

Cryptic evolution of body size in response to climate change in the Alpine marmot (*Marmota marmota*)

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INTRODUCTION

Climate change is profoundly altering ecosystems functioning, leading to significant consequences for biodiversity like population declines and an increased risk of local extinctions (Butchart et al., 2010; Bellard et al., 2012; Román-Palacios and Wiens, 2020). Three primary responses of organisms to climate change have been identified over the last decades: shifts in geographical distribution towards better suited areas (Parmesan, 2006), advanced phenology such as timing of reproduction (Radchuk et al., 2019) and modifications of body size (Gardner et al., 2011). Two main questions arise concerning the responses of organisms to climate change: the adaptive nature of these responses (Merilä and Hendry, 2014), and the proximal causes of such phenotypic response, either it is plasticity or evolutionary driven (Gienapp et al., 2008).

Avoiding the "adaptive story-telling"

Adaptation is essential for the persistence of populations, as prolonged maladaptation can ultimately result in extinction (Gonzalez et al., 2013). Geographical shifts in more-suited habitat and advanced phenology in response to earlier growing seasons are well-documented and generally reflect adaptive responses to climate change (Parmesan, 2006; Charmantier and Gienapp, 2014). Indeed, Parmesan and Yohe (2003) demonstrated that over 80% of a pool of 1570

species exhibited shifts in distribution or abundance consistent with climate change predictions, by moving towards more favorable habitats in northern regions. In the same way, Charmantier et al. (2008) revealed that advanced phenology in response to climate change is overwhelmingly adaptive in birds.

If a phenotypic change is adaptive, it is likely driven by selection (Gienapp and Brommer, 2014). Specifically, adaptation can be inferred when the selection acting on a phenotypic change favors that change (Merilä and Hendry, 2014). The adaptive nature of an observed phenotypic change needs to be formally tested rather than assumed, to avoid an "adaptive story-telling" like stated by Gould and Lewontin (1979), because phenotypic changes do not imply that the observable change is adaptive (Radchuk et al., 2019). For instance, Both et al. (2006)'s study on European flycatchers (*Ficedula hypoleuca*) found that climate change-induced shifts in advanced timing of migration led to a mismatch between the arrival of adult birds at breeding sites and the peak abundance of insect prey for hatchlings, resulting in population declines.

Importantly, only the genetic component of the phenotypic variation under selection is likely to be transmitted from one generation to the next, leading to an evolutionary response (Lynch and Walsh, 1998). Thus, determined the plastic or evolutionary nature of these responses is needed

to study the impact of climate change in wild population (Gienapp and Brommer, 2014).

Plasticity versus evolution

Phenotypic plasticity is the ability of genotypes to express different phenotypes in different environmental conditions (DeWitt et al., 1998). For instance, great tits (*Parus major*) adjust their laying date in response to early spring temperature, leading to a better match between the peak availability of caterpillars and chick needs later in the season (Charmantier et al., 2008). Plastic responses are frequently reported in response to climate change (Charmantier and Gienapp, 2014) as they allow swift tracking of the optimum phenotype maximizing fitness in response to climate change, but it has its limits in a context where the environment is continuously deteriorating (Ghalambor et al., 2007).

Phenotypic changes can also result from evolution (Darwin and Beer, 1951) arising from response to natural selection (adaptive evolution), genetic drift (random genetic changes, likely in small populations), inbreeding, mutation or gene flow (Lynch and Walsh, 1998). From now on, we will focus on adaptive evolution only, as the other mechanisms mentioned are not necessarily adaptive (Lynch and Walsh, 1998). The response to selection of a trait across generations primarily depends on additive variance (Lande, 1979) (see box in Appendix A for further details), as any other sources of variance should cause change only within a generation (Lynch

and Walsh, 1998). Classically viewed as a slow process, evolutionary changes has been proved to occur rather rapidly (Bonnet et al., 2017). An iconic example is provided by Grant and Grant (1993) in Darwin's finches of the Galapagos Islands. Following a severe El Niño event in 1982, the seed composition on the island shifted from large to smaller seeds, leading to a swift evolutionary response toward 1.4% smaller beak sizes of finches within only one generation.

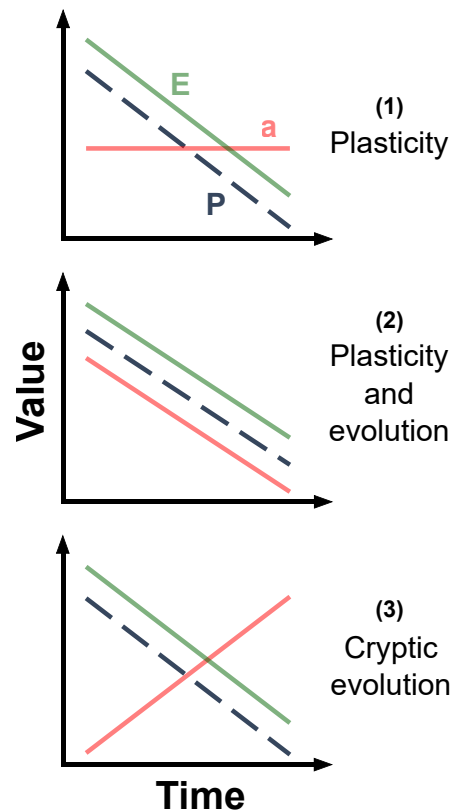


Figure 1: Theoretical relationship between phenotypic genetic and environmental temporal trends. Schematic example of phenotypic temporal changes P (dashed black line) with the associated temporal trend of breeding values a (red solid line) and environmental contribution E (green solid line). Are represented the cases of phenotypic changes due to pure plasticity (first row), plasticity alongside evolution (second row) and cryptic evolution (third row). This overly simplified plot illustrates how it can be misleading to infer on genetic changes (G) only based on observable phenotypic change (P).

Phenotypic changes are not sufficient to infer evolutionary changes

Both evolution and plasticity are likely to simultaneously influence phenotypic changes in response to climate changes (Bonnet et al., 2019; Moiron et al., 2024). For example, Réale et al. (2003) showed that advanced parturition date in Canadian red squirrels (*Tamiasciurus hudsonicus*) is both a plastic response to warmer temperature and increased cone abundance (87% of phenotypic change) and an evolutionary response to natural selection for advanced reproduction time (13% of phenotypic change).

However, plastic and evolutionary response are not always congruent (Merilä and Hendry, 2014). As a result, environmental-induced phenotypic trends can mask the effects of evolution (Figure 1.3), or be the unique factor influencing phenotypic variation despite observable phenotypic changes (Figure 1.1). Evolution and plasticity should be treated as alternative models, rather than one being a null model to be assumed unless rejected by another, like emphasized in Merilä and Hendry (2014). However, numerous studies infer evolution solely from phenotypic data, which can be hazardous if genetic and environmental influences are not explicitly distinguished (Morrissey et al., 2010; Merilä and Hendry, 2014). In fact, a phenotypic-based conclusion about genetics might be correct only when phenotypic and genetic changes are concomitant across time (Figure 1.2). As an ex-

ample, Figure 1.3 illustrates a case of "cryptic evolution", where genetic evolution occurs without observable phenotypic changes (Merilä and Hendry, 2014). Such cryptic evolution has been observed in wild-ranging snow voles (*Chionomys nivalis*), in a ten-years study, where a genetic shift towards lower body mass was shown as an adaptive response to viability selection, likely due to changing snowfall patterns. Despite this genetic change, no phenotypic trend in body mass was observed (Bonnet et al., 2017).

Quantitative genetics is a conceptual and methodological framework that allows to clearly disentangle plastic and genetic influence on phenotypic variation (Kruuk, 2004).

Studying evolution in the wild

Quantitative genetics investigates the genetic basis of complex traits, providing a framework to quantify the contributions of genetic and non-genetic factors to phenotypic variation (Lynch and Walsh, 1998). Notably, quantitative genetics examines how genetic variance is transmitted across generations (Fisher, 1919). The fundamental concept of this field posits that complex traits arise from the cumulative effects of numerous alleles, each exerting a small, additive influence, referred to as the "infinitesimal model" (Fisher, 1919).

In a quantitative genetic framework, population's phenotypic variance (σ_P^2) can be schemati-

cally decomposed as:

$$\sigma_P^2 = \sigma_a^2 + \sigma_E^2 \quad (1)$$

where σ_a^2 represents the additive genetic variance and σ_E^2 represents environmental variance (i.e., all sources of phenotypic variation that will not be transmitted to the next generation, including non-additive genetic variance) (see box in Appendix A for further details).

The influence of individual genotypes on the traits of their offspring is quantified through the concept of breeding values (Lynch and Walsh, 1998). Breeding values represent the proportion of additive effects on an individual's phenotype, and encompass the expected genetic contribution to the phenotypic value that an individual transmits to its offspring (Lynch and Walsh, 1998). Essentially, breeding values estimate the sum of the average effects of alleles an individual possesses, which can be passed on to the next generation (Postma, 2006; Lynch and Walsh, 1998). At the population level, the variance of the individual breeding values is equal to the additive genetic variance σ_a^2 (Lynch and Walsh, 1998). Hence, estimating temporal trend in breeding values is central as they quantified the estimated genetic changes of a population, therefore indicating the presence of evolution (Figure 1.2, Figure 1.3) (Postma, 2006).

Disentangling plastic from genetic responses to environmental change is challenging in natural populations (Merilä and Hendry, 2014). Animal

models, a type of mixed model, can decompose phenotypes into genetic and environmental components and predict individual breeding values using pedigree-based correlations among related individuals (de Villemereuil, 2018). Although obtaining pedigrees in free-ranging animals requires extensive longitudinal studies (Teplitsky et al., 2014; Kruuk and Hadfield, 2007), animal models remain a powerful approach to study evolution in the wild, particularly with recent methodological advancements (Postma, 2006; Hadfield et al., 2010; De Villemereuil et al., 2018).

Body size modification in natural populations

Body size have been proposed as a third universal response to climate change (Gardner et al., 2011; Sheridan and Bickford, 2011). Such responses would be particularly relevant because body size is a critical life history trait in organisms, influencing lifespan (Blueweiss et al., 1978), metabolism (Brown et al., 2004) and reproductive biology (Blueweiss et al., 1978). Thus, understanding the factors driving variation in body size is a crucial goal in ecology because it may ultimately affect demographic parameters (Blueweiss et al., 1978; Brown et al., 1993).

Recent studies have documented body size modifications in response to climate change across various taxa, including birds (Grant and Grant, 2006; Teplitsky et al., 2008; Shipley et al., 2022; Biquet et al., 2022), mammals (Ozgul et al., 2009; Rézouki et al., 2016; Canale et al.,

2016; Fietz et al., 2020; Hantak et al., 2021; Li et al., 2022), amphibians (Reading and Jofré, 2021), and fish (Hattab et al., 2021). Despite the major influence of body size on life history traits (Brown et al., 2004), the question of the adaptive nature and the proximal causes of body size changes in response to climate change remain largely open (Gardner et al., 2011; Teplitsky and Millien, 2014).

