

Coping with climate change.

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



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Comprehensive exam proposal

by

Augustin Birot (300444988)

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Committee members:

Julien Martin (Supervisor)

Vincent Careau (TAC member)

Roslyn Dakin (TAC member)

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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) 2022). Broadly speaking, climate change encompass melting ice caps, rising sea levels. More specifically, main characteristics of this global change, usually documented, includes: **Raising temperature; Changing season lengths; Environmental variability and unpredictability; More frequent and severe droughts; Increasing frequency and severity of extreme weather events** (Intergovernmental Panel On Climate Change (Ipcc) 2022).

Climate change do impact human society, this is, for example, well represented in the city of Ottawa, ON, Canada. Temperature, snowing and raining trends in the Canadian capital over the last century, reveals worrying figures (Walsh and Patterson 2022), and future projections are not much more reassuring (Zhai et al. 2019). A concrete consequences of these changes in Ottawa 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 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) 2022). These profound ecological changes are putting a large number of species at risk, and they must act accordingly to avoid extinction, either by dispersing or adapting (Gienapp and Brommer 2014). 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 resources and must allocate them strategically 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 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 success. In this context, body mass is considered to be an “honest signal” of an individual capacity to accumulate resources and its quality as a reproducer (!!). Therefore body mass can be considered a key LHT influencing directly 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 have been theorized to be an asset in sexual selection (Zahavi 1997), beyond a certain threshold, too large individuals will be counter-selected against smaller ones. Hence, as predicted in Life History Theory, trade-off must be made 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 (usually winter) some species disperse to milder environments, others cope with it and find ways to survive through (!!). A way found by some species to survive through is to enter a specific state of torpor, called “hibernation”.

This strategy consists of reducing the metabolism to a minimum survival level. More specifically, “Fat-storing” hibernators (in opposition to “Food-storing hibernators”) will sustain on their energetic resources, 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 required 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 sufficient energetic stocks to survive without foraging for a full season.

Furthermore, this energy gathering must be done in a short amount 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 must 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 referred to as *global warming*, although this term is often used in climate sceptics rhetoric during unusually intense episodes of cold¹).

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 should be a universal response to climate change (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 1847). Therefore, in a warmer environment, due to global warming, an adaptive response could indeed be a shrinking body size.

However, as noted by Gardner et al. (2011), a lack of large-scale comparative studies prevent us to demonstrate that this response is universal. In addition, 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).

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.

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.

Phenotypic plasticity vs microevolution

Evolution by natural selection was defined by Darwin (1859) as so: individuals that are best adapted to their environment will have better survival and reproductive success. This process result in a population composed mainly of individuals adapted to their environment. So, observed phenotype in natural populations is expected to be the best fit for a specific environment.

However, when this environment changes, as expected with climate change, individuals have two solution to avoid disappearance: **disperse** to a more favorable environment, or **adapt** to their new conditions through phenotypic changes (Gienapp and Brommer 2014).

To adapt, there are two further possibilities: **phenotypic plasticity**, defined as a change in phenotype expressed by a given genotype, which allows for a rapid 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 (!!!). 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.

Hence, adaptation through microevolution can be slow but is a long-term solution, better fitted for a persistent ecological change. 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 those expected with climate change, is evolution through natural selection.

Phenotypic plasticity and microevolution are 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 these mechanisms 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 challenging but fundamental task to understand the adaption and evolution of species.

Quantitative Genetics and Animal Models

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

However, estimating evolutionary signals in natural conditions can be complicated, and an observed phenotypic change is not necessarily due to evolution (i.e., phenotypic plasticity). Fortunately, quantitative genetics provides us a robust and well-established method to address this by decomposing the total phenotypic variance (V_P) into its 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 estimate these variance components from observed phenotypic data 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 (Kruuk et al. 2014; i.e., a "quantitative trait," Lynch and Walsh 1998). An Animal model is a specific kind of mixed model using 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 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-recognised challenge when studying evolution in natural context, is to consider the genetic correlation between several traits, causing **traits coevolution** (Gould and Lewontin 1979; Roff 1992). Indeed a trait cannot evolve independently without impacting other traits. This constraint narrows the range of possibility and reachable outcomes in the adaptive landscape (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 misconception 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); !!!]. To effectively study traits' evolution, it is essential to consider that selection generally acts on multiple traits simultaneously, as 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** (POLS) 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 induces LHT modifications, it is to expect that other key physiological or behavioural trait will coevolve with it. For example, it has been observed that certain behavioural types will be consistently associated with certain 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 LHTs are expected to have even 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 [!!!].

However such models are heavily data-consuming, and the main reason that significant results with such methods are quite rare today is that only a few studies have enough data to support the statistical power required for these complex models. Again, using long-term datasets brings a lot of expectation to address such limitations (Teplitsky et al. 2014).

Individual variation in their plasticity

As explained above, evolution and plasticity are not mutually exclusive, but even more so, plasticity itself can evolve (!!).

Plasticity is usually studied using **Reaction Norm framework** (!!), 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 corresponds to a different phenotypic value associated with a different environment. In this reasoning, 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 regression 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 lost 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 differences 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 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 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, 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 use quantitative genetic methods using Random Regression Animal Model: “RRAM” (Nussey et al. 2007) to decompose this variance into it’s 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 good enough (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. In response to that, Ramakers et al. (2023) proposed a new method, using Environment Specific Mean phenotype (ESM). 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 more efficient than classic the random regression method. Hence, although it’s a progress, 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 kind of mixed model estimating the distribution for both the mean and the residual variance (Lee and Nelder 2006). A DHGLM estimates the residual variance for each individual, then estimates the variance in this residual variance. In other words, DHGLM

estimates the *variance in the residual variance* hereafter referred to as V_{V_e} . This correspond to the variance in the proportion of residual variance attributable to each individual.

We are confident that DHGLM 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 indicate some disparities in the individual contributions to the residual variance. To put it differently, it shows that the range of phenotypic values expressed by each individuals is different, which can be interpreted as an individual variance in their plastic response, so $I * E$.

Although a non-zero variance 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 conditons, 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 regreession with the RRAM, we can use quantitative genetics to also detect $G * E$ if $I * E$ is detected by combining a DHGLM with an Animal model, giving a “Double Hierarchical Animal Model” (DHAM).

This is a very promising method, however, as most new statistical methods, it is often poorly understood/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 it's evolution, in natural condition in a context of climate change.

Bet-hedging

Bet-hedging strategy can be summerized as betting on the best fitness for the long term, even though it means lower a bit your immediate fitness, in order to cope with an unpredictable environment (Starrfelt and Kokko 2012). With climate change, environment are less predictable than ever, therefore, bet-hedging is expected to be a relevant adaptive strategy in such context. Let's take body mass increase as an example again.

On the one hand, an increase body mass, over a certain threshold, can become a handicap for certain species. For example, heavier individuals can be more subject to heat stress; they can be more subject to predation as heavier individuals are slower and more palatable.

On the other hand, an increased body mass, being synonyme of a more important energy stock, allow individuals to “buffer” in a poor year in term of resources. This feature can be very important for species living highly constrained environment, such as high altitude (Inouye and Wielgolaski 2003). Therefore, increase your body mass to “buffer” years with less resources can be expected, especially for hibernating species in alpine environment.

Furthermore, larger body mass can have lower temporal fitness variation as the fitness cost of a poor year would be buffer. Indeed, by increasing the global average body mass in the population, we can expect less phenotypic variation in the population due to environmental change, which should, all else being equal, favoured by selection (Cohen 1966). This correspond to a “Conservative bet-hedging strategy” (Childs et al. 2010).

However, reducing the phenotypic variance is again an important risk as it reduce the adaptation capacity facing changing environment, just like domestication endangered a lot of species by lowering their adaption capacity to new environments due to hyper specialisation (!!).

Indeed, specializing phenotype, in that case “betting” on the long-term fitness, there is a risk of a mismatch with the environment (Stenseth and Mysterud 2002; Visser and Both 2005). This is even more relevant in a context of highly variable and unpredictable environment such as expected with an extremely fast climate change. In such conditions, betting on the future can end in evolutionary traps, where maladapted populations can no longer cope with their environmental constraints and risk local extinctions (Robertson et al. 2013; Schlaepfer et al. 2002).

Species and study

Since 1962, a wild population of Yellow-Bellied Marmots (*Marmota flaviventris*) is monitored continuously, initiated by Kenneth Armitage, and now supervised 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-term wild mammal population monitoring 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 forage to reach a threshold body mass in order to survive hibernation for 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 LHT for the marmots.

