

**THE TIMING OF REPRODUCTION IS RESPONDING PLASTICALLY, NOT
GENETICALLY, TO CLIMATE CHANGE IN YELLOW-BELLIED MARMOTS
(*MARMOTA FLAVIVENTER*).**

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Abstract:

With global climates changing rapidly, animals must adapt to new environmental conditions with altered weather and phenology. Key to adapting to these new conditions is adjusting the timing of reproduction to have offspring when the conditions are best to maximize growth and survival. Using a long-term dataset on a wild population of yellow-bellied marmots (*Marmota flaviventris*) at the Rocky Mountain Biological Laboratory (RMBL), we investigated how the timing of reproduction changed with changing spring conditions over the past 50 years. Marmots are hibernators with a four-month active season. It is thus crucial to reproduce early enough in the season to have time to prepare for hibernation, but not too early so as snow cover prevents access to food. Importantly, climate change in this area has increased spring temperatures by 5 °C and decreased spring snowpack by 50 cm over the past 50 years. This directional change in climate may have caused adaptation. Given that adaptation to environmental conditions could arise from either microevolution or phenotypic plasticity, we evaluated how female marmots adjust the timing of their reproduction and estimated the importance of both genetic variance and plasticity in the variation in this timing. We show that, within a year, the timing of reproduction is not as tightly linked to the date a female emerges from hibernation as previously thought. We report a positive effect of spring snowpack but not of spring temperature on the timing of reproduction. There is inter-individual variation in the timing of reproduction but not in its response to changing spring conditions. Genetic variance in the timing of reproduction is low, and heritability was 8%. Earlier pup emergence date increases the number and weighted proportion of pups surviving their first winter, indicative of directional selection on this trait. The same pattern is not found for litter size with no effect of pup emergence date on the number of pups born. Further, all three of these traits are not under stabilizing selection. Taken together, it seems that

we should expect some changes in this population with changing climatic conditions, but because of plasticity and not due to natural selection. Further, future studies on the marmots should not operate under the assumption that females reproduce immediately following their emergence.

Résumé:

Depuis quelques décennies, le climat global change rapidement. Les animaux doivent s'adapter à des nouvelles conditions environnementales avec une météo et une phénologie modifiée. Pour s'adapter aux nouvelles conditions environnementales, il est, entre autres choses, essentiel de modifier la date de la reproduction pour que les jeunes naissent lorsque les conditions sont optimales pour leur survie et leur développement. En utilisant une base de données à long terme sur une population sauvage de marmottes à ventre jaune (*Marmota flaviventer*) au Rocky Mountain Biological Laboratory (RMBL), nous avons investigué comment la date de la reproduction change avec les changements dans les conditions climatiques printanières pendant les 50 dernières années. Les marmottes à ventre jaunes hibernent durant pratiquement 8 mois pendant l'hiver et sont actives pendant les 4 mois estivaux. Du fait de la contrainte temporelle, il est donc essentiel de se reproduire assez tôt dans la saison active pour avoir le temps de se préparer pour l'hibernation, mais pas trop tôt alors que la neige empêche l'accès à la nourriture. Avec les changements climatiques, nous avons observé dans cette région une augmentation des températures printanières moyennes de 5 °C et une diminution de couvert de neige printanier moyen de 50 cm pendant les 50 dernières années. Étant donné que les adaptations aux conditions environnementales pourraient être dues à la microévolution adaptative ou la plasticité phénotypique, nous avons évalué comment les marmottes femelles ajustent la date de leurs reproduction et nous avons estimé l'importance de la variation génétique et de la plasticité dans la variation d'émergence des marmottons. Nous montrons que, au cours d'une année, la date de reproduction n'est pas aussi étroitement liées à la date d'émergence des femelles, comme considéré auparavant. Nous rapportons un effet positif du montant de neige printanière moyen, mais pas un effet de la température printanière moyenne sur la date de la reproduction. Il y a de la variation

inter-individuelle dans la date de la reproduction, mais pas dans sa réponse aux conditions printanières changeantes. La variation génétique dans la date de la reproduction est faible et l'héritabilité était de 8 %. Une date d'émergence plus hâtive des marmottons, augmente le nombre et la proportion des marmottons qui survivent leur premier hiver, ce qui indique la sélection directionnelle sur ce trait. Il n'y a pas un effet de la date d'émergence sur la taille d'une portée. De plus, ces trois traits ne font pas l'objet de sélection stabilisatrice. Ensemble, il semble que nous pouvons s'attendre à des changements dans cette population avec les conditions climatiques changeantes, mais dû à la plasticité phénotypique et non en raison de la sélection naturelle. De plus, les études futures sur les marmottes ne devraient pas opérer sur le principe que les femelles se reproduisent immédiatement après leur émergence.

