-consuming, and the main reason significant results with such models are quite rare today is that almost no study have enough data to have the statistical power required for theses complex models (Teplitsky et al. 2014).

Again, using long-term datasets brings a lot of expectation to adress such limitations.

Phenotypic plasticity vs microevolution

Phenotype are expected to be the best fit for specific environment as a result of a long evolution by natural selection (i.e., individuals best adapted to their enviromnent will have better survival and reproductive success, Darwin 1859). However, when this environment changes, as expected in today's context of climate change, individuals have two solution to avoid disapearance: **disperse** to a more favorable environment, or **adapt** to their new conditions via phenotypic change (Gienapp and Brommer 2014). For adaptation, two further possibilities exist: **phenotypic plasticity**, defined as a change in phenotype expressed by a given genotype (!!! *probably Nussey or maybe Pigliucci, I think there's a book from the late 90' or early 00'*), which allows for a rapide response within an individual lifetime, is highly flexible and does not involve any changes at the genetic level; and **microevolution**, defined as a change in alleles frequencies in a population over time (!!! *needed?*). When an individual with a better-fitted phenotype for its new environment appears, it would have a better survival and more reproductive success. If this advantage relies on a heritable genetic difference (i.e., transmitted to its descendants, Lynch and Walsh (1998)) the new genotype is going to rapidly increase in proportion in the population, ultimately replacing the old one. Thus, this mecanisme can be slow but is a long-term solution when the ecological change is persistent. However if the change is transient, plasticity is a useful mechanism. 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, presenting costs and limits (DeWitt et al. 1998), to a transient change. 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). The expected optimal answer to a long-term environmental change, as caused by climate change, is evolution through natural selection.

Phenotypic pasticity and microevolution are thus not expected to be mutually exclusive. This is particularly evident in highly plastic traits such as body mass which can vary significantly up and down throughout an individual's life in response to among- and within-year changes in environmental conditions but can also change via microevolution at the population level over the same time period.

Nevertheless, as the consequences of theses mechanism can be highly different on the long term (evolution being more permanent than plasticity), quantifying the extent to which each of these mechanisms contributes to the observed change over a long study period remains a chalenging but fundamental task to understand the adaption and evolution of species. This is even more true today, as populations faces the numerous challenge brought by global climate change.

So Evolution and plasticity are not mutually exclusive, and even more, evolution can even have effect on plasticity itself.

Transition with $I * E$ with the reaction norm framework (Nussey et al. 2007).

Individual variation in their plasticity

Plasticity is usually studied using ***Reaction Norm framework*** (!!! *look at DeWitt & Scheiner, 2004; Schlichting & Pigliucci, 1998; West-Eberhard, 2003 from Thibaut's proposal intro*), so by studying the value of a phenotypic trait (e.g., body masse, size) in response to an environmental proxy (e.g., temperature, precipitation). A plastic response correspond to a different phenotypic value associated to a different environment, so by a slope different from 0 for the reaction norm

(Nussey et al. 2007). A reaction norm has two parameters: **Elevation** (or "Intercept" in statistical terms), which is the expected phenotypic value in the average environment; and the **Slope** (so "Slope" in statistical terms) corresponding to the linear regression of the phenotype over the environmental gradient, so to estimate the phenotypic response to the environment (i.e., phenotypi plasticity) . So that's how phenotypic plasticity is usually studied. But, as emphasized by Nussey et al. (2007), a lot of information is loss if we just study that at the population level (i.e., by just doing a fixed linear model of the phenotype over the environment). First using a linear mixed model is crucial to estimate different elevations for each individual as comonly there's multiple observation per individual, thus not taking that into acount is violation of the independance application condition (*cf every basic stat book*). So doing that allow us to estimate individual variance in the phenotype in the average environment and take into account the fact that all individual in the population doesn't have the same base phenotype. However, that kind of model doesn't allow to estimate individual-level difference in their plastic response to the environment, which can be really important biologically and so must be accounted for. Nussey et al. (2007) proposed a framework to estimate that, which is now fairly accepted and used: ***Random Regression***. Let's go back to the Linear Mixed Models (LMMs), the "classic" way 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 in this compilation, the slope is the same for each individuals; now, if we add a random term also on the slope, not only the model estimate one intercept per individual, but also one slope (so basically, 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 **I * E**.