Yellow-bellied marmots lives in colonies usually composed by one or more matrilineal with one adult male, multiple adult females and their offspring (Armitage 2014). Our population is composed of 7 main and 31 smaller colonies divided between an “up” and a “down valley” (Figure 1) with an elevation difference around 300 m (“up” = 3,000 m; “down” = 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, Figure 2a). Precedent studies concluded that most of this major change was due to phenotypic plasticity (Ozgul et al. 2010). This hypothesis is indeed relevant, with climate change, active season is getting longer and population faces milder conditions (e.g., higher temperature, less snow). Hence, marmots has 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 automatically getting heavier, makes sense!

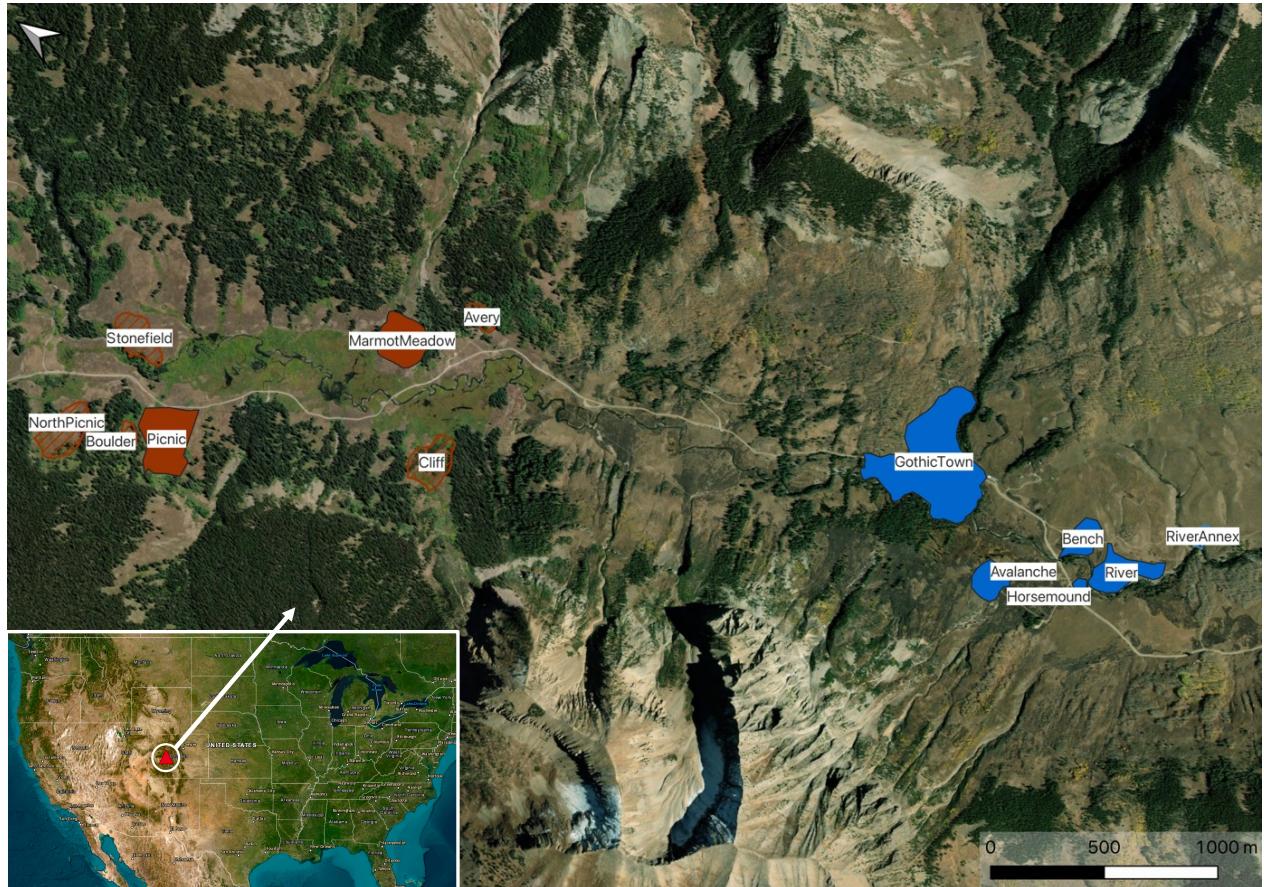


Figure 1: Red colonies represent the “up” valley, blue ones represent the “down” valleys. Plain background polygons represent the seven main colonies. The map was created with QGIS software (QGIS Development Team 2024) and the base map comes from ESRI (“GIS Mapping Software, Location Intelligence & Spatial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

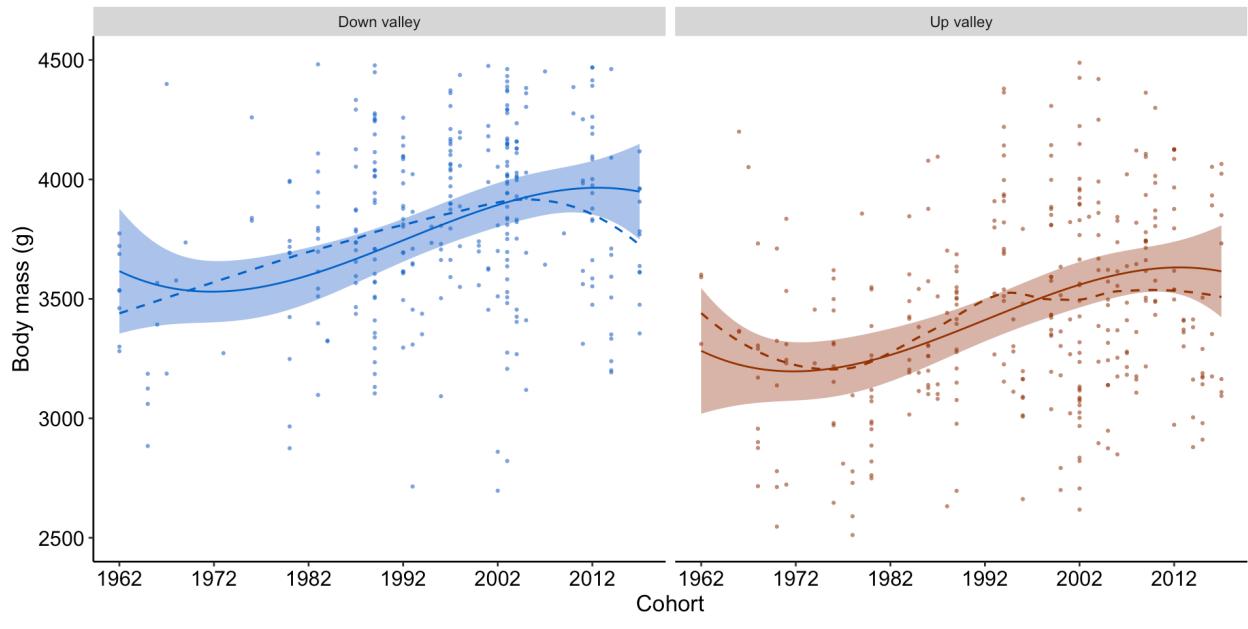
However, with now almost 15 additional years of data, we reanalyzed the body using animal models to properly assess the genetic part of this change and estimate explicitly the trait's evolutionary signal of 199 adult females between 1965 and 2022 (657 observations). Our results show an increase, at the genetic scale, estimated around 400 g, with a heritability of 56%, meaning that around two third of the observed body mass increased is in fact genetic (Birot Blumstein & Martin, 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 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.

