Coping with climate change.

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

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Introduction

Climate change (C.C.)

- The importance of C.C. and its impact in the near future is no longer in doubt, *at the point where it's sad to have to remind people of them once again.*(Intergovernmental Panel On Climate Change (Ipcc) 2023)
- Broadly, C.C. is […] (Polar melting, etc.)
- Which even impact human society (e.g., winter in Ottawa isn't the same anymore: Rideau Canal ice skating future is in jeopardy, the number of days with under -20°C is expected to severly decrease in the near future, etc. (!!! + FACT CHECK everything!))
- Main/Precise impacts of C.C. in natural environments
  - **Raising T°**: Explain + study case (!!!)
  - **Changing season length**: Explain + study case (try to find something at RMBL !!!)
  - **Environmental predictibility**: Explain + study case (!!!)
  - **Drought events**: Explain + study case (!!!)
  - **Extreme weather events**: Explain + study case (!!!)
  - etc.

Ok, so, now, how does C.C. and these precise perturbations impacts concretely natural population? *Study cases* (!!!)

Body size as a Life-History Traits (LHT)

Life history trait (LHT)

Traits impacting directly survival and reproduction, so individual's fitness (Roff 1992)

Link with hibernation

Body mass for hibernating species is so a LHT as it's usually a determining factor for survival over hibernation and reproduction.

Body mass is a LHT as in many species it has direct impact on survival and reproduction (explain + !!!)

C.C. is expected to impact life history traits => **universal C.C. responses (!!! *look for an article explaining the principles of the universal responses to global warming*)**

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 as a rethoric by climate sceptics during cold winters and violent blizzards[1]). 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 C.C. response (Daufresne et al. 2009). This hypotheses follows Bergmann's rules, which state that smaller body size should be expected in warmer environment as it raises the surface to volume ratio, thus favoring heat dissipation (Bergmann, C 1847). 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. And indeed, several studies at higher latitude yield opposite results (i.e., increasing body mass, 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 to milter conditions. As a consequence, 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, allowing individuals to become larger.

, which can also been expected as C.C. is synonym to milder conditions in those latitudes. This change Allows individuals to forage more and thus gain mass.

Q.G. and animal models

Body mass and LHT shifts expected with climate change, **evolution** expected.

{To properly estimate the evolutionary signals of a phenotypic change, quantitative genetic gives us a method to decompose the total phenotypic variance (V_P) into it's genetic (V_A) and environmental (V_{PE}) part: $V_P = V_A + V_{PE}$.} Quantitative Genetics provides a well-established

[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!" Donald J. Trump, Jan 20, 2019.

method for estimating the genetic component of an observed phenotype variation: 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 with small effects (i.e., a "quantitative trait," Kruuk et al. 2014) by fitting a 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 link between the individual of a population, !!!). This method has the advantage of being relatively simple to employ, allowing genetic parameter 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 1996). 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 that kind of study is the lack of power, which could be adress with long-term studies. Such studies would improve our understanding of the relationship between animals and their environment and of the genotype-phenotype-environment relationship, especially in the context of global change.

(Charmantier et al. 2014)

LHT coevolution

Traits can't evolve alone Gould & Lewontin (1979)

Need to show that with multivariate animal model, but no one has enough power for the models (Teplitsky et al. 2014)

POLS

(Dammhahn et al. 2018)

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, 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, !!! *needed? something like Lynch & Walsh, for a definition of heritability sensu stricto*) 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. 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).*

I * E, G * E (individual variation in their plasticity)

Explaine what $I * E$ and $G * E$ is (both in biological and statistical way) (Nussey et al. 2007).

Link plasticity ~ $I * E$ Importance of the environmental proxies to detect slope variation in reaction norm (so $I * E$ and $G * E$) => Environment Specific Mean phenotype (ESM); Difficulty to find the good environmental proxy (Ramakers et al. 2023)

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

(!!! *Ref about bet-hedging*)

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., !!! *def + ref about what phenological mismatch is*), bet-hedging is a bet, so you're not sure to win in the end, and it can end in maladaption…

I * A and G * A

A: AGE => Reaction norm over individual lifetime rather than Environmental gradient

Species and study site

A wild Yellow-Bellied Marmot (*Marmota flaviventris*, "YBM") population in the Upper East River Valley, Colorado, USA, is the subject of one of the longest-term study in the world (1962 - today). 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 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). 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! Hence, knowing all that, we now need to reconsider the evolutionary scenario behind this major phenotypic change.

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.

Chapter 1 - Mechanisms

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

Growth? Baseline? Both?

Double random (Intercept, Slope)

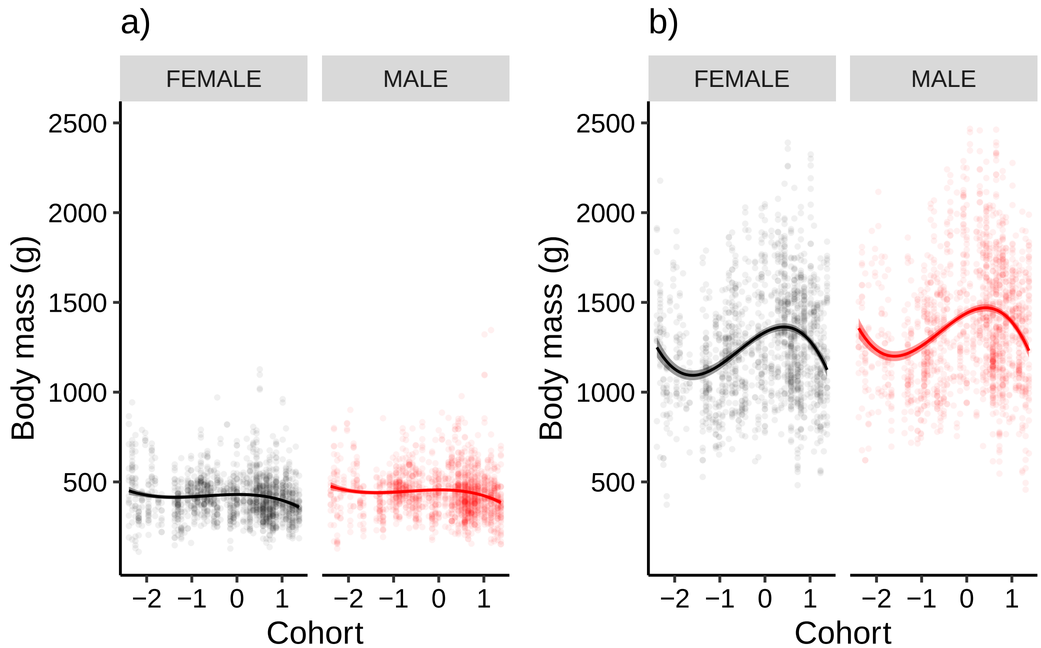

Figure 1: Body mass trend over time cohort for females (black) and males (red) juveniles compared between a) the beginning of the active season (birth weight) and b) the end of the season (mass on August 15th).

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 Dotchermann

Chapter 3 - Triggers

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

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

Predators, Diet?

Chapter 4 - Implications

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

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

Significance and impacts

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