Once we've estimated this between individual variance in plasticity, we can you quantitative genetic methods (i.e., from Animal models, as explained before, but using Random Regression Animal Model: "RRAM", Nussey et al. (2007)) to decompose this variance into it's genetic and permanent environment part to estimate the genetic variation in plasticity, which is called **G * E**. From that we can estimate the heritable variation in reaction norm's slope and have an idea of the evolutionary potential of phenotypic plasticity in itself.

So we have a really good method to do all that, however, as underlyned by Ramakers et al. (2023), if the environmental proxy used for the reaction norm isn't good enough, a lot of this I * E is missed (what they called a "hidden I * E"). Furthermore, it's often impossible to identify the real driver of plasticity in natural conditions (Which is expected as natural environments are exceptionally complex systems, and individuals generally doesn't have only one environmental variable to deal with…), the real driver can be unknown, unmeasurable are a combination of a lot of different variables (Ramakers et al. 2023). In response to that, the authors proposed a new method, using the Environment Specific Mean phenotype (ESM). Although they've shown this method is indeed efficient, they emphasized that we still need a really good knowledge of the studied system, and really specific conditions to be more efficient that the "regular" method. Hence, although it's a progress, more work is needed to deal with this I * E detection in natural environment problem.

The good news is that we have a really promising, fairly new statistical method that could be applied to that: the "Double Hierarchical Generalized Linear Model" (DHGLM, !!! *find citation + maybe explain a little the method*) […] from this method we can estimate the *variance in the residual variance* (i.e., "V_{V_e}" by estimating the residual variance attributable to each individual). Knowing what these models does (*When I'll write it*), we're confident that it can be applied to developp a more powerfull method to detect individual variation in plasticity (I * E) in natural systems. Indeed, a V_{V_e} significantly greater than 0 should indicate that there is some I * E in the system and would

justify investigation by testing different environmental proxies. In contrast, except in very specific conditons, almost impossible in natural conditions (i.e., **perfect** contrary effect), a V_{V_e} equal to 0 indicate that there's no individual variation in plasticity in the studied system. From this method we should be a way to free ourselves from the problems of bad proxies. And obviously, as for the random regreession with the RRAM, we can adapt this method we quantitative genetics to also detect $G * E$ if $I * E$ is detected.

This new method is thus very promising, however, as most new statistical methods, it often poorly understood/used. Hence, a general framework (supervised by someone with good statistical knowledge, i.e., Julien) including the application on how DHGLM could (should) be used to detect I * E would be really helpful for the comunity (especially with the rising need to study efficiently phenotypic plasticity and it's evolution, in natural condition with climate change).

Link with body mass, individual can vary in their growing speed <=> Reaction norm/Plasticity change over time => Evolution directly on the plasticity <=> individual answer to the condition change would be increase their response (i.e., body mass increase within the active season). It would make sense with bet-hedging framework for example

Bet-hedging

(Starrfelt and Kokko 2012)

Bet on the best fitness for the long term (even if it can mean lower a bit your immediate fitness) to cope with an unpredictable environment. With climate change, environment are less predictable than ever (maybe even more in alpine habitat? !!! *fact check + ref about envmt predictability + focus on alpine habitats*). Thus bet-hedging, for example increase you body size to "buffer" is not a crazy strategy, but can be risky in the future => potential phenological mismatch (i.e., […], Stenseth and Mysterud (2002); Visser and Both (2005)), bet-hedging is a bet, so you're not sure to win in the end, and it can end in maladaption…