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Introduction:

Life history traits are those that impact the fitness of an individual through survival and/or reproduction (Braendle *et al.*, 2011). The seasonal timing of these traits is heavily dependent on environmental conditions (Brommer, 2000; Bronson, 2009). These environmental conditions can vary inter-annually (Bright Ross *et al.*, 2020) and seasonally, in both the mean value of the environment and in the timing of important events (*e.g.*, when food becomes available; Nussey *et al.*, 2005). Animals must react to these yearly and seasonal variations by adjusting the timing of their life history traits to coincide with the environmental conditions that will maximize survival and/or reproduction. For example, timing egg laying date so that offspring emerge when food availability is at its highest (Nussey *et al.*, 2005), timing changes in coat colouration to match seasonal changes in the environment and thus avoid predation (Mills *et al.*, 2013), and timing emergence from hibernation to emerge late enough that food resources are not covered by snow, but early enough to maximize the length of the active season (Edic *et al.*, 2020). However, climate change may directionally shift when these environmental conditions occur (Mills *et al.*, 2013; Nussey *et al.*, 2005). Indeed, this has been seen with shifts in the timing of food availability (Nussey *et al.*, 2005) and changes in average season lengths (Cordes *et al.*, 2020). These changes can lead to mismatched timing between animal behaviours and optimal environmental conditions if animals are not able to adjust their timing adequately. Consequently, fitness can be negatively impacted, and indeed declines in both reproductive success (Nussey *et al.*, 2005) and survival (Cordes *et al.*, 2020) have been reported. Animals can alter the timing of their life history traits to coincide with the changed timing of environmental conditions through phenotypic plasticity and/or microevolution (Boutin & Lane, 2014).

Phenotypic plasticity occurs when a phenotype changes in response to a changing environmental condition (Nussey *et al.*, 2007). This can be measured in a wild population by observing how a trait that is expressed multiple times during an individual's life changes in response to changes in climate (Nussey *et al.*, 2007). Phenotypic plasticity is an important mechanism by which individuals respond to their environment as it allows for a fast change in the phenotype that can accurately track sudden changes in environmental conditions (Charmantier *et al.*, 2008). Plasticity therefore also provides a potentially important solution in terms of climate change response because while the trend in climatic changes is expected to be directional (Boutin & Lane, 2014), variability is expected to increase (Childs *et al.*, 2010). Indeed, Charmantier *et al.* (2008) outlined how the egg-laying date of a population of great tits (*Parus major*) in the UK has become earlier by 14 days. They attributed this finding to phenotypic plasticity in response to changing spring temperatures with microevolution playing no role. While there is population-level plasticity, they reported no inter-individual variation in plasticity amongst females. This lack of variation indicated that there is no individual by environment interaction (IxE; Nussey *et al.*, 2007) for the date of egg-laying in this population.

However, the capacity of phenotypic plasticity to respond to these global environmental changes may be limited over the long-term (Boutin & Lane, 2014). Certain studies have shown that to fully adapt to changes in climatic conditions, populations will need to undergo microevolutionary changes as phenotypic plasticity will not be enough on its own (Phillimore *et al.*, 2010; Mills *et al.*, 2013). For instance, Phillimore *et al.* (2010) examined the response of first spawning date in British populations of the common frog (*Rana temporaria*) to changes in temperature. They found that even though spawning date is plastic, plasticity alone will not be enough to adapt to the degree of change in temperature expected in these areas. They outlined that

the upper limit of plasticity in this population is a 5–9-day advancement in spawning date. However, to maintain fitness, these populations will need to spawn 21–39 days earlier. Therefore, microevolutionary changes will be needed to allow the population to fully adapt. Further, the timing at which certain animals molt to match their environment has become mismatched with current environmental conditions (Mills *et al.*, 2013). In these systems, spring snow melt now begins before coat colouration has changed, leaving individuals vulnerable to predation (Mills *et al.*, 2013). Mills *et al.* (2013) studied wild populations of snowshoe hares (*Lepus americanus*) and determined that while there was plasticity in the rate of molting in the spring, it is not enough to cope with the magnitude of expected climate change. Indeed, they reported that with current climate change projections, in the next hundred years hares will be exposed four to eight times longer than presently unless microevolutionary changes occur in the timing of spring molt.