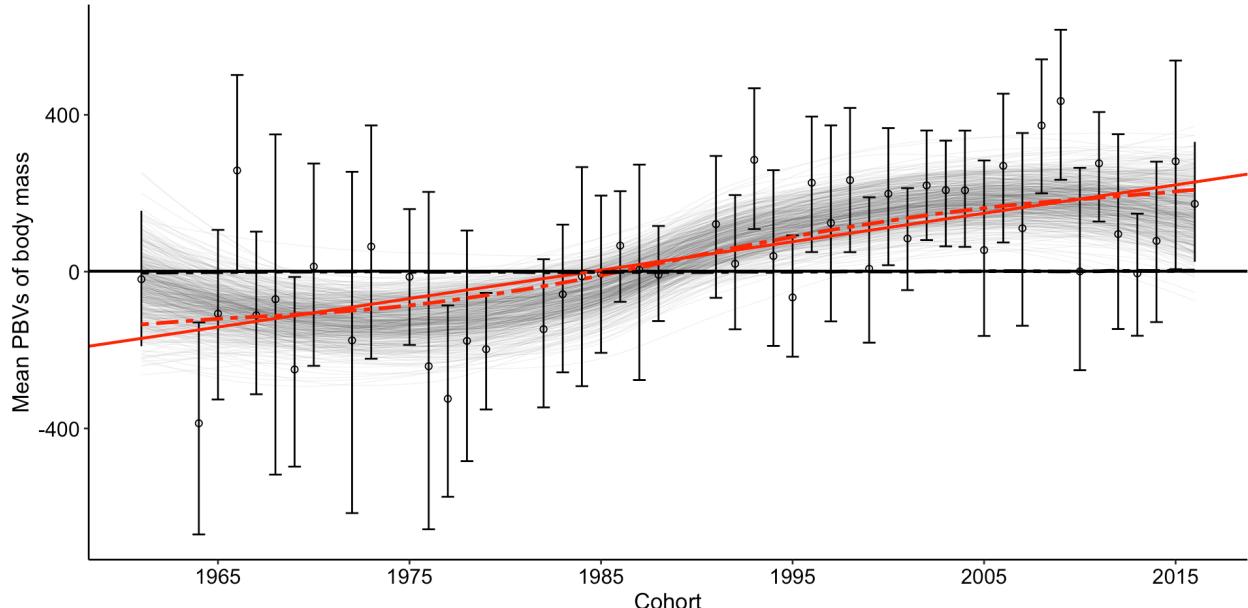
As explained earlier, body mass is a keystone phenotypic trait for the yellow-bellied marmots. It is therefore crucial to understand how this trait and this population is responding to climate change, both for conservation purposes and better comprehension of the links between phenotype and environment. 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 Spring-Summer (May - 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 ($81 * 25 * 30\text{cm}$) situated near burrow entrances. If the individual is captured for the first time, it is identified by placing a unique numbered ear tag on both ears, and with a nontoxic black Nyzanol dye fur mark for distant identification during behavioral observations. Over 95% of individuals are captured between the first two years of their lives and thus have known year of birth and age, from that each we define four age classes, the **juveniles** between 0 and 1 year old, **yearlings** between 1 and 2 years old, **subadults** between 2 and 3 years old, and **adult** over 3 years old (Jebb et al. 2021).



(a)



(b)

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.

Pedigree (i.e., parental links between individuals) is known for most individuals in the population (4,652 individuals to this date). This was first estimated through behavioral observations, meaning that only the mother-daughter links could be determined, then pedigree was estimated with genetic methods (details in Blumstein et al. 2010; Olson et al. 2012).

Behavioral observations and experiments (running speed and Flight Initiation Distance (FID) (!!!)) are conducted all along the season. Upon each capture, individuals are sexed, weighted (initially with a spring scale ($\pm 50g$) and now with a digital balance ($\pm 10g$)) 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 Amospheric 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 2024), analysis will be performed on R (R Core Team 2024), Animal models will be performed using R package “MCMCglmm” (Hadfield 2010), DHGLM and other bayesian analysis (excluding MCMCglmm) will be done with “brms” (Bürkner 2021), figures will be made with “ggplot2” (Wickham 2016).

Research objective

As explained before, the observed major body mass increase (20%) in Yellow-Bellied marmots has been miss considered. We have shown a strong evolutionary signal in this change, meaning that we need to rethink the evolutionary scenario explaining this phenotypic change.

First, I will study which specific aspects of the marmots body mass has changed. We need to understand if individuals are born with a greater constitution (so the intercept in statistical term), if their growing capacity has increased (slope) or both.

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, there is a pressing need to develop new 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, using our extensive datasets on the weather and environment of the marmots, I am going to study the changes during the last half-century in order to understand which factors could have triggered this body mass increase.

Finally, we expect that such modification in a crucial LHT in natural population will not be the only major phenotypic change. Therefore, as theorized by the extended POLS, I am going to investigate potential behavioral changes linked to body mass in marmots.

Chapter 1 - Mechanisms behind the body mass increase.

To investigate the body mass increase in the last-half century, the first step is to understand what has exactly changed. Understanding the mechanism of this increase means understand if cohorts have now a bigger constitution than before (i.e., born bigger), or does the growing capacity of each cohorts has increased? To explain that in statistical term, we have to understand if the intercept (constitution), the slope (growing) or both has changed over time cohorts.

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. That prediction was the main explanation for a stable body mass in adults marmots even if it was linked to a better fitness. This stable body mass in Juvenile, holding its evolution in the subsequent age classes, is called the “invisible fraction” and is explained by Jebb et al. (2021).

However, looking at body mass in Juvenile over time cohort for both males and females reveals interesting details (Figure 3). 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 1,206.18 g in 1976 (Males) and 1,130.64 g in 1979 (Females) to 1,519.71 g in 1998 (Males) and 1,363.03 g in 2001 (Females, Estimations from local regression on raw data)*. These changes represent a body mass increase of 23% in 22 years (22 cohorts), meaning that between the mid 1970s and the 2000s, each cohort was in average 1% heavier than the last one at the end of their first foraging season (Figure 3).

The relax of the evolutionary constraint on body mass in Juvenile could be a serious clue to explain the sudden increase observed in adults arround the same period.

First, I will study the body mass patternst through time cohorts at the beginning and end of the active season for each age classes at both phenotypic and genetic level to understand the changes in the last half century. Then, I will investigate the reaction norms (at cohort scale) by looking both the average cohorts mass at these two moments, and slopes over the active season.

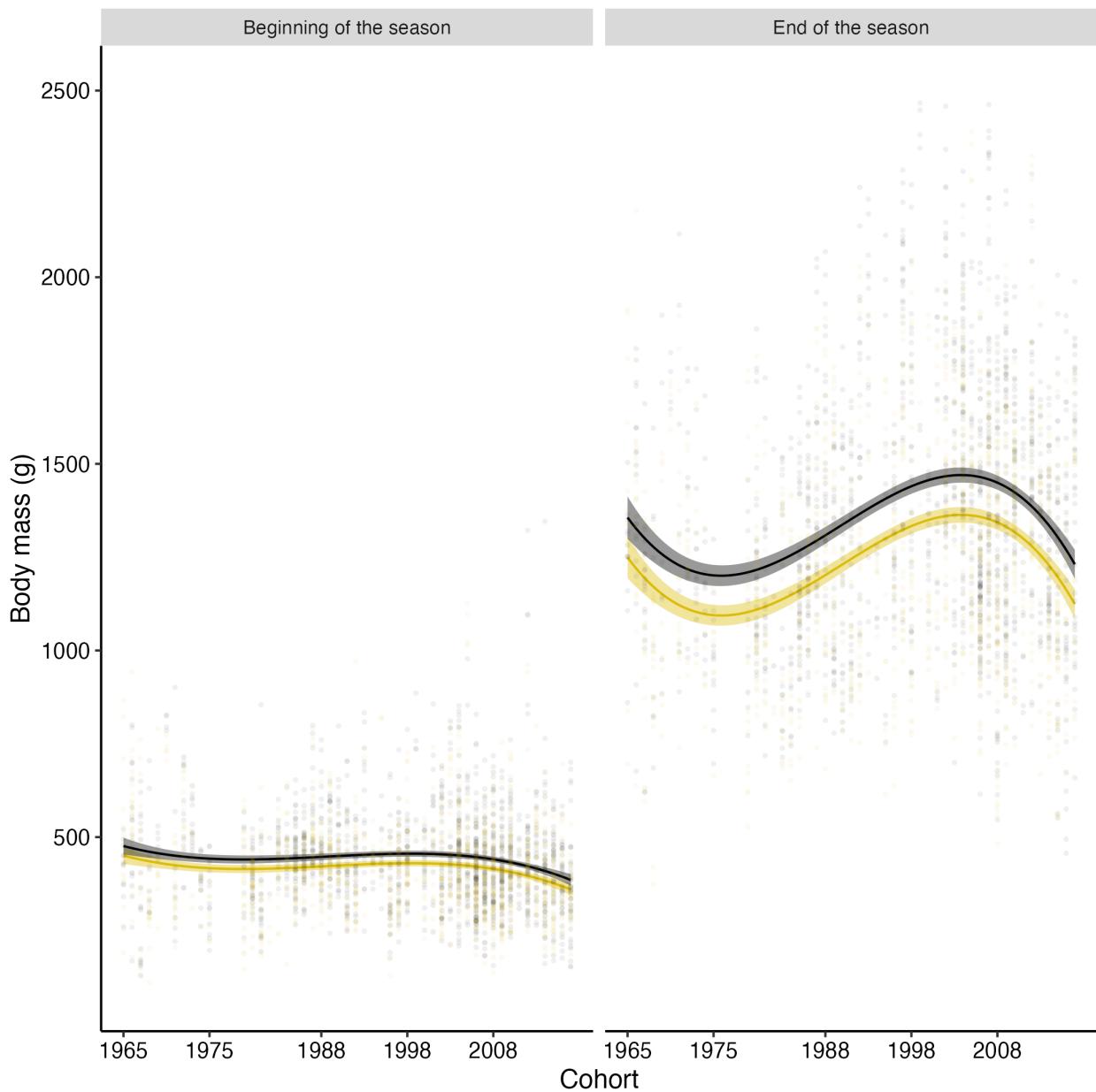


Figure 3: Body mass trend over time cohort for females (yellow) and males (black) Juveniles compared between the beginning (birth weight) and end of their first active season (mass on August 15th).