Species and study site

Since 1962, a wild population of Yellow-Bellied Marmots (*Marmota flaviventris*, "YBM") is followed yearly, first supervised by Kenneth Armitage, and today by Julien Martin and Daniel Blumstein, at the Rocky Moutain Biological Laboratory (RMBL) in Gothic, Colorado, USA, this is the second longest-term study of a natural mammal population in the world. YBM is a ground-dwelling sciurid (rodentia, sciurideae) inhabiting alpine habitats in western North America with a life cycle divided between an "active season" representing approximately a third of the year (from May to September) where individuals must forage to reach a threshold body mass in order to survive hibernation for the remainder of the time (Armitage 2014). Individuals experience high seasonal flutuation in body mass, with a critical threshold to be reached before the onset of hibernation in order to 1) survive through the next active season and 2) have sufficient energy left for hibernation (which occurs in the first weeks of the active season, Armitage 1965, 2014). Consequently, body mass is consider being a critical LHT for the marmots. YBM lives in colonies composed usually by one or more matriline with on adult males, multiple adult females and their offspring (Armitage 2014). Our population is composed of seven main colonies divided between an "up" and a "down valley" with a elevation difference arround 300m ("up" = 3,000m; "down" = 2,700m) implying some difference in weather (Armitage 2014; e.g., delayed snowmel and vegetation growth onset, temperature difference up to 2

°C, Blumstein et al. 2004) and so delayed emergence up to two weeks in the up-valley (Blumstein 2009; Monclús et al. 2014). This two differents condition offers an amazing opportunity to test the impact on environment on several factors while working in natural conditions.

This hibernation (life) cycle is highly environemntally dependant, with the onset and end of the active season believed to be mediated mostly by weather variable such as temperature and snow cover of the region (Armitage 2014). Thus, body mass is expected to be a keystone phenotypic trait for the marmots. It is therefore crucial to understand how this trait and this species responds to global warming, both for conservaion purposes and to elucidate links between phenotype and environment.

Body mass increase in Yellow-Bellied Marmots (YBM)

An important body mass increase has been observed in this population over the past half-century (estimated arround 600 g for the adult females). Precedent studies attributed this major change mostly to phenotypic plasticity (Ozgul et al. 2010). This hypothese made in fact a lot of sense, with climate change active season is getting longer (milder condition, higher temperature, less snow, shorter winter, etc.), hence marmots have more time to forage, gain weight, and the hibernation period is getting shorter so less time for the individuals to lose mass, at the end of the day, we have heavier individuals, makes sense! However, using animal models to properly assess the genetic attributable part of this change, estimating explicitely the body mass' evolutionary signal for the adult females over the time cohort (i.e., year of birth) during the study period, we found an increase, at the genetic scale, estimated arround 400 g, with a heritability of 56% (Birot & Martin, Manuscript in progress, Figure 1). So, in fact, arround two third of the body mass increase seems to be due to evolution, not just plasticity. Furthermore, although the lengthening active season is indeed a good potential explanation for the body mass increase through phenotypic plasticity, it doesn't match with the observed evolutionary signal. If the main selective pressure on body mass is survival through hibernation (i.e., heavier individuals having more chance to survive through winter as they have more ressources), then the expected evolutionary response (i.e., average body mass increase) is occuring when the pressure is decreasing, which doesn't makes sense!
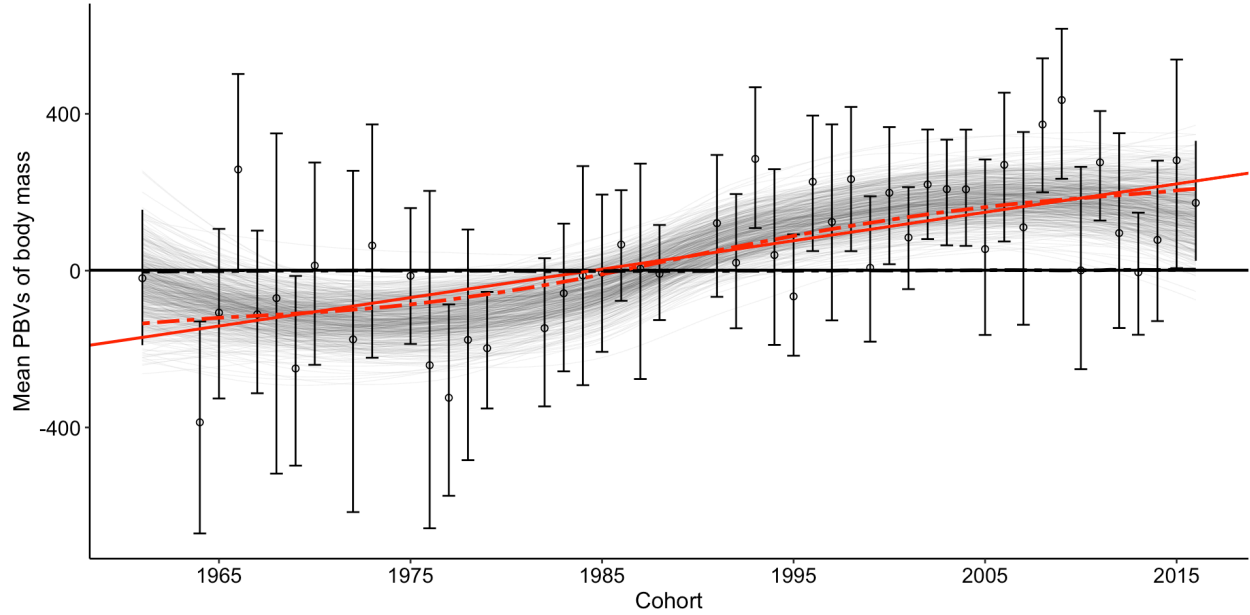
Figure 1: Mean cohort's predicted breeding values trend over 5,000 iterations (gray lines). The median trends of the observations (red line) and under the null scenario (drift alone, black line) are represented, according to linear (solid line) or generalized additive models (two dashed lines). Points and error bars represent the median and 95% credibility interval of the posterior mean PBV for each cohort.