These microevolutionary changes can occur in plasticity or in the mean of the trait if there is inter-individual variation, heritability, and selection. In terms of microevolution in plasticity, Nussey *et al.* (2005) found increased selection pressures for higher plasticity in the egg-laying date in a population of great tits (*Parus major*) in response to warming temperatures. They concluded that selection for increased plasticity is being observed because those individuals that can adjust the timing of their egg-laying date to better match environmental conditions (*i.e.*, those that have increased plasticity), will have more food available for their young when they hatch. This would increase offspring survival compared to those individuals with lower plasticity. They also found that plasticity is heritable and there is inter-individual variation in the degree of plasticity expressed. In terms of microevolution on the mean of the trait, Réale *et al.* (2003) reported that over the course of a decade, the date of reproduction in a wild population of red squirrels

(*Tamiasciurus hudsonicus*) became 18 days earlier. By finding that this trait is heritable and under strong negative selection, they concluded that this change in birth date is due, in part, to microevolutionary changes in the mean of the trait (but see Boutin & Lane, 2014). However, while microevolution may offer a long-term solution in responding to climate change, there may be a mismatch between the two (Gienapp *et al.*, 2007; Boutin & Lane, 2014). Microevolution is a relatively slow, and not easily adjustable process in contrast to phenotypic plasticity; this may prove problematic as a response to climate change which can occur quickly and vary inter-annually (Charmantier *et al.*, 2008).

Despite the extensive background research on these topics, studies examining the relative contributions of phenotypic plasticity and/or microevolution in the response of a wild population to climate change, remain rare (de Villemereuil *et al.*, 2020; Nussey *et al.*, 2005; Lane *et al.*, 2018). This is because studies of this nature require long-term data, a known pedigree, a sizeable population (Boutin & Lane, 2014; Nussey *et al.*, 2005), and a study site that is impacted by climate change (Lane *et al.*, 2018). One example of a study system that meets these requirements are the yellow-bellied marmots (*Marmota flaviventer*) of the Rocky Mountain Biological Laboratory (RMBL) in Colorado, USA. Since 1962, this study system has generated annual data on individual marmots, maternity has been assigned behaviourally since the study's beginning and paternity assignment began in 2000. For the past 50 years, there has been a steady increase in mean temperatures and decrease in mean snowpack, with one of the fastest reported changes globally. Specifically, there has been an increase of 5 °C in average spring temperatures and a decrease of 50 cm in average spring snowpack over the past 50 years (Figure 1).