Several hypotheses have been advanced to body size response to climate change (Yom-Tov and Geffen, 2011). A widely discussed pattern is that body size varies with latitude and elevation, with species tending to be larger in colder climates, a phenomenon referred to as "The Bergmann's rule" (Bergmann, 1847). This pattern could explain in theory the observed tendency of organisms to become smaller in response to global warming (Fietz et al., 2020; Hattab et al., 2021). Bergmann's rule generally receives support at large temporal or geographical scale. For example, a meta-analysis by Millien et al. (2006) suggests that 62% to 83% of vertebrate fossils conform to Bergmann's rule. However, the application of Bergmann's rule at the population level is more questionable (Gardner et al., 2011) and leads to unclear expectations (Teplitsky et al., 2008). Although originally attributed to the selective advantage of larger body size in reducing heat loss in cold environments, the proximate causes underlying Bergmann's rule remain ambiguous

(Yom-Tov and Geffen, 2011). Multiple environmental factors, beyond temperature alone, likely influence body size (Blois et al., 2008; Yom-Tov and Geffen, 2011). For instance, in Alaskan shrews (*Sorex*), increased food availability during warmer winters, rather than temperature alone, led to higher metabolic rates and smaller body sizes across a temporal scale in response to global warming (Ochocińska and Taylor, 2003).

Regardless of the proximate mechanisms, predictions from the Bergmann's rule suggest body size shrinking to be an adaptive response to climate change. However, although shrinking body size in response to climate change have been observed, the adaptive nature of such response have rarely been investigated (Gardner et al., 2011; Teplitsky et al., 2014), and if so, poorly support this pattern (Table 1).

In contrast, environment-induced body size shrinking could be maladaptive (Ozgul et al., 2009), especially given the strong selection for increased body size (Andersson, 1994). Body size reduction could simply result from environmental constraints such as food availability (Yom-Tov and Geffen, 2011). In mammals, adult body size is primarily determined during the growth period in early life stages (Lumey, 1992), and numerous studies have investigated the effects of poor environmental conditions during early development and their negative long-term impacts (Metcalf and Monaghan, 2001;

Table 1: Adaptive evolution of body size in response to climate change. A synopsis of long-terms studies in the wild that tested for adaptive evolution of body size modification in response to climate change while controlling for prediction error for breeding values (Hadfield et al., 2010) and temporal phenotypic trend (Postma, 2006). We reported the species studied, the proxy of body size used, the time range of study, the direction of the phenotypic change and the presence of adaptive evolution in the phenotypic changes observed. A change was considered as adaptive if the sign of phenotypic change matched the sign of selection.

Species	Trait	Time	Sign of change	Genetic	Adaptive	Reference
Red-billed gull (<i>C. scopulinus</i>)	body mass	1958-2004	-	N	N	(Teplitsky et al., 2008)
Soay sheep (<i>Ovis aries</i>)	body mass	1986-2006	-	N	N	(Ozgul et al., 2009)
Great tits (<i>P. major</i>)	body mass	1979-2008	-	N	N	(Husby et al., 2011)
Great tits (<i>P. major</i>)	wing length	1979-2008	-/+	N	N/Y	(Husby et al., 2011)
Great tits (<i>P. major</i>)	wing length	1979-2008	-/+	N	N/Y	(Husby et al., 2011)
Snow vole (<i>C. nivalis</i>)	body mass	2006-2014	=	Y	N	(Bonnet et al., 2017)
Atlantic salmon (<i>S. salar</i>)	body size	1977-1989	=	N	N	(Hajduk et al., 2020)

Dmitriew, 2011). Although compensation mechanisms exist, characterized by increased growth rates following a "poor start" compensation is often incomplete and are associated with a cost (Metcalf and Monaghan, 2001), resulting in maladaptive smaller adult size (Ho et al., 2010) that reduced fitness (Hantak et al., 2021).

Prediction of evolution

Given the importance of body size in mammalian biology, predicting the evolutionary response of body size is crucial for assessing the state of a population and its odds of persistence facing climate change (Gonzalez et al., 2013). Furthermore, comparing the estimated genetic changes (through the breeding values) of population to the prediction of response to climate change to selection provides insights into how organisms respond to selection (the underpinning of adap-

tive evolution) in the wild and tests our ability to predict evolutionary changes and to decrypt the underlying mechanisms (Morrissey et al., 2010; Gienapp et al., 2008).

The per-generation evolutionary response to selection in a given trait, R , can be predicted using the Breeder's equation: $R = h^2 S$ (Morrissey et al., 2012), where h^2 represents the trait heritability (σ_a^2/σ_P^2), and S is the directional selection differential (the change of mean trait value within a generation) (Morrissey et al., 2010; Lynch and Walsh, 1998). The Breeder's equation (BE) has the strong advantage to give insight on how selection act on the trait studied by explicitly differentiate h^2 and S (Morrissey et al., 2010). However, the BE relies on the strong assumption of causality between the trait and the fitness, and require that all traits that covariate with fitness

are included in the model to yield correct predictions (Morrissey et al., 2010).

In addition to the BE, responses to selection in natural populations can be obtained by Robertson-Price's Secondary Theorem of Natural Selection (STS) (Price et al., 1970). The STS postulates that the additive genetic covariance between a trait and relative fitness is a direct measure of the expected response to selection (Robertson, 1966; Price et al., 1970). By considering solely the genetic relationship between a trait and relative fitness, the STS does not necessitate measuring all traits that influence fitness to be measured, nor does it assume that selection on the phenotype is equal to selection on the genotype, as in the BE. STS is thus considering as a more robust model than BE to predict evolutionary changes (Morrissey et al., 2010, 2012). However, it does not provide any information about the underlying selection processes driving the evolutionary responses, unlike the BE (Morrissey et al., 2010). Thus, evaluating both the BE and the STS provide a complementary approach (Morrissey et al., 2012). Integrating both predictions allows for a more thorough understanding of trait evolution in natural populations under natural selection (Morrissey et al., 2012).

The present study

During recent decades, Alpine habitats have experienced more pronounced environmental alterations due to climate change than other low elevation areas, marked by a 2°C increase in min-

imal temperature, coupled with decreased summer precipitation and snowfall (Büntgen et al., 2014; Beniston, 2006). These changes particularly endanger endemic species, especially hibernating ones that are heat sensitive and highly seasonal (Wells et al., 2022).

In this context, the Alpine marmot (*Marmota marmota*) serves as an excellent model to study species' responses to climate change. The Alpine marmot is a highly social, hibernating rodent that lives in family groups organized around a dominant breeding pair (Allainé, 2000). Body size is critical for survival during hibernation, influenced by both social factors and environmental factors (Arnold, 1990; Farand et al., 2002). Notably, the body mass and size of Alpine marmots has decreased in recent years (Rézouki et al., 2016; Canale et al., 2016). Furthermore, various biological processes have been impacted by climate change, including smaller group size (Rézouki et al., 2016) and litter sizes (Tafari et al., 2013), and a significant drop in juvenile annual survival from 0.85 ± 0.16 to 0.42 ± 0.07 over 23 years (Rézouki et al., 2016).

The response of marmots to climate change appears to be maladaptive (Rézouki et al., 2016). This research aims (i) to establish body size variation of juveniles, (ii) to test for the adaptive nature of these changes, and (iii) to identify the mechanisms underlying these changes (plasticity or evolution). We used animal models (Wilson et al., 2010) to examine the genetic contri-

butions to changes in body size and mass over a 26-year period (1997-2023) in a population of Alpine marmots in the French Alps and quantified the selection pressures acting on body mass and body size. Our focus was on young-of-the-year, because this age class is particularly susceptible to environmental changes (Rézouki et al., 2016) and because early environment is known to affect adult fitness Alpine marmots (Berger et al., 2015).

According to either Bergmann's rule or the environmental constraints' hypothesis, a decrease in the body size of juvenile marmots is anticipated at the phenotypic level, particularly considering the trend of diminishing body size observed in prior research (Rézouki et al., 2016). However, the expected direction of selection varies between these hypotheses. Bergmann's rule suggests that smaller individuals have higher fitness (indicating negative selection on body size) (scenario of Figure 1.2). Conversely, the "environmental constraint hypothesis" posits that larger individuals have greater fitness, suggesting positive selection on body size (scenario of Figure 1.3).

MATERIAL AND METHODS

Study population

Study species

The Alpine marmot (*Marmota marmota*) is a cooperative breeder rodent, living in family groups formed of 2 up to 16 individuals (Allainé, 2000).

They are highly territorial, socially monogamous with groups composed of a dominant couple, mature subordinates of 2–4 years old, yearlings and young of the year, also called pups (Perrin et al., 1993). Territories remain stable over time and are mostly defended by the dominant male against other male intruders (Arnold, 1990).

Reproduction is despotic, where dominant individuals monopolize reproduction by suppressing reproduction of same-sex mature subordinates through harassment and antagonistic behaviors (Hackländer et al., 2003). Nevertheless, extra-pair paternity is common, especially from dispersing males (Goossens et al., 1998; Cohan et al., 2006). The dominance is established across years until death or eviction by another individual (Lardy et al., 2011). Subordinates attempt to take over dominance either in their natal group or another territory by leaving the family group between 2 and 4 years of age, either dispersing willingly or being chased by dominants. If dispersers cannot access dominance, they will surely die because dispersers never integrate a new family group as subordinate (Magnolon, 1999) and no lone marmot can survive hibernation (Arnold, 1988). Members of a family group hibernate in a same *hibernaculum* from mid-October to mid-April and pups emerge from the natal burrow between mid-June and mid-July (Arnold, 1988).

Alpine marmot is an altricial species with pups born hairless, eye closed and barely mov-

ing (Dupont, 2017). Pups emerge from the *hibernaculum* for the first time after weaning at 40 days (Allainé et al., 1998). At emergence, pups can vary greatly in their mass (8—96g) and body size (19—32cm), primarily due to stochastic variations among cohort (i.e. year of birth), sex and litter size (Allainé et al., 1998). Pups will reach adult size during their third active season (mean body mass : 4000g [1900—5600]; mean body size : 49cm [44—49]) (Dupont, 2017).

Data collection

The study was conducted at the Grande Sassièrre Nature Reserve (French Alps, 45°29'N, 6°59'E). The study area represents a fraction of the reserve area, hosting up to 34 marmot families.