Research objectives & Methodology

Since this major phenotypic shift for the YBM in the last half-century has been miss considered, knowing that there is in fact a strong evolutionary signal, we need to reconsider the evolutionary scenario behind this body mass increase.

I will explore which environmental factors could have triggered this shift, but also the mechanism behind this increase and finally the potential implication for the population's future.

Data from the long-term study

Each year during the active season (May - September), most individuals in the population are regularly trapped. At each capture, individuals are measured, weight, DNA samples are taken. Meanwhile, behavioral observations and experiments are conducted all along the season.

Data are stored in the R package "ybamaRmot" (Martin 2024)

Analysis will be perofrmed on R (R Core Team 2024); Animal models will be performed using R package "MCMCglmm" (Hadfield 2010); DHGLM and other bayesian analysis (non using MCMCglmm) will be done with "brms" (Bürkner 2021). Figures will be made with "ggplot2" (Wickham 2016)

Morphological data

Population pedigree for most of the individuals (4,652 individuals to this date)

Morphological data

Body mass measured

Chapter 1 - Mechanisms

Marmot's Biology: What mechanisms are behind the body mass increase?

As emphasized in the introduction, we know that the body mass has increased in the last half-century, however we still know very few about it. And for starter, we don't know yet what has changed in the marmots in the last decades: do they have a bigger constitution (i.e., are they born bigger, their Intercept in statistical term), or does their growing capacity has increased through time (in statistical term again, this would correspond to their slope)?

I * A and **G * A** A: AGE => Reaction norm over individual lifetime rather than Environmental gradient

Growth? Baseline? Both?

Double random (Intercept, Slope)

Body mass in juvenile was predicted to stay stable as it favour a higher running speed allowing juvenile to escape predators more efficiently during foraging (Jebb et al. 2021). This was one of the main argument to explain why YBM body mass was (before the 70s) stable in adults, the "invisible fraction" explained by Jebb et al. (2021).

However, by looking at Figure 2 we see that even if the body mass at birth (*a*)) is indeed stable, the mass at the end of the individuals first season however, shows a pattern found in Figure 1. Indeed, the body mass at the end of our juveniles' first foraging season has increased by 23% in 23 years (23 cohorts), meaning that between 1977 and 2000, each cohort was 1% heavier than the last one at the end of their first foraging season (*b*)). This could be a serious clue to explain the sudden body mass increase observed in adults arround the same period. We can hypothesized that a relax on the juvenile body mass constrained has occured. Now we must find which constraint has change during this specific period of time (see Section).