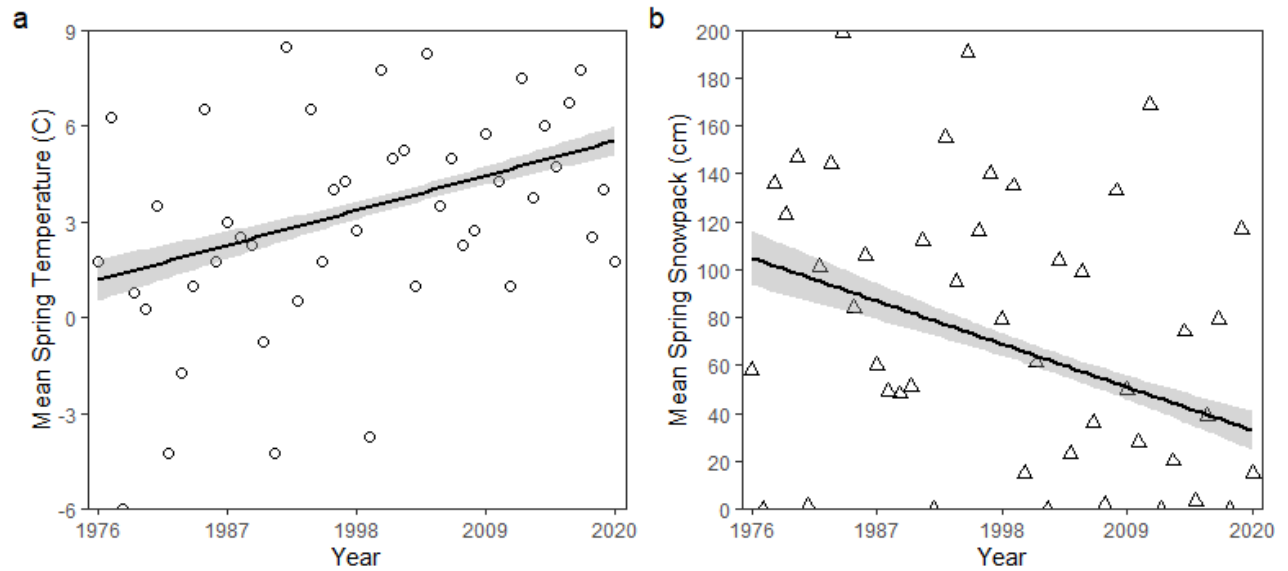


Figure 1. Relationship between year and mean spring (for definition of mean spring see results) temperature (panel a) and snowpack (panel b). Grey shading represents standard errors.

Coupled with these climatic changes are changes in the marmots' life history: adult emergence date from hibernation has advanced (Edic *et al.*, 2020), pups are being weaned earlier (Ozgul *et al.*, 2010), and overwinter survival is decreasing while summer survival is increasing (Cordes *et al.*, 2020). Indeed, a marmot's life history is heavily constrained by climate (Cordes *et al.*, 2020). During the short four-month growing season, marmots must gain as much weight as possible to survive hibernation (Ozgul *et al.*, 2010). Notably limiting the ability of marmots to gain mass is when they are born their first year and when they reproduce the years after. Individuals that are born later are less likely to survive overwinter than those born earlier in the season (Monclús *et al.*, 2014). Similarly, if a female is investing energy and resources into lactating late into the season, she may also have a harder time surviving overwinter than those that invest earlier (Andersen *et al.*, 1976). We might assume that marmots should emerge and reproduce earlier to increase the length of this crucial growing season. However, emerging and reproducing too early

also poses problems. If there is still snow on the ground covering food resources when marmots emerge, they must draw on depleted energy stores for longer (Cordes *et al.*, 2020). This could potentially lead to starvation, decrease the number of pups in a litter, or cause marmots to forgo reproduction altogether (Inoyue *et al.*, 2000). Nevertheless, there has been a documented advance in the emergence date from hibernation (Edic *et al.*, 2020).

Since marmots are thought to reproduce immediately following emergence, we expected the timing of reproduction, pup emergence date, and adult emergence date to be strongly linked and to follow a similar pattern. However, how the timing of reproduction varies from year to year and the impact of climate change on the timing of reproduction remains unknown. Therefore, we were interested in examining whether the timing of reproduction is changing in response to changes in average spring temperatures and average spring snowpack. Given that these changes can occur through microevolution and/or phenotypic plasticity, we further investigated the relative contributions of each by examining whether the trait is heritable, whether there is selection on the timing of reproduction in response to climate change, and whether there is phenotypic plasticity in the trait in response to changes in both average spring temperature and snowpack. As reproduction is expected to occur immediately following adult emergence, we expected the results for the timing of reproduction and adult emergence to be similar. Therefore, following Edic *et al.* (2020), we expected there to be low, but estimatable heritability for the trait, strong plasticity, and an impact of both spring temperature and snowpack. We further expected IxE in plasticity and stabilizing selection on the timing of reproduction.

Methods:

Study species and data collection:

Yellow-bellied marmots are large (adult females weighing on average 2.5 kg and adult males weighing on average 3 kg; Armitage, 2014) hibernating rodents living up to 15 years. They have a four-month active season, from late-April/early-May to late-September, during which they need to reproduce and accumulate fat reserves to survive the eight months of hibernation (Armitage, 2014). A population of yellow-bellied marmots has been studied at the Rocky Mountain Biological Laboratory (RMBL) in Gothic, CO, USA since 1962.