Chapter 2 - Detecting individual variation in plasticity with DHGLMs.

As explained previously, detecting more efficiently individual variation in plasticity ($I * E$) in natural condition is essential to better understand individual responses to climate change. However, although some good methods exists today (Nussey et al. 2007; Ramakers et al. 2023), a lot of biases coming from environmental proxies still limit these methods today. As said in the introduction again, we believe that using Double Hierarchical Generalized Models (DHGLM) can drastically reduce these problems and help us improve the efficiency of $I * E$ detection in natural populations.

DHGLMs will estimate the residual variance for each individuals, then the variance in this residual variance: V_{V_e} . When fitting a DHGLM on a focal phenotypic trait with multiple values for each individuals, if there is no $I * E$ (i.e., each individual's phenotypic response will be the same, Figure 4 a), there will be no variance in the residual variance as each individual will exhibit the same range of phenotypic values (Figure 4 b), so $V_{V_e} = 0$.

However, if there's individual variation in their plastic response ($I * E$) for the focal phenotypic trait (Figure 4 c), there, the residual variance won't be the same for each individual, hence there will be a V_{V_e} different from 0 (Figure 4 d).

Therefore, although a V_{V_e} significantly different from 0 isn't a proof of $I * E$ in itself (as it could come from something else), such result show that investigation on this focal trait are worth doing. On the contrary, unless in very specific case, almost never met in natural conditions (i.e., exact opposite effect, Figure 5 c, d), leading to false negatives, a $V_{V_e} = 0$ most likely indicate that there is no individual variation in their plastic response for the focal trait.

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 vamues. 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 6 d). In other words, a false positive.

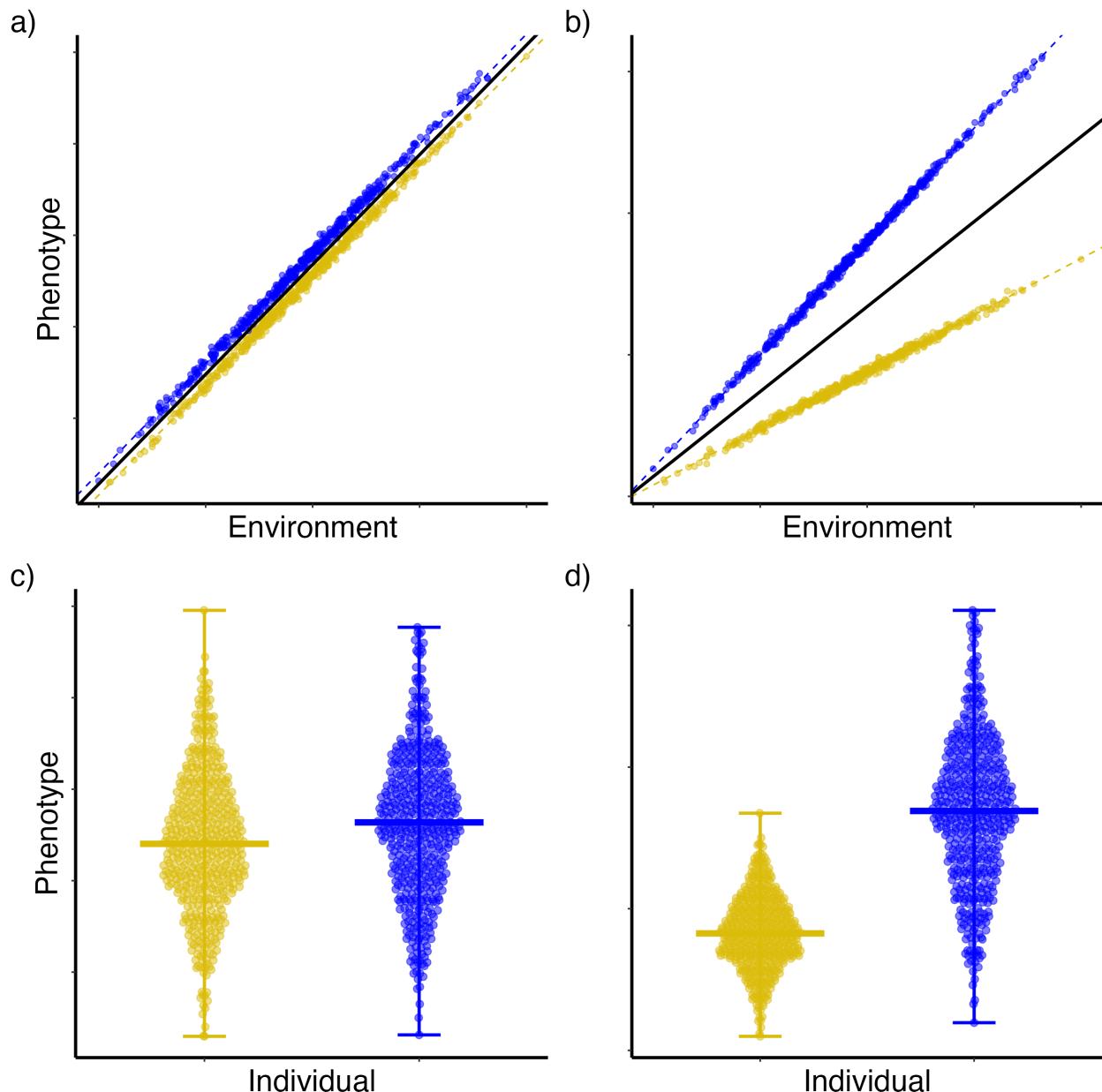


Figure 4: Reaction norms for two individuals (blue and yellow) for a trait a) without and b) with individual variations in plasticity. c) In the absence of I^*E , both individual express the same range of phenotypic values. d) However, with I^*E , individuals express different range of values.

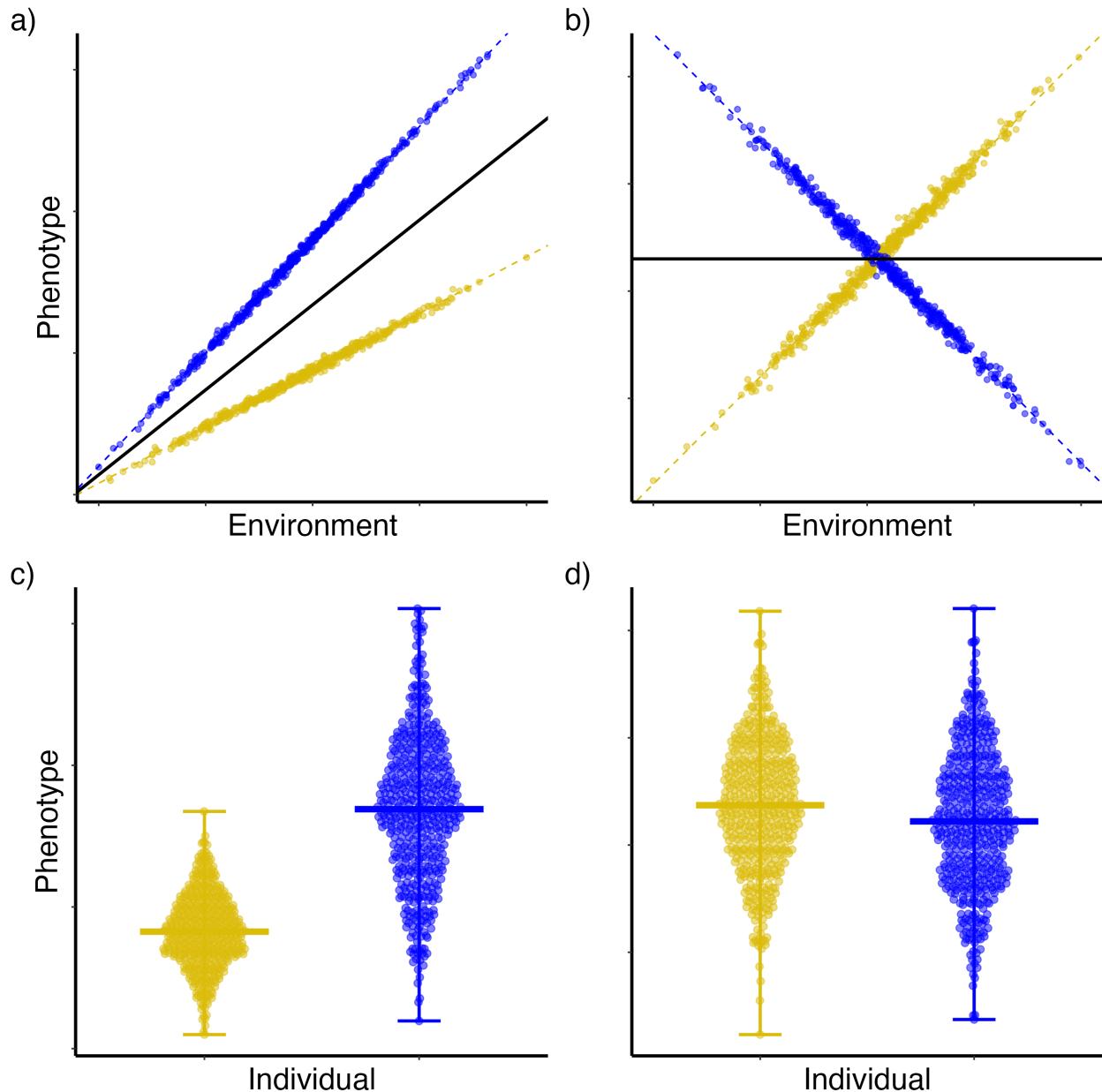


Figure 5: Reaction norms for two individuals (blue and yellow) for a trait a) with individual variation in their relationships and b) with the exact opposite effects. Here, although individuals in the first case c) express different ranges of phenotypic value, d) in the second case, they express the same range despite the $I * E$.