Every year since 1990, from mid-May to mid-July, individuals within the study area are captured with two-door live traps baited with dandelions (*Taraxacum densleonis*). These traps are set near the entrance of the main burrow on each territory, facilitating the assignment of captured individuals to their respective family groups. Upon capture, marmots are temporarily housed in Hessian bags and tranquilized using Zolétil 100 (0.1 mL.kg⁻¹). Annual probability of capture ranged from 0.76 ± 0.07 to 0.92 ± 0.03 (Rézouki et al., 2016). Once tranquilized, individuals are sexed based on their ano-genital distance and morphological measures are taken. Then, we weight the individuals using a hand-held spring balance with a precision of 5 grams and tibia length with a caliper at a precision of 1

millimeter. All captured individuals are released on their territory after processing. All captured marmots are uniquely identified through a combination of a transponder chip implanted under the skin of the neck (Trovan Ltd, Germany), and metal ear tags. Further details about the capture protocol can be found in Rézouki et al. (2016).

Data selection and estimation of fitness

We focused our study on pups aged between 0 and 15 days old and used the tibia length as a proxy of overall body size. Although pups might have been captured and measured several times for both body mass and size, we only included the measure corresponding to the first capture in subsequent analyses, as only 100 and 14 pups (over 1287) have been measured several times for body mass and size respectively. We excluded years 1990 to 1996 from the analyses because tibia length data were not available for that period.

In Alpine marmots, morphology of pups is influenced by body growth (Allainé et al., 1998) and from mass gain during active season (Armitage et al., 1976). As weaning occur inside burrows, accurate estimations of birth were not possible. Hence, we defined pups age as the number of days after initial emergence to account for growth effect on body size. Additionally, the earlier young marmots are weaned, the more they weight at hibernation (Armitage et al., 1976). So, we defined the *capture time*, the relative lateness of emergence of pups, as the emergence

date (in days) relative to the within-cohort's minimal emergence date. In addition, we reconstitute from the data the group size and the litter size at birth of pups.

Estimation of selection parameters require assessing the relative individual fitness. We used the lifetime breeding success (LRS) which is the total number of pups produced during the whole life of an individual, as a proxy of fitness (Bonnet et al., 2022). As the LRS needs to be computed on the entire life of individuals, we carried out the models to estimate selection parameters on a subset of the data in order to select individuals with complete LRS. Thus, we only included extinct cohorts in our analysis. We considered cohorts extinct (i.e. all individuals of this cohort realized their LRS) if they last 7 years after the year of birth, which represent the 80% of the cumulative age of motherhood in our data

Social pedigree

Quantitative genetics analyses hinge upon disentangling the genetic contribution to individual phenotypic variation based on the phenotypic resemblance between relatives (Kruuk and Hadfield, 2007). The expected relatedness can be derived from the information contained in the population pedigree (Wilson et al., 2010).

In Alpine marmots, the social structure makes parentage inference straightforward: the mother is the current territory's dominant female, and the father is the dominant male for each co-

hort of pups. A genetic pedigree of our study was available up to 2015 and based on 16 microsatellites. To avoid different degree of pedigree reliability throughout the study, we thus only relied on the social pedigree. Although social pedigree can be less precise than genetic based pedigree, we observed a high correlation of both pedigrees in our population: 98.3% maternal match and 90.2% paternal match. Mismatches were likely due to extra-pair reproductions (Cohas et al., 2006), with 75 out of 872 instances of extra-pair paternities ($8.6\% \pm 0.4$) and 11 out of 917 instances of extra-pair maternities ($1.2\% \pm 0.9$). Although misassigned paternities could slightly underestimate the additive genetic variance, we assumed this effect to be quite negligible at the observed level of extra-pair reproduction and any bias would be conservative (Charmantier and Réale (2005)). We also computed the inbreeding coefficient from the pedigree, as mating between relatives occur in the Alpine marmots (Goossens et al., 2001). We performed pedigree analyses using the `kinship2` (Sinnwell et al., 2014) and `pedantics` (Morrissey and Wilson, 2010) packages in R software (R Core Team et al., 2024). A visualization of the pedigree is available in Appendix B.

After removing non-informative individuals (*pedigree pruning*, Wilson et al. (2010)), the study's pedigree included 1417 individuals across nine generations, representing 198 families over 32 years, originating from 100 founder

individuals. The mean inbreeding coefficient was $6.2\% \pm 0.3$, with 167 individuals (11.9%) exhibiting intermediate inbreeding levels ($f = 0.25$) and 24 individuals exhibiting high inbreeding rates ($f \geq 0.4$).

Quantitative genetic analysis

Partition of phenotypic variance

Phenotypic variance partitioning was conducted using animal models, a form of mixed model which include breeding values as random effect (Kruuk and Hadfield, 2007). The estimations of fixed and random effects and the underlying modeling hypothesis in an animal model are entirely similar to those of a 'classic' mixed linear model (Wilson et al., 2010), although a relatedness matrix allows estimating the additive genetic variance parameter σ_a^2 .

We partitioned phenotypic variation, controlling for other sources of variance of body mass and size that could be confounded with resemblance between relatives (Kruuk, 2004). Furthermore, as body mass and body size are likely to be genetically correlated (Huxley et al., 1993), we estimated their (co)variance using a bivariate animal model with both traits as the response variable. We then fitted the model:

$$\begin{pmatrix} \text{mass} \\ \text{size} \end{pmatrix}_{i,t} \sim \mathbf{X}\mathbf{b}_{i,t} + \mathbf{a}_i + \mathbf{m}_i + \mathbf{c}_t + \mathbf{r}_{i,t} \quad (2)$$

where $\begin{pmatrix} \text{mass} \\ \text{size} \end{pmatrix}_{i,t}$ is the vector of observed body mass and body size of individual i at time t mod-

elled as Gaussian traits, \mathbf{X} is the design matrix for the fixed effects, $\mathbf{b}_{i,t}$ is the vector of fixed effect parameter estimates, and \mathbf{a}_i , \mathbf{m}_i , \mathbf{c}_t are the random effects with which to estimate the breeding values (Equation 4), mother identity (effect of the mother on its offspring) and cohort year, respectively. The vector \mathbf{r}_i represents the residuals.

As both body mass and body size are included as response variables, random effects $i \in [m, c, r]$ are assumed to be drawn from a multivariate normal distribution MN from which (co)variance components σ_i^2 and cov_i are estimated for each random effect between body size and body mass, such as:

$$\mathbf{i} \sim \mathcal{MN}\left(0, \begin{pmatrix} \sigma_i^2(\text{mass}) & cov_i \\ cov_i & \sigma_i^2(\text{size}) \end{pmatrix}\right) \quad (3)$$

The predicted breeding values \mathbf{a}_i are also assumed to be drawn from a multivariate normal distribution (notations are taken from de Villemereuil (2012)):

$$\begin{pmatrix} \mathbf{a}_{\text{mass}} \\ \mathbf{a}_{\text{size}} \end{pmatrix} = \begin{pmatrix} a_{1,\text{mass}} \\ \vdots \\ a_{n,\text{mass}} \\ a_{1,\text{size}} \\ \vdots \\ a_{n,\text{size}} \end{pmatrix} \sim \mathcal{N}\left(\begin{pmatrix} 0 \\ 0 \end{pmatrix}, \mathbf{G} \otimes \mathbf{A}\right) \quad (4)$$

Where \mathbf{A} the relatedness matrix derived from pedigree with $A_{ij} = 2\phi_{ij}$ with ϕ_{ij} the coefficient

of co-ancestry, with $2\phi_{ij}$ corresponding to the expected proportion of shared alleles between individual i and j (e.g. $\phi = 0.50$ between one mother and its offspring) and \mathbf{G} is the additive genetic (co)variance matrix, containing the additive genetic (co)variances between body mass and body size :

$$\mathbf{G} \otimes \mathbf{A} = \begin{pmatrix} \sigma_a^2(mass)\mathbf{A} & cov_a\mathbf{A} \\ cov_a\mathbf{A} & \sigma_a^2(size)\mathbf{A} \end{pmatrix} \quad (5)$$

Weighted by the relatedness matrix \mathbf{A} , this method allowed to estimate the additive genetic variance parameter σ_a^2 of body mass and body size as the expected variation arising from resemblance between relatives, and thus the individual breeding values (Wilson et al., 2010).

Variance parameters are typically expressed relative to the total phenotypic variation (Lynch and Walsh, 1998). However, variance can also arise from fixed effects, which is often neglected, although it can underestimate the total phenotypic variance (De Villemereuil et al., 2018). Thus, following the indication of De Villemereuil et al. (2018), we included the variance from fixed effect σ_f^2 in the computation of the total phenotypic variance for the trait z , $\sigma_{P,z}^2$, such as:

$$\sigma_{P,z}^2 = \sigma_{a,z}^2 + \sigma_{m,z}^2 + \sigma_{c,z}^2 + \sigma_{r,z}^2 + \sigma_{f,z}^2 \quad (6)$$

with σ_i^2 the variance component $i \in [a, m, c, f]$, σ_P^2 the total phenotypic variance, σ_a^2 the additive genetic variance, σ_m^2 the maternal

identity variance, σ_c^2 the cohort year variance, σ_r^2 the residual variance and σ_f^2 the variance of fixed effects for the trait z (De Villemereuil et al., 2018).

Fixed effects selection and modelling the non-linear association between year and body size

Additional fixed effect to the animal model allow to control for effect that could artificially increase the differences between relatives, like differences due to age (Kruuk and Hadfield, 2007). Also, properly controlling for temporal variation in phenotypes is crucial to estimate breeding values correctly, as part of phenotypic variation may be confounded with temporal trends in predicted breeding values (Postma, 2006). Failure to do so can lead to erroneous conclusions about the genetic trends in evolution (Postma, 2006; Hadfield et al., 2010; Morrissey et al., 2010).

We entered the age of the pups, the time of capture, the litter size and group size at birth as linear covariates, and sex as a factor as fixed effects in the animal model. All variables significantly influenced body mass and body size. Inbreeding coefficient was included as a covariate, although it was not in the selected model, because it can bias upwards the estimates of additive genetic variance (Reid and Keller, 2010).

Pre-visualization of temporal variation of tibia length suggested a highly non-linear relationship between cohort year and tibia length (Figure 2), making a simple linear regression in-

adequate. We implemented a new methodology, not included in packages to run animal models, using generalized additive model (GAM) (Wood, 2017).

GAMs are non-parametric regression methods based on non-linear smoothing functions, providing a more flexible fit than simple regression methods. The GAM model is expressed as:

$$y_i = \sum_{j=1}^q f_j(x_i) + \epsilon_i \quad (7)$$

with y_i the response variable, $f(x_i)$ the unknown smoothed function of the i^{th} predictor x , q the number of dimension of the model and $\epsilon \sim \mathcal{N}(0, \sigma_\epsilon^2)$ the residuals. To be implemented into the animal model, the f functions need to be defined so that the Equation 7 becomes a linear model. To that end, we define an ensemble of basis functions so that $g_j(x)$ the j^{th} function is:

$$f(x) = \sum_{j=1}^q g_j(x) \gamma_j \quad (8)$$

For this study, we chose a cubic spline basis following the method described in Gu and Gu (2002) (p.37). A cubic spline approximates a function using connected cubic polynomials, with knots defining sections based on the quantile distribution of the predictor variable (here, cohort year).