Marmots were live trapped in Tomahawk traps regularly during the active season. When they were caught, data on their weight, sex, and reproductive status were collected. Upon first trapping, marmots were assigned a unique identifier and given a permanent ear tag for identification. For observations at a distance, Nyanzol-D, a semi-permanent dye, was applied in a unique pattern on each marmot. Starting in 2000, parentage has been determined using genetic assignment (for detailed methodology on genetic assignment see Blumstein *et al.*, 2010). Prior to this, maternal identity could be reliably determined via behavioural observations while paternal identity remained unknown since males do not contribute to parental care. Daily climate data were collected by an on-site weather station since 1975. Data collected included daily minimum and maximum temperatures, daily precipitation, and depth of the snowpack. Mass on June 1st and August 15th were estimated for each individual every year using best linear unbiased predictors from age- and sex-specific linear mixed models (for detailed methods see Kroeger *et al.*, 2018). For pups, mass was estimated for emergence date and not June 1st. Age was calculated using birth

year and the year of capture. Since 83% of females are captured for the first time when they are juveniles, they are of known age. The study is divided into an up-valley and a down-valley that differ in elevation by 165 m (Ozgul *et al.*, 2010) resulting in a delay in the phenology of the up-valley by about two weeks compared to the down-valley (Monclús *et al.*, 2014). For our analysis, we restricted our dataset to include only main colonies which are observed with a higher frequency (near daily) compared to satellite colonies and we can thus have a more accurate estimation of emergence dates.

To estimate the timing of reproduction, we used the date pups first emerge from their burrow after being weaned as a proxy. Since the length of gestation and lactation are considered fixed in the marmots, with 30 days spent gestating and 25 days spent lactating (Armitage, 2014), and pups emerge immediately following weaning (Monclús *et al.*, 2014) this is an excellent proxy for the timing of reproduction. Given that adult emergence in the spring is related to average spring temperature and average spring snowpack, we focused on these two environmental variables for our analysis of pup emergence date. Since seasonal averages of environmental variables can be estimated between any two arbitrary timepoints (Bailey & van de Pol, 2016), we used a statistical approach to determine which phenological window of these two variables had the greatest association with pup emergence date. This was done using the statistical approach built in the R package *climwin* (Bailey & van de Pol, 2016; van de Pol *et al.*, 2016). This package allows the fitting of multiple models with different phenological windows used to estimate environmental averages and determine, using AIC based model comparison, which window has the strongest relation with the biological variable of interest.

Statistical Analyses:

All statistical analyses were conducted in R v.4.0.3 (R Core Team, 2020) using packages *climwin* v1.2.3 (Bailey & van de Pol, 2016; van de Pol *et al.*, 2016), *lme4* v1.1.26 (Bates *et al.*, 2015), *asreml-R* v4.1 (Butler, 2021), *ggplot2* v.3.3.3 (Wickham, 2016), *tidyverse* v.1.3.1 (Wickham *et al.*, 2019), *nadiv* v.2.17.1 (Wolak, 2012), *lubridate* v.1.7.10 (Grolemund & Wickham, 2011), *gridExtra* v.2.3 (Auguie, 2017), *ggeffects* v.1.1.2 (Lüdtke, 2018), *lmerTest* v3.1.3 (Kuznetsova *et al.*, 2017), and *car* 3.0.10 (Fox & Weisberg, 2019).

One of the key assumptions in a marmot's life history is that they reproduce immediately following their emergence. We wanted to investigate this assumption by estimating the relationship between female emergence from hibernation and pup emergence date from weaning in a given year. To do so, we used a restricted dataset from the years 2003-2017 where we had all female emergence dates from hibernation and pup emergence from weaning in each year. We then ran a linear mixed model with the package *lme4* (Bates *et al.*, 2015) using pup emergence date as our response variable. We used female emergence date as the only fixed effect. Year and female identity were fitted as random effects. Since we were expecting a 1:1 ratio between pup and female emergence date, we also used a t-test to compare the slope of the female emergence date to 1.

To determine during which phenological window temperature and snowpack had the strongest association with pup emergence date, we used the R package *climwin* (Bailey & van de Pol, 2016; van de Pol *et al.*, 2016). For both environmental variables, we fit a model in *climwin* with pup emergence date as our response variable and either average temperature or snowpack as our independent variable. Our specified reference day was June 1st, and the starting date of the

window varied from June 1st to November 13th (200 days before June 1st) the previous year. We allowed any length of window from 1 to 200 days.

To investigate whether climate change was impacting the timing of reproduction in the yellow-bellied marmot, we fitted a univariate animal model of pup emergence date using the *asreml-R* package (Butler, 2021). For this model, we restricted the dataset to include those females of known age, with a known mass in June, who reproduced that year. Fixed effects included mother's age, valley (up- or down-valley), average spring snowpack, average spring temperature, and the mother's mass in June. Random effects were the year, permanent environment (see Kruuk & Hadfield, 2007), additive genetic, and colony effects. Year was added to control for inter-annual variation in conditions experienced. Permanent environment effect was added to control for any inter-individual variation in pup emergence date not due to genetic effects. Additive genetic effects were added to estimate the amount of variation in the phenotype associated with additive genetic variation. Colony was added to control for potential micro-environmental differences between them. Significance of the random effects was determined using a log-likelihood ratio test. Starting from our full model, random effects were dropped one at a time and the log-likelihood ratio of each model were compared.