Based on that, I will simulate phenotypic and environmental values for populations with and without $I * E$, with balanced and unbalanced models and fit DHGLMs on it to test the detection capacity of this method. Then I will apply this method on our Yellow-Bellied Marmots population to illustrate it with a real condition example.

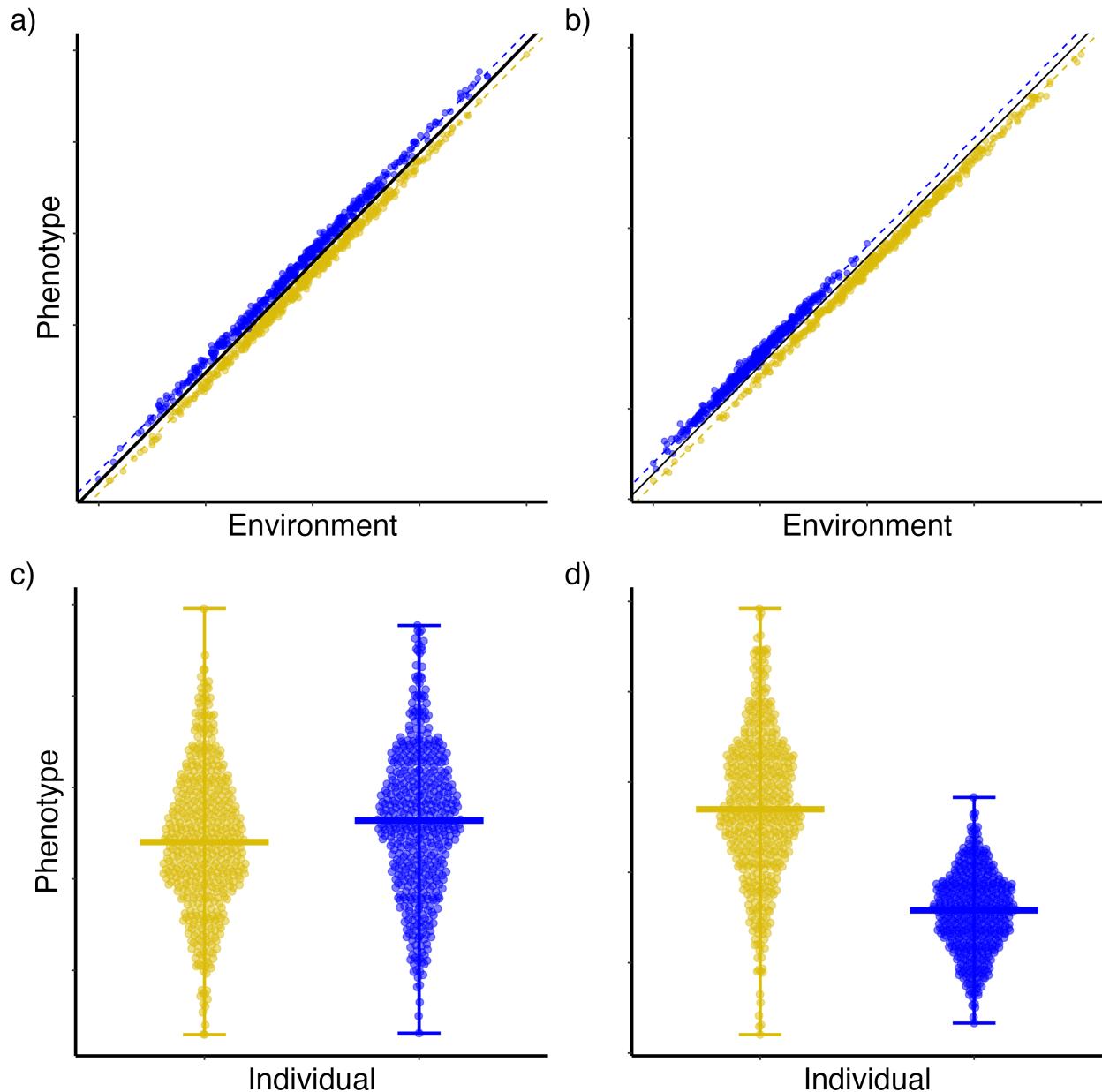


Figure 6: Reaction norms for two individuals (blue and yellow) for a trait without individual variation in their plasticity in a) balanced and an b) unbalanced design. c) In the balanced design there is indeed no individual difference in the range of expressed phenotypic values. d) But in the unbalanced design, although both individuals have the same slope (i.e., phenotypic response), there is a difference in the range of expressed phenotypic values.

Chapter 3 - Identifying the predictors of increased body mass.

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

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.

Extensive and detailed weather data at site from 1975 to 2022 (Prather et al. 2023)

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

Predators, Diet?

Using our extensive weather data, I will perform multivariate analyses (Principal Components Analysis, PCA with “ade4” package, Dray et al. 2023)

(Biro, Blumstein & Martin, Manuscript in progress, Figure 7)

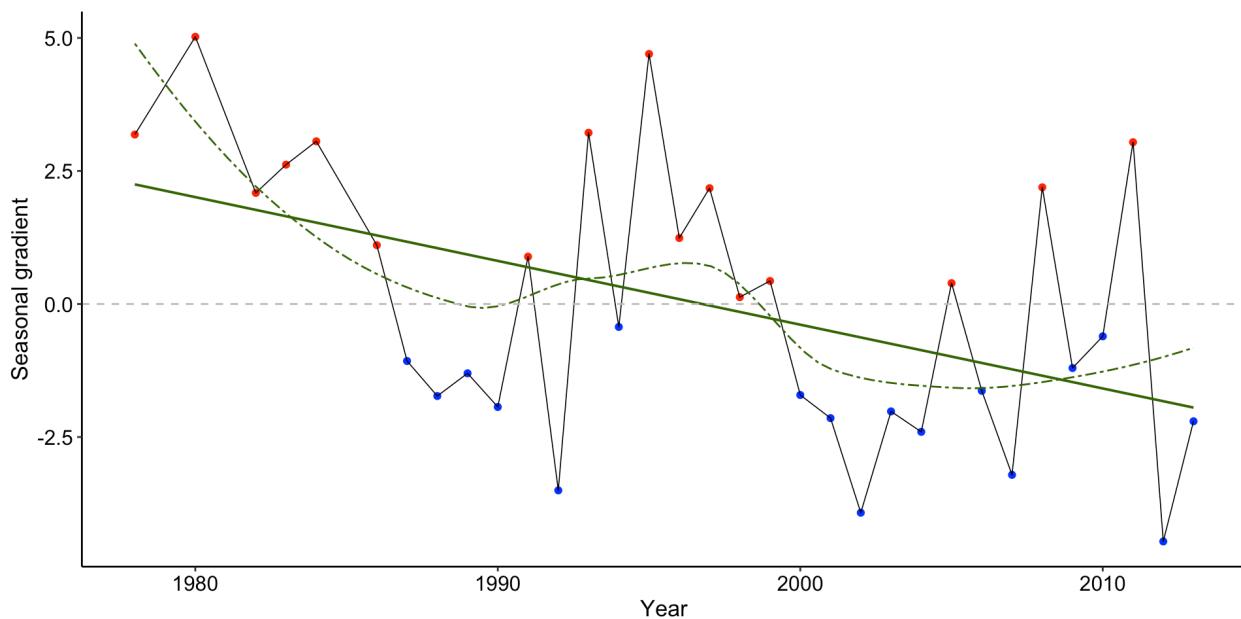


Figure 7: [...]