Knots determine the smoothness of the resulting curve (Wood, 2017). The spline method decomposes the cohort year variable into g_j vari-

ables, which were included in the design matrix $X_{i,t}$ of the animal model of Equation 2 to estimate the associated γ_j , thereby modeling non-linearity. We determined the optimal number of knots for each trait by sequentially adding g_j and determined if they were different from 0 for body mass and tibia length. Consequently, mass variation was modeled with a simple linear relationship, while tibia length variation was modeled with three knots (Figure 2).

After previewing the effect of the year on body mass and body size, we have identified two distinct periods. The first period between 1997 and 2005 corresponds to a strong decline of body size, which could reflect a period of strong selection pressure. The second period, between 2006 and 2023, correspond to a stabilization of body size. Hence, we performed the subsequent analysis for the overall study time and for both identified periods. Results of fixed effects estimates of the animal model of Equation 2 can be found in Appendix C.

Bayesian framework

We fitted the animal model for the marmot body mass and size data with the MCMCglmm package (Hadfield, 2010) in the R software (version 4.2.1) (R Core Team et al., 2024). We worked in a Bayesian framework and produced *posterior* probabilistic distributions and *prior* probabilistic distribution of the parameters to be estimated (Hadfield, 2010, 2014). We reported all parameters with the mode of the *posterior* distribution

and its 95% credible interval ([lower IC; upper IC]). The main advantage of a Bayesian inference is that it enables to propagate uncertainty of estimation when computing composite parameters like heritability and when estimating the temporal trend of breeding values of body mass and body size (Hadfield, 2010).

Priors for fixed effect were set as normal distribution with mean 0 and uniform distribution. We used a Fisher’s prior with parameters expanded priors for the variance components (Gelman, 2006). Parameter expansion consists into splitting the random effect u_i into two independent components : $u_i = \alpha\eta_i$ with $\eta_i \sim \mathcal{N}(0, \sigma_\eta^2)$. Parameter $\alpha \sim \mathcal{N}(0, \sigma_\alpha^2)$ is the working parameter allowing for bigger *jump* during parameters space exploration and prevent the MCMC chains to get stuck near 0 thus improving mixing of the chains and convergence (Gelman, 2006).

We set the number of iteration to $1.2 * 10^7$ with a burning of 300,000 and a thinning interval of 5000 to ensure every fixed and random effects have an effective sample size (independent draws from *posterior* distribution) of 1000 as recommended by Hadfield (2014).

The significance of variance components becomes complex in Bayesian context framework, because direct comparisons to zero are not feasible as variance terms are always superior to 0. While permutations can generate null distributions to produce pseudo p-values (Pick et al., 2023), the associated computational costs have

prompted us to defer this analysis for future publication. Hence, only credible intervals of variance will be reported.

Estimating evolutionary change

We investigated evolutionary changes by studying (i) the temporal trend of estimated breeding values of body mass and size and (ii) the predicted response to selection based on the relationship between body mass, tibia length and fitness.

Temporal trend of breeding values

From the bivariate animal model of Equation 2, we extracted the complete posterior distribution of breeding values (Hadfield et al., 2010) of body mass and size for each individual and tested for temporal changes over the course of the study. We assessed the temporal trends of predicted breeding values by regressing the mean cohort year breeding values of each MCMC iteration as a function of the cohort year (Hadfield et al., 2010). Thus, we obtained a distribution of regression slopes reflecting the estimated genetic change over time of our marmot population.

To assess whether genetic changes are due to adaptive evolution or random genetic changes, we compared the estimated change in breeding values to expected genetic changes under scenarios of genetic drift, i.e. random fluctuation of genes flow (Hadfield et al., 2010). To this end, we simulated random breeding values for body mass and size following the approach of Had-

field et al. (2010). We also assessed the temporal trends of these generated breeding values by regressing the mean cohort year breeding values of each MCMC iteration on the cohort year. Then, we calculated the proportion of the posterior distribution of these simulated slopes under the drift scenario that returned a regression value more positive than the posterior mode of the observed temporal slopes. Thus, we obtained the posterior probability that the estimated genetic changes were higher than those expected by drift alone.

We expressed the predicted breeding values slopes per generation, by multiplying the slopes by 5.94 which correspond to the mean generation time in days of the Alpine marmots of our population of La Grande Sassi re.

Prediction of responses of body mass and body size to selection

Prediction of response to selection require the covariance between trait and the relative fitness for prediction of evolutionary changes. We expressed relative LRS (Lifetime Reproductive Success) (Lande and Arnold, 1983) as:

$$w(z) = \frac{W(z)}{\bar{W}(z)_t} \quad (9)$$

With $w(z)$ representing the relative fitness of phenotype z , $W(z)$ the absolute fitness, and \bar{W}_t the mean fitness per cohort (Lande, 1979), LRS was calculated for individuals born up until 2016 (see "Data selection and estimation of fitness").

We used trivariate animal models with $\begin{pmatrix} \text{mass} \\ \text{size} \end{pmatrix}_{i,t}$ as a response variable to estimate the covariance between trait and fitness $\sigma_P(z, w)$ (the selection differentials) and the phenotypic (co)variance matrix \mathbf{P} for the multivariate breeder equation (MBE). We also estimated the additive genetic covariance between trait and fitness $\sigma_a(z, w)$ require for the secondary theorem of selection (STS).

As body mass and body size are likely to be correlated (Huxley et al., 1993), we used the Multivariate formulation of the Breeder Equation (MBE) (Lande, 1979), expressed as:

$$\mathbf{R} = \mathbf{G}\mathbf{P}^{-1}\mathbf{S} \quad (10)$$

with \mathbf{R} the vector of expected response to selection, \mathbf{G} the additive genetic (co)variance matrix between mass and size, \mathbf{P} the phenotypic (co)variance matrix of both traits and \mathbf{S} the vector of selection differentials.

In order to estimate \mathbf{S} and \mathbf{P} , we conducted a trivariate animal model $\begin{pmatrix} \text{mass} \\ \text{size} \end{pmatrix}_{i,t}$ as response variables with no random effect to simply extract $\sigma_P(\text{mass}, w)$ and $\sigma_P(\text{size}, w)$, the selection differentials for body mass and body size, respectively, from the (co)variance matrix of residuals. Similarly, \mathbf{P} was computed based on the matrix of residuals of this model, for which we also added the variance arising from fixed effects, like described in "Partition of phenotypic variance" (De Villemereuil et al., 2018). The additive genetic (co)variance matrix \mathbf{G} was derived from the

bivariate animal model of Equation 2.

Selection differentials reflect the total selection (direct and indirect) acting on each trait (Price et al., 1970). We also computed the variance-normalized selection gradient:

$$\beta_{\sigma} = \begin{pmatrix} 1/\sigma_{mass} & 0 \\ 0 & 1/\sigma_{size} \end{pmatrix} \mathbf{P}^{-1} \mathbf{S} \quad (11)$$

with σ_{mass} and σ_{size} the standard deviation of body mass and body size, respectively. Selection gradients are conceptually equivalent to a standard multiple regression analysis estimates (Lande and Arnold, 1983; Hereford et al., 2004). In contrast to selection differentials, selection gradients measure the strength and direction of direct selection only on body mass (or size), accounting for indirect selection from size (or mass) through trait genetic correlation.

In order to assess the importance of genetic correlation in the response to selection, we also evaluated the predictions from the MBE assuming no genetic correlation, thus $\sigma_a(mass, size) = 0$ (Morrissey et al., 2012).

The STS (Robertson, 1966; Price et al., 1970) posits that evolutionary change in phenotype between successive generation is equal to the additive genetic covariance between the trait and relative fitness $\sigma_a(z, w)$. Three models were conducted to estimate $\sigma_a(z, w)$ for the following time periods: between 1997 and 2016, and the two periods identified in "Fixed effects selection and modelling the non-linear association

between year and body size": 1997 to 2005 and 2006 to 2016. The models were similar to Equation 2 except that relative fitness $w(z)$ was included. No fixed effects were fitted for $w(z)$. Hence, STS prediction response to selection was computed straightforward as:

$$R = \sigma_a(z, w) \quad (12)$$

According to Bergmann's rule or the environmental constraint hypothesis, a decrease in body mass and body size is expected at the phenotypic level. However, under Bergmann's rule, this negative trend should be associated with negative temporal trends in breeding values, as well as negative selection differentials \mathbf{S} and selection gradients β_{σ} for body mass and body size. Also, predictions of smaller body size by the MBE and the STS are expected. In contrast, under the environmental constraint hypothesis, we would expect a positive temporal trend in breeding values and positive selection differentials and selection gradients, associated with positive response predictions to selection by the MBE and the STS.

Using the full potential of Bayesian inference and following the considerations of Muff et al. (2022), we used an evidence-based language to interpret our results rather than the classical dichotomy "significant versus non-significant" that has been overly discussed as misleading in discussing confidence in statistical inferences (Goodman, 2008). Strength of confidence in the parameters of selection and response predictions