As the body mass was previously hypothesized to be stable as an anti-predator strategy, it seems logical to look for a change in predators populations or behaviour between the 1970s and the 2000s at our study site.
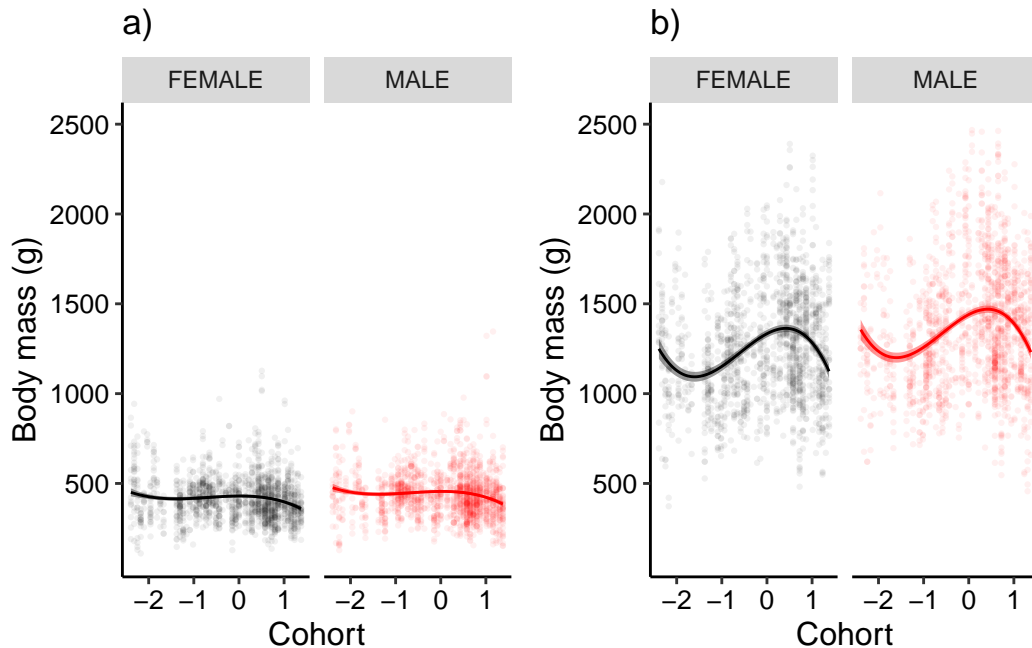
Figure 2: Body mass trend over time cohort for females (black) and males (red) juveniles compared between a) the beginning of the active season (birth weight) and b) the end of the season (mass on August 15th).

Chapter 2 - Methodology

*Methodology: I * E detection with double random mixed models*

(Nussey et al. 2007) –> double random

So we're doing something different –> examining the residuals of the model (if I * E, still a lot of residual variance ?)

**Look at this one: (Westneat et al. 2015)

DHGLM, brms, Julien's code

Vve (Variance dans la variance résiduel, estime la variance résiduel pour chaque individu et regarde la variance dans cette variance résiduelle, si I * E Vve > 0)

Attention aux modèle débalancés si pas d'effet fixes corrige pour les variations par effet fixes, puis test pour le I * E, si y'en a tu pexu chercher la variable environnemental pour lesquels on a de la variation dans la plasitcité (I * E)

Ned Dochtermann

Chapter 3 - Triggers

Marmot's Biology: Which environemntal factors have triggered the phenotypic shift?

E1 - E10 (T°, Precipitation, ...), Seasonal Gradient

Predators, Diet?

We have precise weather data from Billy Barr

Chapter 4 - Implications

Marmot's Biology: What could be the implications of that for the population's future?

POLS

Manuscript models Body Mass/active season with survival => Phenological mismatch?? (e.g., thermal stress)

Significance and impacts

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