Chapter 4 - Links between increasing body mass and behavior in marmots.

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

POLS

With the POLS, we expect to see a clear effect of the body mass on the behavior. However, by looking at some preliminary results, although some results seems statistically significant, the biological effect is really small

fig => effect of the **experience** compared to the physiological effect (i.e., body mass seems to impact the behavior more in Juveniles than in adults)

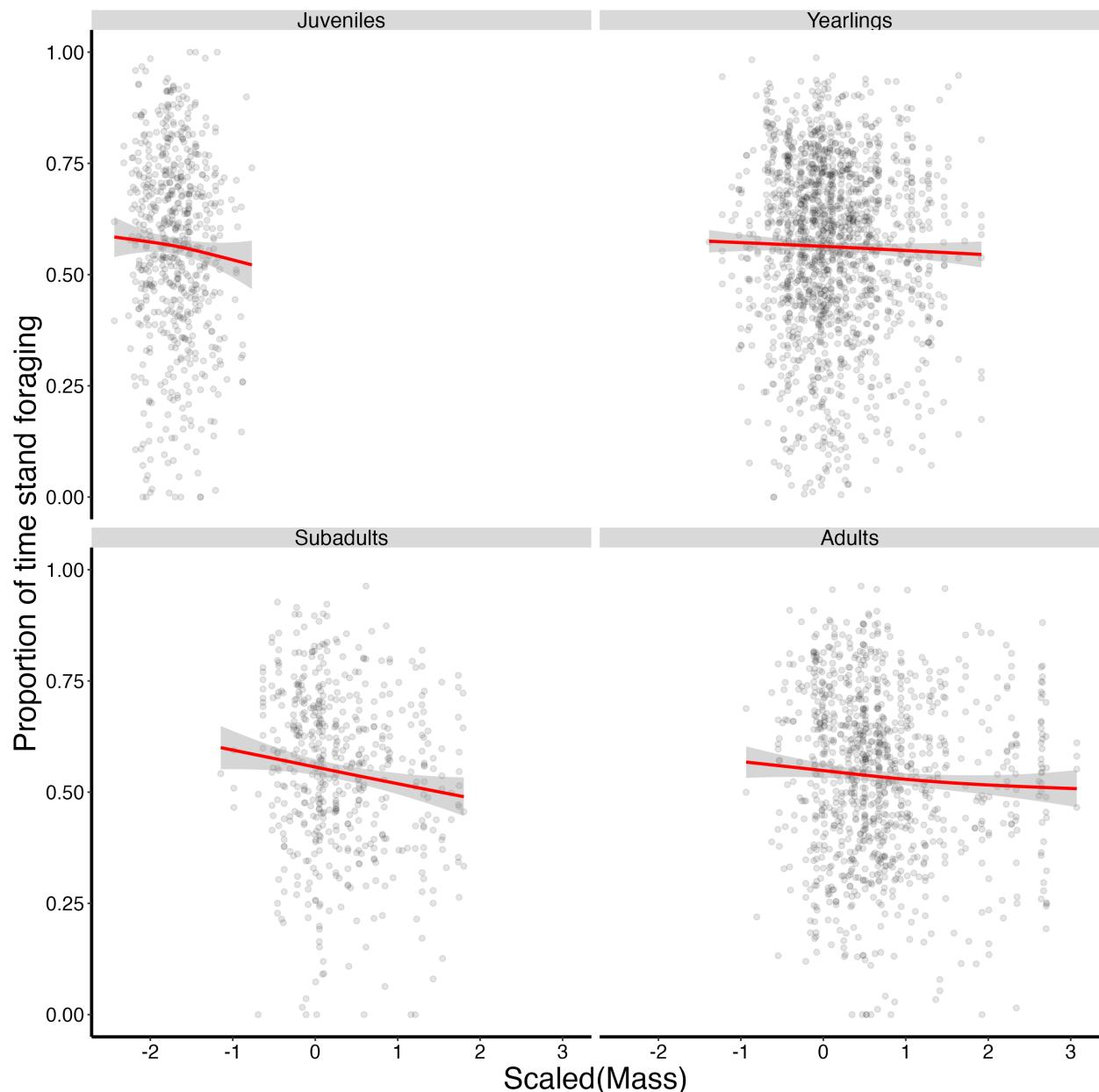


Figure 8: [...]

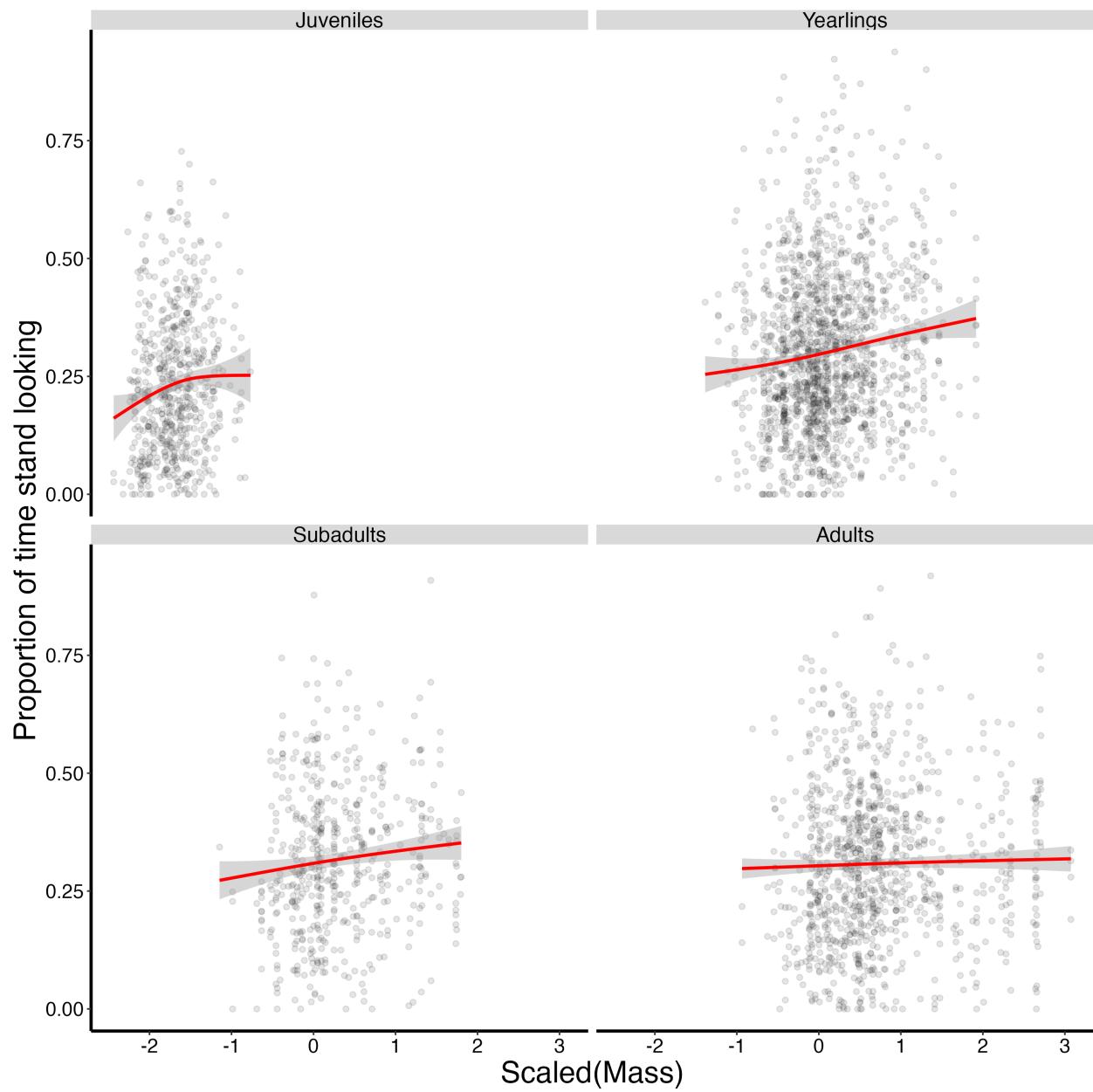


Figure 9: [...]

Significance and impacts

This research uses one of the most extensive natural population databases in the world to better understand how can natural populations cope with climate change. The quality and quality of data provided by this study system will allow conducting powerful and complete analysis that can't be done on most natural population (such as powerful multivariate animal models). This will provide crucial insight to guide conservation policies in a context of rapidly changing environments.