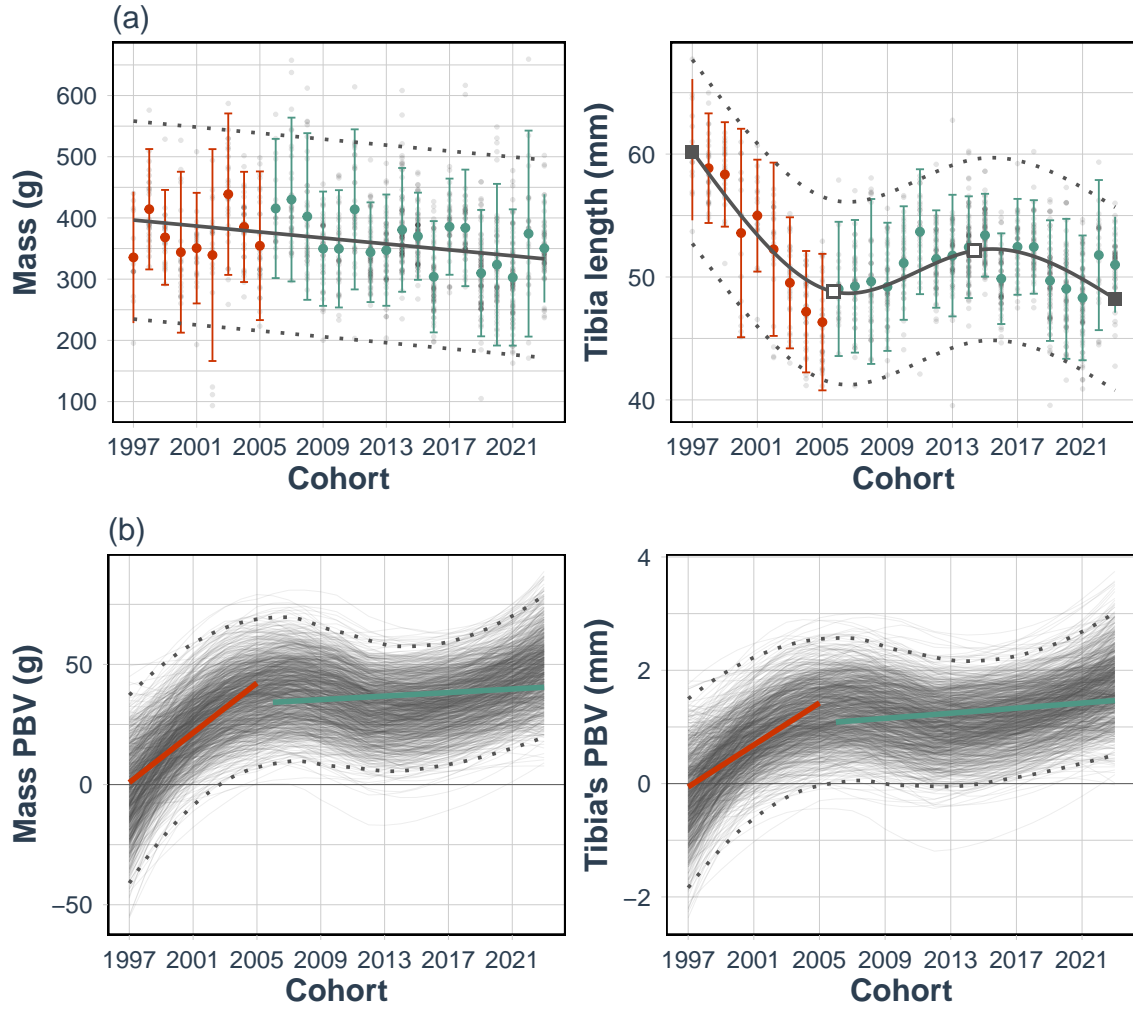


Figure 2: Temporal variation of phenotype and breeding values. (a) Temporal variation of mass and size (corrected for age, capture time and sex) of under-one-years old Alpine marmots (*Marmota marmota*) in the French Alps between 1997 and 2023. Solid black lines represents the linear and splined trends for mass and size, respectively. White squares represent the knots used to account for the non-linearity association of size and year. (b) Temporal trend of predicted breeding values (PBV), the contribution of additive genetic effect to trait's value. Each gray line represents the cohort's year average estimated breeding value for one iteration of the MCMC chain of the bivariate animal model using loess regression. Red elements of the plots correspond to the period 1997-2005, and pale blue elements correspond to the period 2006-2023. Dotted lines represent the 95% interval of predicted values.

were assessed as the mean number of MCMC iterations greater than 0, following our initial hypothesis.

Details and code of the statistical analysis are available in the following link: [github link](#).

RESULTS

Phenotypic variation of body size

In total, 1287 individuals were used to estimate phenotypic and genetic variation across the study period (44.8 [16—96] per year). Mean body mass of pups was $380.87\text{g} \pm \text{sd} = 100.38$ and mean tibia length was $52.40\text{mm} \pm \text{sd} = 4.58$.

As expected by previous studies results

(Rézouki et al., 2016; Canale et al., 2016), the mean mass of pups decreased by -2.44g per year ($\text{CI}=[-3.02, -1.186]$, $p < 0.001$) and mean tibia length decreased by -0.15mm per year ($\text{CI}=[-0.18, -0.12]$, $p < 0.001$) over the entire study period (1997-2023) (Figure 2.a). A negative phenotypic trend was also observed for the size of the pups between 1997 and 2005 with a sharp decreased of -1.86mm per year ($\text{CI}=[-2.04, -1.69]$, $p < 0.001$), while no evidence of trend in phenotypic variation for mass was detected ($\beta = 1.05\text{mm}$, $\text{CI}=[-2.83, 4.94]$, $p = 0.59$) (Figure 2.a). However, mass decreased by -4.49g ($\text{CI}=[-5.4, -3.56]$, $p < 0.001$) during the period 2005-2023, while we found only a weak support for a negative temporal trend in the size of pups during this period ($\beta = -0.04\text{mm}$, $\text{CI}=[-0.09, 0]$, $p < 0.053$) (Figure 2.a).

Selection acting on body size

Estimation of selection differentials and selection gradient were estimated using animal model including $(mass, size, w(z))$ as response variables. Congruent with the environmental stress hypothesis, the selection differentials were positive for mass and size for all periods considered, despite the observed negative phenotypic trend Table 2. Furthermore, they were systematically qualitatively greater in the period 1997-2005 than in the period 2005-2023 Table 2, although no evidence of difference of selection was found between both period for body mass ($P(1997-2005 > 2006-2023) = 48.3\%$)

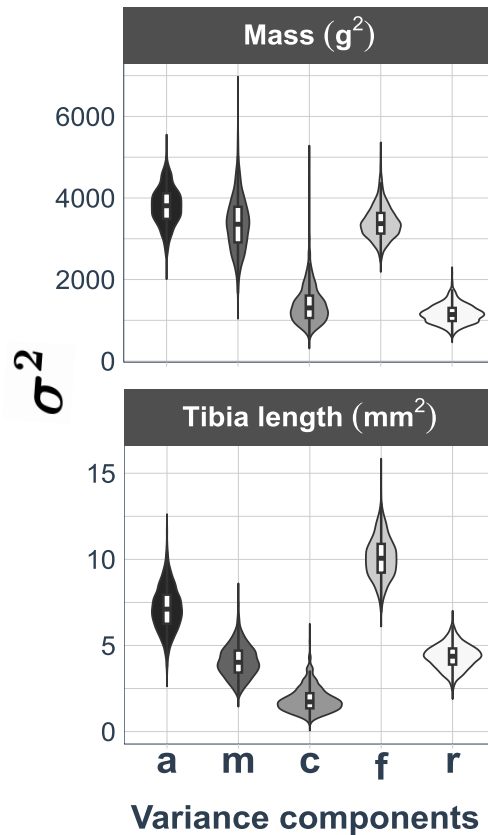


Figure 3: Variance component posteriors. Posterior distribution from the bivariate animal model $(mass, size)_t$ of the variance component influencing phenotype of body mass and body size in a population of alpine marmots (*Marmota marmota*) of the French Alps between 1997 and 2023. Violins represents the posterior distribution of additive genetic a, maternal identity m, cohort's year c, variance arising from fixed effect f and the residuals' variance r. Box plots represent the median and the 25% and 75% quantiles.

and size ($P(1997-2005 > 2006-2023) = 42.2\%$).

The normalized selection gradients β yielded a different pattern than selection differentials, and strong evidence for positive directional selection was only observed for the period 1997-2005 for size. Weaker evidence of positive directional selection was observed for the overall study period for both trait Table 2.

Table 2: Selection parameters. Selection parameters of body size of a population of an Alpine marmots population of the French Alps obtained from a multivariate animal model [*mass, size, fitness*]. Are represented the posterior mode and 95% credible interval of the selection differentials S and variance-normalized selection gradient β_σ for mass and size for the three periods. Parameters are expressed as within per generation change. Element in bold and italic represent the parameters with less than 5% and 10%, respectively, of MCMC iteration ≤ 0 .

	Mass (g)			Tibia length (mm)		
	Overall study	1997-2005	2006-2023	Overall study	1997-2005	2006-2023
S	24.347 [3.060; 41.782]	<i>22.416</i> [-8.006; 55.849]	19.444 [-3.202; 40.369]	1.239 [0.439; 2.106]	1.558 [0.163; 2.738]	0.965 [-0.006; 2.065]
p	0.003	0.088	0.047	0.005	0.012	0.032
β_σ	<i>0.160</i> [-0.083; 0.402]	0.139 [-0.166; 0.451]	0.079 [-0.186; 0.364]	<i>0.139</i> [-0.059; 0.321]	0.204 [0.032; 0.427]	0.172 [-0.144; 0.446]
p	0.088	0.186	0.289	0.074	0.024	0.140

Potentiality of response to selection

Results from the animal model showed that both mass and size of pups were heritable. Additive genetic variance was detected for both traits, contributing to 29% [22, 36] of total phenotypic variation of mass ($\sigma_a^2=3803.9$, $CI=[2878.3, 4727.5]$) and 26% [18, 34] of size ($\sigma_a^2=7.2$, $CI=[4.5, 9.5]$). Maternal identity contributed to 26% [18, 33] of mass variation ($\sigma_m^2=3376.7$, $CI=[2222.3, 4773.9]$) and to 15% [9, 20] of size variation ($\sigma_m^2=4.1$, $CI=[2.3, 5.7]$). Stochastic among-year variance contributed the least for both trait, explaining 11% [6, 17] of mass variation ($\sigma_c^2=1394.0$, $CI=[684.1, 2273.8]$) and for 7% [3, 11] of size variation ($\sigma_c^2=1.9$, $CI=[0.7, 3.3]$). A summary of the contribution of each random effect can be found in Appendix D.

Additionally, mass and size exhibited a strong correlation at both the phenotypic level ($r=0.73$, $CI=[0.67, 0.78]$, $p < 0.001$) and the genetic level ($\rho=0.94$, $CI=[0.88, 0.98]$, $p < 0.001$),

indicating that both traits share almost all of their additive genetic variance.

Estimated genetic change

As expected, genetic changes towards larger marmots were found. The temporal trend of breeding values indicate strong evidence of genetic changes toward larger individuals during the overall study and the 19997-2005 period for body mass and for body size. Only weak evidences of such genetic change were found for the 2006-2023 period (Table 3; Figure 4).

The comparison with the observed slope of PBV with random slopes generated under genetic drift indicates that the probability of increasing more than expected by drift alone was 84.8% and 84.3% for the overall study, 90.4% and 90.1% between 1997 and 2005, and 64.1% and 70.7% between 2006 and 2023 for mass and size, respectively. Although posterior probability indicated weak to medium evidence, it should be

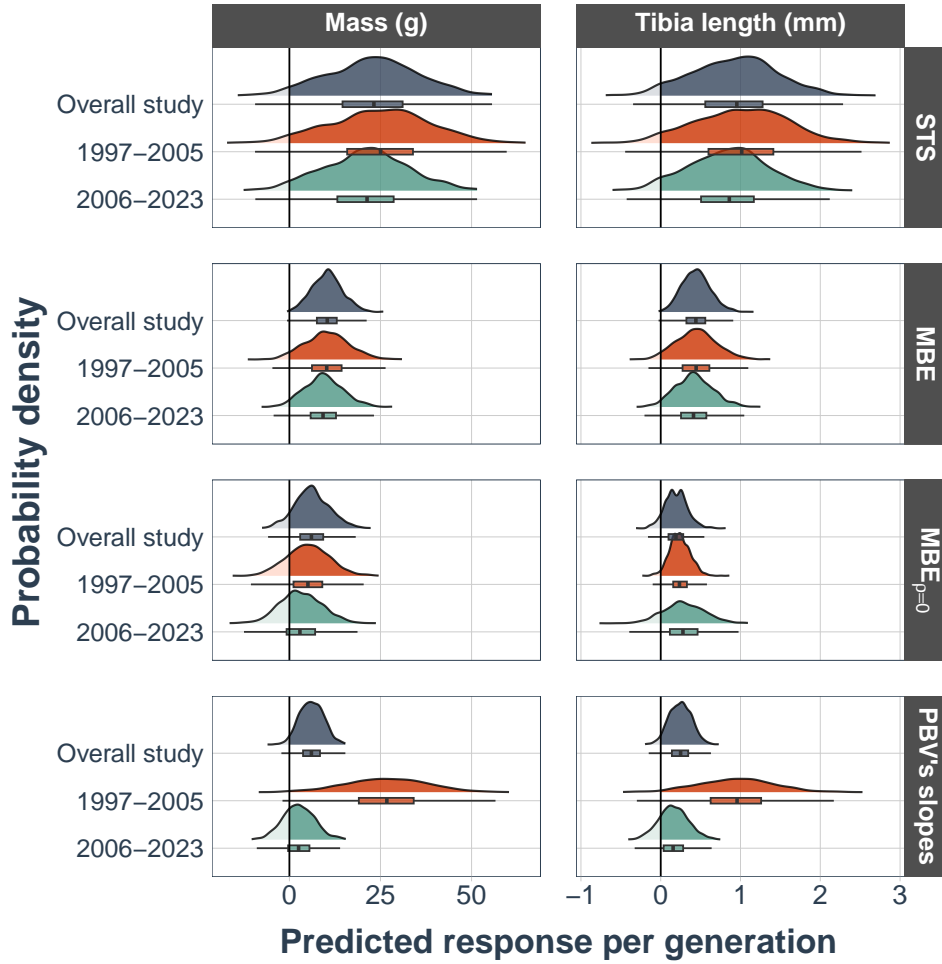


Figure 4: Posterior distributions of predicted responses to selection and estimated genetic change. Posterior of the predicted response to selection and estimated genetic changes of a population of Alpine marmots (*Marmota marmota*) of the French Alps. Results are expressed per generation for mass and tibia length for all cohort's year ('overall study'), between 1997-2005 corresponding to a phenotypic decrease of size and between 2006-2023 corresponding to a stabilization of size's phenotype. Predictions were made with the Robertson-Prince's secondary theorem of evolution (STS) (Robertson, 1966; Price et al., 1970) using the additive genetic covariance between trait and fitness, the multivariate breeder equation accounting for genetic correlation between both trait (MBE) and without genetic correlation ($MBE_{\rho=0}$) and the slopes of predicted breeding values (PBV's β) as function of cohort's year (Hadfield et al., 2010).

noted that this method provides highly conservative results (Hadfield et al., 2010).

Prediction of evolutionary responses

As a prerequisite for the use of the secondary theorem of selection (STS), we observed significant additive variance for relative fitness for all period considered (overall study: 0.282 [0, 0.645]; 1997-2005: 0.284 [0, 0.1.036]; 2006-2016: 0.286 [0, 0.802]). In line with the environmental stress

hypothesis, the MBE and the STS predicted positive evolutionary changes for both body mass and size (Table 3; Figure 4). No evidence were found for different responses between both periods, according to the prediction of the MBE for body mass ($P(1997-2005 > 2006-2023) = 54.4\%$) and body size ($P(1997-2005 > 2006-2023) = 53.2\%$). In contrast, medium evidence was found for stronger response during the 1997-2005 period compared to the 2006-2016 pe-

Table 3: Predicted response to selection and estimated genetic change. Predicted responses to selection per generation for mass and tibia length in a population of Alpine marmots (*Marmota marmota*) of the French Alps between 1997 and 2023. Predictions were made with the Robertson-Prince's secondary theorem of evolution (STS) (Robertson, 1966; Price et al., 1970) using the additive genetic covariance between trait and fitness, the multivariate breeder equation accounting for genetic correlation between both traits (MBE) and without genetic correlation (Overall study $_{\rho=0}$). Estimated genetic change is represented by the slopes of predicted breeding values as function of cohort's year (Hadfield et al., 2010). Element in bold and italic indicate parameters that are significantly greater than 0 with less than 5% and 10% of MCMC iteration ≤ 0 , respectively.

	Mass (g)			Tibia length (mm)		
	Overall study	1997-2005	2006-2023	Overall study	1997-2005	2006-2023
STS	21.63 [-2.37,44.38]	23.85 [-5.27,47.11]	19.70 [-2.25,40.78]	0.83 [-0.22,1.74]	0.93 [-0.16,2.06]	0.75 [-0.16,1.67]
<i>p</i>	0.035	0.035	0.038	0.043	0.041	0.048
MBE	10.13 [1.50,17.43]	14.35 [-1.73,31.65]	6.83 [-2.87,18.48]	0.44 [0.08,0.77]	0.65 [-0.06,1.36]	0.30 [-0.25,1.46]
<i>p</i>	0.001	0.044	0.032	0.002	0.032	0.027
MBE $_{\rho=0}$	<i>4.58</i> [-3.66,13.96]	<i>2.87</i> [-17.43,22.74]	<i>3.31</i> [-6.03,13.76]	<i>0.26</i> [0,0.59]	0.53 [-0.12,1.22]	<i>0.16</i> [-0.19,0.61]
<i>p</i>	0.088	0.186	0.289	0.074	0.024	0.140
PBV's β	6.04 [0.83,11.03]	26.74 [8.14,44.43]	<i>2.52</i> [-4.53,9.60]	0.25 [0.02,0.47]	0.96 [0.18, 1.69]	<i>0.15</i> [-0.15,0.48]
<i>p</i>	0.029	0.006	0.280	0.032	0.021	0.187

riod according to the STS, for body mass weak evidence that it was lower for the period ($P(1997-2005 > 2006-2023) = 79.8\%$) and for 2006-2016 ($P(MBE > MBE_{\rho=0}) = 86.0\%$). body size ($P(1997-2005 > 2006-2023) = 80.02\%$). Only weak evidences were found for

Surprisingly for marmots, when the genetic body size for the 1997-2005 period correlation between body mass and size was ($P(MBE > MBE_{\rho=0}) = 81.4\%$) and for the not included (comparing MBE versus $MBE_{\rho=0}$ 2006-2016 period ($P(MBE > MBE_{\rho=0}) = 71.1\%$) predictions in Table 3 and Figure 4), no clear The estimated breeding values yielded similar pattern than the STS for the period 1997-2005 mass response was predicted by the MBE for for body mass ($P(PBV > STS) = 54.6\%$) and for any of the periods 1997-2005 and 2006-2016. for body size ($P(PBV > STS) = 47.7\%$). However, the On the other hand, selection response of size body size STS predictions were higher than the estimated were always clearly positive even when genetic STS predictions were higher than the estimated covariance with mass was set to 0 (Table 3; change in breeding values for the overall study Figure 4). Furthermore, we found strong evidence for body mass ($P(PBV > STS) = 92.3\%$) and for body size ($P(PBV > STS) = 87.7\%$) according to the $MBE_{\rho=0}$ were lower in the and for the 2006-2016 period for both first period ($P(MBE > MBE_{\rho=0}) = 97.6\%$), and traits (mass: $P(PBV > STS) = 92.3\%$; size:

$P(\text{PBV} > \text{STS}) = 89.3\%$).

DISCUSSION

Based on a 34-years long longitudinal study on Alpine marmots, we investigated the temporal trend of body mass and size of pups marmots since 1997. We aimed to explore the adaptiveness of those changes, as well as their plastic and/or evolutionary nature, using animal models. Our results confirm that pups' body size in Alpine marmots decreases with time (Rézouki et al., 2016; Canale et al., 2016) (Figure 2). Additionally, we demonstrate that this body size reduction is partially buffered by natural selection favoring larger individuals (Table 3, Figure 4). Thus, the body size shrinking observed in the Alpine marmots is non-adaptive. These results contradict Bergmann's rule (Bergmann, 1847), which states that body size shrinkage is an adaptive reaction to increased temperature, and rather supports the hypothesis of an environmental constraint of marmot's bodies development. Notably, the effect of natural selection is masked by an opposing phenotypic trend, illustrating a rarely documented case of 'cryptic evolution' (Merilä and Hendry, 2014) (Figure 1.3; Figure 2.b).

Non-adaptive body size shrinkage in response to climate change

Our results contradict the Bergmann's rule and suggest that the observed reduction in body

size and mass in Alpine marmots is a consequence of environmental deterioration. Although we did not directly measure environmental variables, previous studies have documented increased winter harshness, including colder temperatures and deeper frost penetration at La Grande Sassièrè natural reserve (Tafari et al., 2013; Rézouki et al., 2016). Reduced snow cover decreases insulation, causing frost to penetrate deeper and lower *hibernaculum* temperatures (Tafari et al., 2013). These harsher winter condition have negatively affected the mass and the size of marmots (Rézouki et al., 2016; Canale et al., 2016), who spend significant more energy to maintain their body temperature above the required 5°C threshold during hibernation (Arnold et al., 1991; Tafari et al., 2013). As a result, mother's condition have decreased over time (Tafari et al., 2013) which strongly impacts the body mass at emergence of the pups because mother in poor condition produce offspring with lower mass at emergence (Allainé et al., 1998; Plard et al., 2021). Such pattern of response stress out the importance of not assume phenotypic changes are adaptive based on observed phenotypic trend only to avoid an "adaptive storytelling" (Gould and Lewontin, 1979).

Similar non-adaptive morphological decreases have been observed in Soay sheep, where positive selection favored larger body size, but environmental factors like extended grass-growing seasons and high population

density led to a decline in body weight over time. As a consequence, lighter mothers produced lighter offspring due to physiological constraints, counteracting the positive effects of selection (Ozgul et al., 2009).

In the closely related Yellow-Bellied marmots (*Marmota flaviventris*), a stark contrast is observed: body mass of the population and population have increased in the last decades (Ozgul et al., 2010) and the annual survival rate of juveniles has remained constant (Boero, 1999), despite experiencing similar environmental changes (Armitage, 2014). To our knowledge, evolutionary responses to climate change have not been investigated in this species, but it highlights that while both species exhibit plastic responses to climate change, these responses can vary significantly, emphasizing the complexity of evaluating the impact of climate change on organisms, even among closely related species.