Potential side projects

- Dig the conservative bet-hedging hypothesis
- Continue a previously started work at NTNU with Yimen Araya-Ajoy about developing a path between Social Network Analysis (SNA) and metapopulation dynamics studies

Expected Products

Introduction (*MSc second year project*)

Manuscript is being prepared for submision to Evolution

1. Beyond plasticity: Study of the evolutionary character of the increase in body mass in the Yellow-bellied Marmot. Augustin Birot, Dan Blumstein and Julien Martin

Lorem ipsum

Thesis

2. What has changed in Yellow-bellied Marmots' body mass. Augustin Birot, Dan Blumstein and Julien Martin

Lorem ipsum

3. Break free from bad envrionmental proxies when detecting I^*E , the DHGLMs solution. Augustin Birot, Ned Dochtermann and Julien Martin

Lorem ipsum

4. Why have Marmots only gotten bigger now? Augustin Birot, Dan Blumstein and Julien Martin

Lorem ipsum

5. Is there a link between an increased body mass and behavior? Augustin Birot, Vincent Careau, Denis Réale, Dan Blumstein and Julien Martin

Lorem ipsum

Side projects

6. Buffer environmental instability by increasing your body mass: an application of conservative bet-hedging in a hibernant rodent Augustin Birot, Dan Blumstein and Julien Martin

Lorem ipsum

7. How can social network analysis help us understand metapopulation dynamics? Augustin Birot, Yimen Araya-Ajoy, Bernt-Erik Sæther, Henrik Jensen, Jonathan Wright, Pierre Bize and Julien Martin

Lorem ipsum

Timeline

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

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

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

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

References

- Armitage, K. B. (1965), “Vernal behaviour of the yellow-bellied marmot (*Marmota flaviventris*),” *Animal Behaviour*, 13, 59–68. [https://doi.org/10.1016/0003-3472\(65\)90072-2](https://doi.org/10.1016/0003-3472(65)90072-2).
- Armitage, K. B. (2014), *Marmot Biology: Sociality, Individual Fitness, and Population Dynamics*, Cambridge University Press. <https://doi.org/10.1017/CBO9781107284272>.
- Arnold, S. J., Pfrender, M. E., and Jones, A. G. (2001), “The adaptive landscape as a conceptual bridge between micro- and macroevolution,” in *Microevolution Rate, Pattern, Process*, eds. A. P. Hendry and M. T. Kinnison, Dordrecht: Springer Netherlands, pp. 9–32. https://doi.org/10.1007/978-94-010-0585-2_2.
- Bergmann (1847), “About the relationships between heat conservation and body size of animals,” *Goett Stud*, 1, 595–708.
- Biro, P. A., and Stamps, J. A. (2008), “Are animal personality traits linked to life-history productivity?” *Trends in Ecology & Evolution*, 23, 361–368. <https://doi.org/10.1016/j.tree.2008.04.003>.
- Blumstein, D. T. (2009), “SOCIAL EFFECTS ON EMERGENCE FROM HIBERNATION IN YELLOW-BELLIED MARMOTS.”
- Blumstein, D. T., Im, S., Nicodemus, A., and Zugmeyer, C. (2004), “Yellow-bellied Marmots (*Marmota flaviventris*) Hibernate Socially,” *Journal of Mammalogy*, 85, 25–29. [https://doi.org/10.1644/1545-1542\(2004\)085%3C0025:YMMFHS%3E2.0.CO;2](https://doi.org/10.1644/1545-1542(2004)085%3C0025:YMMFHS%3E2.0.CO;2).
- Blumstein, D. T., Lea, A. J., Olson, L. E., and Martin, J. G. A. (2010), “Heritability of anti-predatory traits: Vigilance and locomotor performance in marmots,” *Journal of Evolutionary Biology*, 23, 879–887. <https://doi.org/10.1111/j.1420-9101.2010.01967.x>.
- Bürkner, P.-C. (2021), “Bayesian item response modeling in R with brms and Stan,” *Journal of Statistical Software*, 100, 1–54. <https://doi.org/10.18637/jss.v100.i05>.
- Carey, H. V., Andrews, M. T., and Martin, S. L. (2003), “Mammalian Hibernation: Cellular and Molecular Responses to Depressed Metabolism and Low Temperature,” *Physiological Reviews*, 83, 1153–1181. <https://doi.org/10.1152/physrev.00008.2003>.
- Childs, D. Z., Metcalf, C. J. E., and Rees, M. (2010), “Evolutionary bet-hedging in the real world: Empirical evidence and challenges revealed by plants,” *Proceedings of the Royal Society B: Biological Sciences*, 277, 3055–3064. <https://doi.org/10.1098/rspb.2010.0707>.
- Cohen, D. (1966), “Optimizing reproduction in a randomly varying environment,” *Journal of Theoretical Biology*, 12, 119–129. [https://doi.org/10.1016/0022-5193\(66\)90188-3](https://doi.org/10.1016/0022-5193(66)90188-3).
- Dammhahn, M., Dingemanse, N. J., Niemelä, P. T., and Réale, D. (2018), “Pace-of-life syndromes: A framework for the adaptive integration of behaviour, physiology and life history,” *Behavioral Ecology and Sociobiology*, 72, 62, s00265-018-2473-y. <https://doi.org/>

[10.1007/s00265-018-2473-y](https://doi.org/10.1007/s00265-018-2473-y).

Darwin, C. (1859), *The Origin of Species: By Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life*, Cambridge University Press. <https://doi.org/10.1017/CBO9780511694295>.

Daufresne, M., Lengfellner, K., and Sommer, U. (2009), “Global warming benefits the small in aquatic ecosystems,” *Proceedings of the National Academy of Sciences*, 106, 12788–12793. <https://doi.org/10.1073/pnas.0902080106>.

DeWitt, T. J., Sih, A., and Wilson, D. S. (1998), “Costs and limits of phenotypic plasticity,” *Trends in Ecology & Evolution*, 13, 77–81. [https://doi.org/10.1016/S0169-5347\(97\)01274-3](https://doi.org/10.1016/S0169-5347(97)01274-3).

Dray, S., Dufour, A.-B., Thioulouse, J., Jombart, T., Pavoine, S., Lobry, J. R., Ollier, S., Siberchicot, A., and Chessel, D. (2023), *Ade4: Analysis of Ecological Data: Exploratory and Euclidean Methods in Environmental Sciences*.

Durant, J., Hjermann, D., Ottersen, G., and Stenseth, N. (2007), “Climate and the match or mismatch between predator requirements and resource availability,” *Climate Research*, 33, 271–283. <https://doi.org/10.3354/cr033271>.

Gardner, J. L., Peters, A., Kearney, M. R., Joseph, L., and Heinsohn, R. (2011), “Declining body size: A third universal response to warming?” *Trends in Ecology & Evolution*, 26, 285–291. <https://doi.org/10.1016/j.tree.2011.03.005>.

Geiser, F. (2013), “Hibernation,” *Current Biology*, 23, R188–R193. <https://doi.org/10.1016/j.cub.2013.01.062>.

Gienapp, P., and Brommer, J. E. (2014), “Evolutionary dynamics in response to climate change,” in *Quantitative Genetics in the Wild*, eds. A. Charmantier, D. Garant, and L. E. B. Kruuk, Oxford University PressOxford, pp. 254–274. <https://doi.org/10.1093/acprof:oso/9780199674237.003.0015>.

“GIS Mapping Software, Location Intelligence & Spatial Analytics | Esri” (n.d.). <https://www.esri.com/en-us/home>.

Gould, S. J., and Lewontin, R. C. (1979), “The spandrels of San Marco and the Panglossian paradigm: A critique of the adaptationist programme,” *Proceedings of the Royal Society of London. Series B. Biological Sciences*, 205, 581–598. <https://doi.org/10.1098/rspb.1979.0086>.

Guillemain, M., Elmberg, J., Gauthier-Clerc, M., Massez, G., Hearn, R., Champagnon, J., and Simon, G. (2010), “Wintering French Mallard and Teal Are Heavier and in Better Body Condition than 30 Years Ago: Effects of a Changing Environment?” *AMBIO*, 39, 170–180. <https://doi.org/10.1007/s13280-010-0020-9>.