Cryptic evolution of body size

To our knowledge, few studies that took into account the prediction error of breeding values (Postma, 2006) and that controlled for potentially confounding phenotypic temporal trend (Hadfield et al., 2010) have found evidence for a genetic change underlying phenotypic changes in response to climate change. Convincing evidence of genetic changes in response to climate change have been found in body mass of snow voles *Chionomys nivalis* (Bonnet et al., 2017),

in male plumage coloration in collared flycatchers *Ficedula albicollis* (Evans and Gustafsson, 2017), in parturition date of red deer *Cervus elaphus* (Bonnet et al., 2019) and in migration timing in the common terns *Sterna hirundo* (Moirion et al., 2024). Altogether with the present study, these studies emphasize the role of rapid pace evolutionary changes in response to climate change (Gonzalez et al., 2013). It also emphasizes that temporal genetic changes do not necessarily need to be manifested at the phenotypic level (Merilä and Hendry, 2014), cryptic evolution representing an extreme case of this phenomenon, as both phenotypic and genetic changes are in opposite direction (Bonnet et al., 2017).

Most environmental perturbations of development are likely to reduce fitness, and thus selection would usually be expected to favor genetic changes that restore the ancestral phenotype (Conover and Schultz, 1995), a phenomenon refers to as "genetic compensation" (Grether, 2005). Ongoing climate changes operates continuously in our study population, with linear decreased of snow cover over the year (Rézouki et al., 2016). As marmots needs to reach a certain threshold condition to survive during hibernation (Allainé et al., 1998), such genetic compensation (Grether, 2005) might play a role in buffering a deteriorating environment and explain this cryptic evolution observed in the Alpine marmot. Moreover, this statement is supported by the fact

that genetic changes towards larger and heavier individuals were more pronounced in the period between 1997 and 2005 (Table 2) where phenotypic changes of size (and thus probably environmental deterioration) were the highest Figure 2. Despite this, we noted a decrease in selection pressure between 2006 and 2023, even though body size and mass did not return to their original values. Further analysis explicitly linking environment and selection is required to understand the ongoing evolutionary processes.

As review in Hadfield et al. (2011), cryptic evolution could have occurred due to evolutionary change itself, that result in genetic-based environmental deterioration. This deterioration happens because, as evolution progresses, successful lineages must compete against an increasing number of other successful lineages. For instance, in pigs breeding programs, selection for growth rate leads to a response to selection in the opposite direction than expected. This is because, by selecting for increased growth rate, individuals monopolizing resources to the expense of other individuals are favored and so, generations after generations, the environment has a more and more negative impact on individual growth rate (Camerlink et al., 2015). However, it is unlikely to be the case in our population, as induced-climate social deterioration have been thoroughly described in the Alpine marmot (Tafari et al., 2013; Rézouki et al., 2016) and because density-dependence effect are negligible at

the family group in the Alpine marmot (Allainé, 2000).

Different responses for different morphological measures

We found different selection patterns of the response of body mass compared with the response of body size. Indeed, a significant proportion of the changes in marmot body mass partially arises from its genetic correlation with body size, especially during the 1997-2005 period where the negative phenotypic trend is the strongest (Table 2). These results suggest the presence of an indirect selection acting on body mass.

Although body mass is crucial for winter survival, as the fat accumulated during summer is the sole energy source during hibernation (Armitage, 2003), it varies significantly throughout the life of an Alpine marmot. For example, adults typically weigh around 2.2kg when they emerge from hibernation in April and can reach up to 6.5kg before re-entering hibernation (Körtner and Heldmaier, 1995). During hibernation, they may lose up to 30% of their fall body mass (Arnold, 1990). Furthermore, in Alpine marmots, juvenile survival is not influenced by their body mass when measured shortly after weaning (Armitage et al., 1976). It might be due that at this stage, body mass reflects environmental or maternal condition rather than the crucial body condition before hibernation (Armitage et al., 1976; Allainé et al., 1998), which is sup-

ported by the strong influence of maternal effect for mass (Figure 3). Given this high variability of mass and the fact that we measured the pups soon in the active season, body size at this early age might be a better predictor of the future fat reserve that the pups will reach at the need of the active season. Furthermore, body size do not vary when growth is finished (Lumey, 1992) and any late start can rarely be caught up at the adult stage (Ho et al., 2010). Thus, body size might better reflect the body condition in which pups will enter into hibernation, and probably a better predictor of the future reproductive success than mass.

This supports previous findings that different body size measures can lead to varying conclusions about climate change effects (Bailey et al., 2020), as natural selection may favor specific morphological changes over overall size modifications (Ryding et al., 2021). For instance, Allen’s rule emphasizes the size of body appendages like tails, beaks, and legs rather than overall body size (Allen, 1877). It argues that larger appendages provide more surface area to effectively dissipate body heat (Allen, 1877). Galapagos finches (*Geospiza fortis*), provide a clear example of Allen’s rule. Beausoleil et al. (2019) studied disruptive selection based on bill size, a key thermoregulatory feature. They found that bill size impacted survival differently during high temperatures, with small-billed morphs showing decreased survival compared to large-

billed morphs. Further analysis revealed that temperature significantly impacted both population changes and bill size, suggesting that larger bills help dissipate heat more effectively.

Estimated breeding values mismatch the predictions

The estimated genetic trend of breeding values yielded a qualitatively different result than the prediction of the secondary theorem of selection (STS) for the overall study period and after 2005 (Table 2; Figure 4). In theory, the STS should yield similar result than the temporal trend of breeding values (Morrissey et al., 2012) if $w(z)$ is a good proxy of fitness. Indeed, Equation 12 can be rewritten as:

$$R = \sigma(a_z, w) \quad (13)$$

where a_z is the breeding value for z . Hence, the STS only consider the selection acting on breeding values, thus, on the part of the variance transmitted to the next generation (Price et al., 1970). Several elements could explain this discrepancy between estimated breeding values and prediction from the STS.

First, we modelled fitness as a Gaussian trait while lifetime reproductive success (LRS) follows a 0 inflated Poisson distribution. Although this provides an easy direct interpretation of the covariance trait-fitness in the original scale of the trait (Lande and Arnold, 1983), it could have influenced the prediction of the STS especially

in Alpine marmots in which social structure implies that very few individuals reproduce (Allainé, 2000). Generalized animal model methods have recently been developed (de Villemereuil, 2018) but their strong computation times were incompatible with the time frame of this work.

Second, we modeled relative fitness based on the LRS. Although LRS can be a good approximation of fitness (Lande, 1979), it can be poorly appropriate in Alpine marmots. Indeed, Alpine marmots are cooperative breeders (Allainé, 2000) and thus survival also contribute to inclusive fitness (Hamilton, 1963), notably through social thermoregulation increasing pups overwinter survival (Allainé and Theuriau, 2004). An integrative proxy of fitness including survival could have been more adequate.

One possibility is the λ (McGraw and Caswell, 1996) integrating survival, timing of reproduction and reproduction, which can yield subsequent differences with the mere lifetime reproductive success. Indeed, McGraw and Caswell (1996) (in the figure 2 of their article) showed that the use of λ or LRS in the European Sparrow hawk (*Accipiter nisus*) leads to opposite sign of selection of the age at first reproduction, mostly because the λ does include timing of reproduction, and LRS does not. This illustrates the strong potentiality of coupling evolutionary biology with population dynamic to estimate evolutionary parameters.

Conclusion

Our study stresses the importance of separating environmental from genetic influences on phenotype when inferring the adaptiveness of observable changes. This is especially true in the extreme case of cryptic evolution, where phenotype-based conclusions might lead to opposite interpretations because phenotypic and genetic changes are opposed. Quantitative genetics offers a powerful tool to distinguish between hypotheses that would not be distinguishable otherwise. Moreover, our research contributes to the growing evidence that evolution can occur over short time scales and act as a mechanism to counter the effects of climate change (Gienapp et al., 2008). This reinforces the importance of long-term monitoring of wild populations to determine the impact of climate change on organisms (Teplitsky et al., 2014). However, although not studied in this work, the underlying adaptive evolution must not be taken too optimistically and draw conclusion on the persistence of the Alpine marmots into facing undergoing climate changes. Indeed, Radchuk et al. (2019) meta-analysis have suggested that the rate of adaptation of species is most likely to be insufficient in reaction to the pace of climate changes. Overall, this work contribution enhances the understanding of how animal populations adapt to global change and contribute to an improved predictive framework that might aid future conservation management efforts.

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SUPPLEMENTARY MATERIALS

Appendix A : Important concepts in quantitative genetics

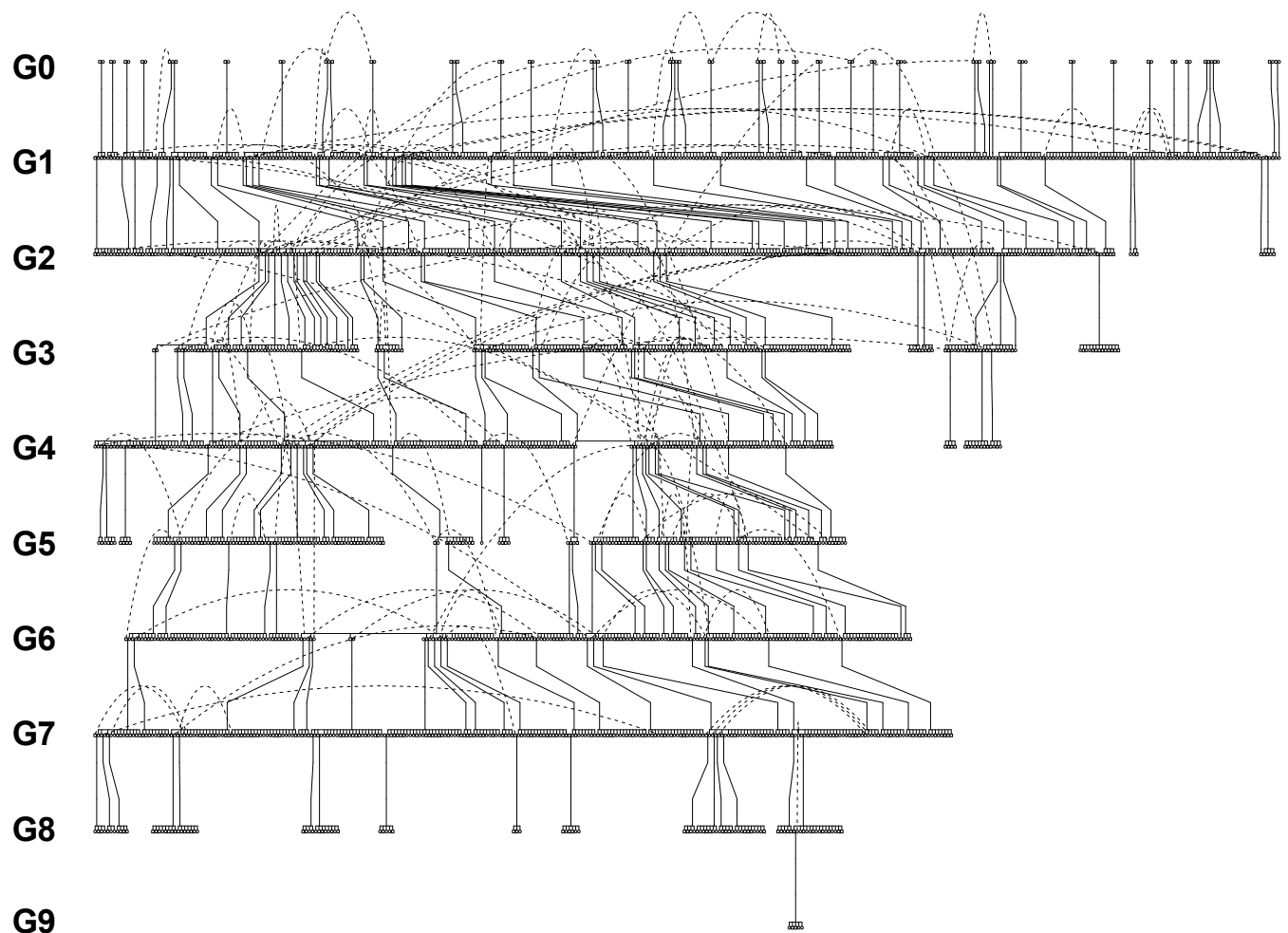
Breeding values and additive genetic variance

Additive genetic variance refers to the portion of the total genetic variance in a population that is due to additive effects of alleles (Lynch and Walsh, 1998). As alleles are the units passed through generations, additive component effects can be predicted over generations. Typically, these effects explain the resemblance between relative (Galton, 1886). As a consequence, the additivity of a trait is often emphasized as it represents (i) the majority of the total genetic variance (Hill et al., 2008), (ii) the opportunities of genetic change that selection can act upon (Lynch and Walsh, 1998). Additive components are directly predictable from parent's genotype (Lynch and Walsh, 1998). In contrast, non-additive effects stem from the interaction between the haplotype of both parents (Lukaszewicz, 2001). Non-additivity encompasses intra (dominance effect) and inter (epistasis effect) alleles interaction (Lynch and Walsh, 1998). As sexual reproduction changes the genetic context of each allele every generation, non-additive genetic contribution to phenotype from one generation to the next is more complex to assess (Lynch and Walsh, 1998).

Additive genetic variance plays a central role in quantifying the potential for evolutionary change through selection (Lynch and Walsh, 1998). Because additive effects are directly predictable from an individual's genotype, they provide a basis for predicting how traits will respond to selection pressures over successive generations (Lynch and Walsh, 1998). Breeding values represent the additive effects of an individual's genotype on a particular trait (Lynch and Walsh, 1998). They are determined by the sum of the effects of the alleles that an individual carries for that trait (Lynch and Walsh, 1998). By selecting individuals with favorable breeding values, breeders or natural selection can effectively alter the frequency of alleles in a population, leading to changes in the average phenotype of future generations (Bijma et al., 2007).

Appendix B: Pedigree of the population studied

Pedigree of Alpine marmot of la Grande Sassièrè. Pedigree of the Alpine marmot of the population studied at the natural reserve La Grande Sassièrè in the French Alps. Dashed lines represent events of dispersion, each row represents a generation, with G0 the generation of founder individuals of unknown parents.



Appendix C: MCMCglmm results of fixed effects

MCMCglmm result for biivariate model for mass and tibia length. Estimates mean and 95% credible interval, effective sample size ES (number of independent draws in the *posterior* distribution), and p-values for mass and tibia length. Predictors are mean centered to allow comparison between both traits. "V" variables corresponds to the cubic splines estimators for cohort's year effect described in part "??".

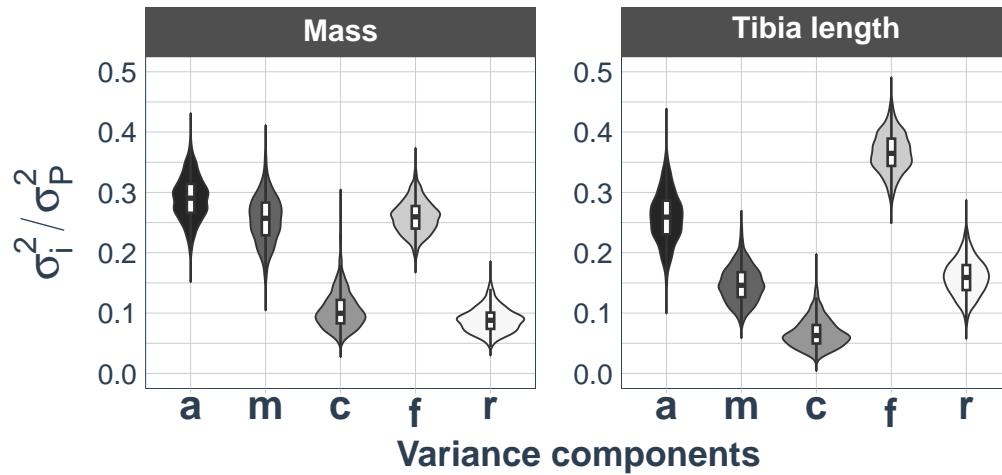
	Mass			Tibia length		
	Mean [95% IC]	ES	p-value	Mean [95% IC]	ES	p-value
μ	337.00 [310.30; 364.20]	1409	<0.001	50.70 [49.48; 51.62]	1000	<0.001
Capture time	4.12 [2.82; 5.31]	1000	<0.001	0.15 [0.10; 0.21]	935	<0.001
Sex	12.84 [6.14; 19.13]	1000	<0.001	1.10 [0.76; 1.43]	1109	<0.001
Age	8.74 [6.65; 10.80]	1000	<0.001	0.45 [0.35; 0.56]	1000	<0.001
Litter size	-38.62 [-42.07; -34.61]	715.4	<0.001	-1.17 [-1.36; -1.00]	1000	<0.001
Group size	-5.09 [-6.95; -3.28]	1000	<0.001	-0.28 [-0.38; -0.19]	845.5	<0.001
Inbreeding	-10.82 [-118.29; 93.26]	1000	0.816	-3.18 [-7.57; 0.83]	1000	0.142
V2	-11.34 [-29.17; 4.51]	881	0.168	-3.25 [-4.06; -2.37]	1000	<0.001
V3	-	-	-	-6.59 [-8.69; -3.98]	1090	<0.001
V4	-	-	-	2.68 [0.33; 4.53]	1100	0.006
V5	-	-	-	-3.28 [-5.59; -0.68]	1101	0.004

Appendix D: Variance component estimations

Variance components estimation variance components of mass, tibia length and fitness (as relative LRS) from a bivariate animal model expressed in original scale and in ratio of the total phenotypic variance. Values between brackets represents the 95% credible intervals.

	Mass (g)		Tibia length (mm)		Fitness	
	σ^2	σ^2/σ_P^2	σ^2	σ^2/σ_P^2	σ^2	σ^2/σ_P^2
Additive genetic	3803.9 [2878.3; 4727.5]	0.29 [0.22; 0.36]	7.2 [4.5; 9.5]	0.26 [0.18; 0.34]	0.28 [0; 0.64]	0.03 [0; 0.06]
Mother	3376.7 [2222.3; 4773.9]	0.26 [0.18; 0.33]	4.1 [2.3; 5.7]	0.15 [0.09; 0.20]	0.18 [0; 0.50]	0.02 [0; 0.05]
Cohort	1394.0 [684.1; 2273.8]	0.11 [0.06; 0.17]	1.9 [0.7; 3.3]	0.07 [0.03; 0.11]	-	-
Fixed effect	3404.6 [2632.5; 4187.5]	0.26 [0.21; 0.32]	10.1 [8.0; 12.6]	0.37 [0.30; 0.43]	-	-
Residuals	1156.4 [730.6; 1619.9]	0.09 [0.05; 0.13]	4.4 [3.0; 5.7]	0.16 [0.10; 0.22]	9.75 [8.65; 10.67]	0.95 [0.91; 0.99]

Variance components. Variance posterior distribution from the bivariate animal model [mass, size]. Violins represents the additive genetic σ_a^2 , maternal identity σ_m^2 , cohort's year σ_c^2 , variance arising from fixed effect σ_f^2 and residuals variance σ_r^2 on phenotype expressed as ratio of the total phenotype variability σ_P^2 for mass and size.



Master de modélisation en écologie de l'Université de Rennes 1

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RÉSUMÉ

La réduction de la taille corporelle, parallèlement aux changements géographiques dans de meilleurs habitats et une phénologie plus précoce, a été proposée comme une troisième réponse universelle au changement climatique. Alors que la nature adaptative et plastique/évolutive des changements géographiques et de la phénologie sont bien documentés, des questions persistent concernant les modifications de la taille corporelle, malgré son impact significatif sur les traits de l'histoire de vie. Diverses hypothèses, y compris la règle de Bergmann, stipulant une diminution de la taille corporelle avec l'augmentation de la température, et l'hypothèse du stress environnemental, ont été avancées pour expliquer les réponses de la taille corporelle au changement climatique. Dans une étude longitudinale de 34 ans sur les marmottes alpines depuis 1997, nous avons examiné les changements de masse corporelle et de taille pour explorer leur caractère adaptatif et plastique/évolutif à l'aide de modèles de génétique quantitative. Nos résultats montrent une diminution de la taille corporelle des juvéniles au fil du temps, partiellement atténuée par la sélection naturelle favorisant les individus plus grands. Cette réduction de la taille corporelle non adaptative contredit la règle de Bergmann, suggérant une contrainte environnementale sur le développement corporel des marmottes. De plus, l'effet de la sélection naturelle est obscurci par une tendance phénotypique opposée, illustrant un cas rare d'« évolution cryptique ».

Mots clé : Sélection naturelle, changement climatique, évolution cryptique, second théorème de la sélection, équation du sélectionneur, modèle animal, marmottes alpines, *Marmota marmota*.

ABSTRACT

Body size shrinking, alongside geographical shifts in better suited areas and advanced phenology, has been proposed as a third universal response to climate change. While the adaptive and plastic/evolutionary nature of geographical shifts and phenology are well-understood, questions persist regarding body size modifications, despite its significant impact on life history traits. Various hypotheses, including Bergmann's rule, stating body shrinking with increased temperature, and the environmental stress hypothesis, have been proposed to explain body size responses to climate change. In a 34-year longitudinal study on Alpine marmots since 1997, we investigated changes in body mass and size to explore their adaptiveness and plastic/evolutionary nature using quantitative genetics models. Our findings show a decrease in juvenile body size over time, partially mitigated by natural selection favoring larger individuals. This non-adaptive body size reduction contradicts Bergmann's rule, suggesting an environmental constraint on marmot body development. Furthermore, natural selection's effect is obscured by an opposing phenotypic trend, illustrating a rare case of 'cryptic evolution'.

Key words: Natural selection, climate change, cryptic evolution, secondary theorem of selection, breeder's equation, animal model, Alpine marmots, *Marmota marmota*.