Hadfield, J. D. (2010), “MCMC methods for multi-response generalized linear mixed models:

- The MCMCglmm R package,” *Journal of Statistical Software*, 33, 1–22.
- Inouye, D. W., and Wielgolaski, F. E. (2003), “High Altitude Climates,” in *Phenology: An integrative Environmental Science*, pp. 195–214.
- Intergovernmental Panel On Climate Change (Ipcc) (2022), *Climate Change 2022 – Impacts, Adaptation and Vulnerability: Working Group II Contribution to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change*, Cambridge University Press. <https://doi.org/10.1017/9781009325844>.
- Jebb, A. H. M., Blumstein, D. T., Bize, P., and Martin, J. G. A. (2021), “Bigger is not always better: Viability selection on body mass varies across life stages in a hibernating mammal,” *Ecology and Evolution*, 11, 3435–3445. <https://doi.org/10.1002/ece3.7304>.
- Kruuk, L. E. B. (2004), “Estimating genetic parameters in natural populations using the ‘animal model’,” *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, 359, 873–890. <https://doi.org/10.1098/rstb.2003.1437>.
- Kruuk, L. E. B., Charmantier, A., and Garant, D. (2014), “The study of quantitative genetics in wild populations,” in *Quantitative Genetics in the Wild*, Oxford University PressOxford, pp. 1–15. <https://doi.org/10.1093/acprof:oso/9780199674237.003.0012>.
- Lee, Y., and Nelder, J. A. (2006), “Double hierarchical generalized linear models,” *Journal of the Royal Statistical Society Series C: Applied Statistics*.
- Lynch, M., and Walsh, B. (1998), *Genetics and Analysis of Quantitative Traits*, Sinauer.
- Martin, J. (2024), [*ybamaRmot: A r package for the database of the marmot study in the east river valley, colorado*](#).
- Monclús, R., Pang, B., and Blumstein, D. T. (2014), “Yellow-bellied marmots do not compensate for a late start: The role of maternal allocation in shaping life-history trajectories,” *Evolutionary Ecology*, 28, 721–733. <https://doi.org/10.1007/s10682-014-9705-z>.
- Nedergaard, J., and Cannon, B. (1990), “Mammalian hibernation,” *Philosophical Transactions of the Royal Society of London. B, Biological Sciences*, 326, 669–686. <https://doi.org/10.1098/rstb.1990.0038>.
- Nussey, D. H., Wilson, A. J., and Brommer, J. E. (2007), “The evolutionary ecology of individual phenotypic plasticity in wild populations,” *Journal of Evolutionary Biology*, 20, 831–844. <https://doi.org/10.1111/j.1420-9101.2007.01300.x>.
- Olson, L. E., Blumstein, D. T., Pollinger, J. R., and Wayne, R. K. (2012), “No evidence of inbreeding avoidance despite demonstrated survival costs in a polygynous rodent,” *Molecular Ecology*, 21, 562–571. <https://doi.org/10.1111/j.1365-294X.2011.05389.x>.
- Ozgul, A., Childs, D. Z., Oli, M. K., Armitage, K. B., Blumstein, D. T., Olson, L. E., Tuljapurkar, S., and Coulson, T. (2010), “Coupled dynamics of body mass and population growth in response to environmental change,” *Nature*, 466, 482–485. <https://doi.org/10.1038/nature09120>.

1038/nature09210.

- Phillips, P. C., and Arnold, S. J. (1989), “VISUALIZING MULTIVARIATE SELECTION,” *Evolution*, 43, 1209–1222. <https://doi.org/10.1111/j.1558-5646.1989.tb02569.x>.
- Prather, R. M., Underwood, N., Dalton, R. M., Barr, B., and Inouye, B. D. (2023), “Climate data from the Rocky Mountain Biological Laboratory (1975–2022),” *Ecology*, 104, e4153. <https://doi.org/10.1002/ecy.4153>.
- QGIS Development Team (2024), “QGIS Geographic Information System,” QGIS Association.
- R Core Team (2024), *R: A language and environment for statistical computing*, Vienna, Austria: R Foundation for Statistical Computing.
- Ramakers, J. J. C., Reed, T. E., Harris, M. P., and Gienapp, P. (2023), “Probing variation in reaction norms in wild populations: The importance of reliable environmental proxies,” *Oikos*, 2023, e09592. <https://doi.org/10.1111/oik.09592>.
- Réale, D., Garant, D., Humphries, M. M., Bergeron, P., Careau, V., and Montiglio, P.-O. (2010), “Personality and the emergence of the pace-of-life syndrome concept at the population level,” *Philosophical Transactions of the Royal Society B: Biological Sciences*, Royal Society, 365, 4051–4063. <https://doi.org/10.1098/rstb.2010.0208>.
- Robertson, B. A., Rehage, J. S., and Sih, A. (2013), “Ecological novelty and the emergence of evolutionary traps,” *Trends in Ecology & Evolution*, 28, 552–560. <https://doi.org/10.1016/j.tree.2013.04.004>.
- Roff, D. A. (1992), “The evolution of life histories : Theory and analysis.”
- Schlaepfer, M. A., Runge, M. C., and Sherman, P. W. (2002), “Ecological and evolutionary traps,” *Trends in Ecology & Evolution*, 17, 474–480. [https://doi.org/10.1016/S0169-5347\(02\)02580-6](https://doi.org/10.1016/S0169-5347(02)02580-6).
- Sheridan, J. A., and Bickford, D. (2011), “Shrinking body size as an ecological response to climate change,” *Nature Climate Change*, 1, 401–406. <https://doi.org/10.1038/nclimate1259>.
- Siepielski, A. M., Morrissey, M. B., Carlson, S. M., Francis, C. D., Kingsolver, J. G., Whitney, K. D., and Kruuk, L. E. B. (2019), “No evidence that warmer temperatures are associated with selection for smaller body sizes,” *Proceedings of the Royal Society B: Biological Sciences*, 286, 20191332. <https://doi.org/10.1098/rspb.2019.1332>.
- Sih, A., Ferrari, M. C. O., and Harris, D. J. (2011), “Evolution and behavioural responses to human-induced rapid environmental change,” *Evolutionary Applications*, 4, 367–387. <https://doi.org/10.1111/j.1752-4571.2010.00166.x>.
- Stamps, J. A. (2007), “Growth-mortality tradeoffs and ‘personality traits’ in animals,” *Ecology Letters*, 10, 355–363. <https://doi.org/10.1111/j.1461-0248.2007.01034.x>.

- Starrfelt, J., and Kokko, H. (2012), “Bet-hedging—a triple trade-off between means, variances and correlations,” *Biological Reviews*, 87, 742–755. <https://doi.org/10.1111/j.1469-185X.2012.00225.x>.
- Stearns, S. C. (1992), *The evolution of life histories*, Oxford University Press. <https://doi.org/10.1093/oso/9780198577416.001.0001>.
- Stenseth, N. Chr., and Mysterud, A. (2002), “Climate, changing phenology, and other life history traits: Nonlinearity and match–mismatch to the environment,” *Proceedings of the National Academy of Sciences*, 99, 13379–13381. <https://doi.org/10.1073/pnas.212519399>.
- Teplitsky, C., Robinson, M. R., and Merilä, J. (2014), “Evolutionary potential and constraints in wild populations,” in *Quantitative Genetics in the Wild*, eds. A. Charmantier, D. Garant, and L. E. B. Kruuk, Oxford University PressOxford, pp. 190–208. <https://doi.org/10.1093/acprof:oso/9780199674237.003.0012>.
- Visser, M. E., and Both, C. (2005), “Shifts in phenology due to global climate change: The need for a yardstick,” *Proceedings of the Royal Society B: Biological Sciences*, 272, 2561–2569. <https://doi.org/10.1098/rspb.2005.3356>.
- Walsh, C. R., and Patterson, R. T. (2022), “Precipitation and Temperature Trends and Cycles Derived from Historical 1890–2019 Weather Data for the City of Ottawa, Ontario, Canada,” *Environments*, 9, 35. <https://doi.org/10.3390/environments9030035>.
- Wickham, H. (2016), *ggplot2: Elegant graphics for data analysis*.
- Wilson, A. J., Réale, D., Clements, M. N., Morrissey, M., Postma, E., Walling, C., Kruuk, L., and Nussey, D. (2010), “An ecologist’s guide to the animal model.” *The Journal of animal ecology*, 79 1, 13–26. <https://doi.org/10.1111/j.1365-2656.2009.01639.x>.
- Wolf, M., Van Doorn, G. S., Leimar, O., and Weissing, F. J. (2007), “Life-history trade-offs favour the evolution of animal personalities,” *Nature*, 447, 581–584. <https://doi.org/10.1038/nature05835>.
- Yom-Tov, Y., Yom-Tov, S., and Jarrell, G. (2008), “Recent increase in body size of the American marten *Martes americana* in Alaska: GLOBAL WARMING AND BODY SIZE OF THE AMERICAN MARTEN,” *Biological Journal of the Linnean Society*, 93, 701–707. <https://doi.org/10.1111/j.1095-8312.2007.00950.x>.
- Zahavi, A. A. (1997), *The handicap principle: A missing piece of darwin’s puzzle*, Oxford University Press. <https://doi.org/10.1093/oso/9780195100358.001.0001>.
- Zhai, Y., Huang, G., Wang, X., Zhou, X., Lu, C., and Li, Z. (2019), “Future projections of temperature changes in Ottawa, Canada through stepwise clustered downscaling of multiple GCMs under RCPs,” *Climate Dynamics*, 52, 3455–3470. <https://doi.org/10.1007/s00382-018-4340-y>.