To investigate inter-individual variation in the plasticity of the timing of reproduction, we extended the previous animal model by adding random slopes for average spring snowpack and temperature in two separate models using *asreml-R* (Butler, 2021). We tested the significance of the random slope terms and the random intercept by comparing the log-likelihood of the models with and without each of these effects. We did not include additive genetic effects in this model.

We estimated the existence of selection (directional and/or stabilizing) on pup emergence date. To do this, we ran generalized linear mixed models with three different fitness proxies in lme4 (Bates *et al.*, 2015). For each litter, we used the total number of pups surviving to one year old, the proportion of pups surviving to one year old, and the total number of pups. We used the same model structure for the three models. Fixed effects were the linear and quadratic orthogonal polynomials of pup emergence date, mother's age, mother's mass in June, average spring snowpack, average spring temperature, and valley. Random effects were female identity, colony, and year. We used a Poisson distribution for number of pups surviving to one year old and the number of pups in the litter. We used a Binomial distribution for the proportion of pups surviving to one year old.

For all models, all continuous variables fit as fixed effects were scaled to have a variance of one and a mean of zero.

Results:

Female emergence date was a significant predictor of pup emergence date, with females that emerged later producing pups that emerged later (Estimate \pm SE = 0.286 ± 0.072 ; Table 1, Figure 2).

Table 1. Linear mixed model (LMM) to analyze the association of female emergence date with pup emergence date. Pup emergence date was scaled and mean-centered. (number of females = 88, number of litters = 171).

	Estimate	Standard Error	DF	T-Value	P-value
Intercept	0.004	0.111	16.611	0.038	0.97
Female Emergence Date	0.286	0.072	134.136	3.98	<0.001

However, the slope of the relationship between pups' and females' emergence dates was also significantly different from 1 (t-value = -10.3, df = 134.1, p-value < 0.001). This indicated that there was substantial variation in the timing of reproduction after emergence (Figure 2). Some females are having their pups emerge earlier than would be expected based on their emergence date, while the majority are having their pups emerge later than would be expected (Figure 2). This indicated that some females reproduced before emerging and most delayed reproduction after emergence (Figure 2).

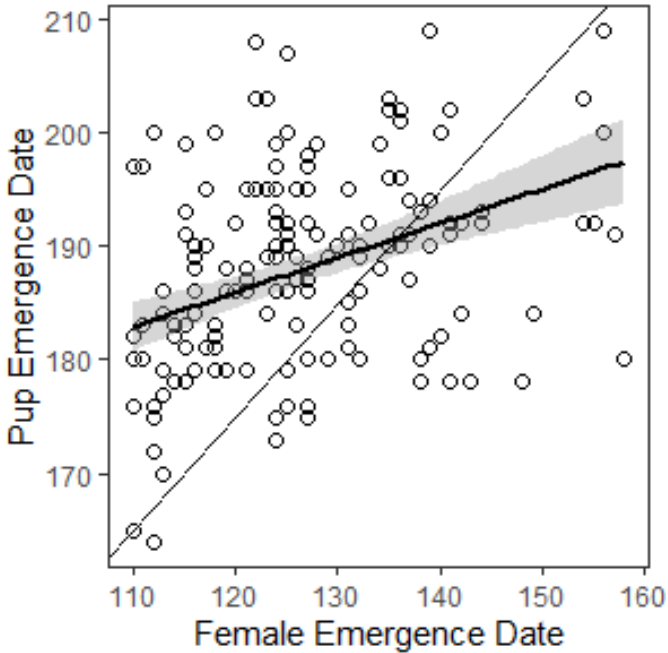


Figure 2. Relationship between female emergence date and pup emergence date. Thin black line represents the predicted slope if females were reproducing immediately after emerging. Darker black line represents the observed relationship between pup emergence date and female emergence date (number of females = 88, number of litters = 171).

The window of mean temperature and mean snowpack that had the strongest association with pup emergence date was between mid-April to early-May (Figure 3). Using these results, mean spring temperature and snowpack were defined as between April 15th and May 5th.

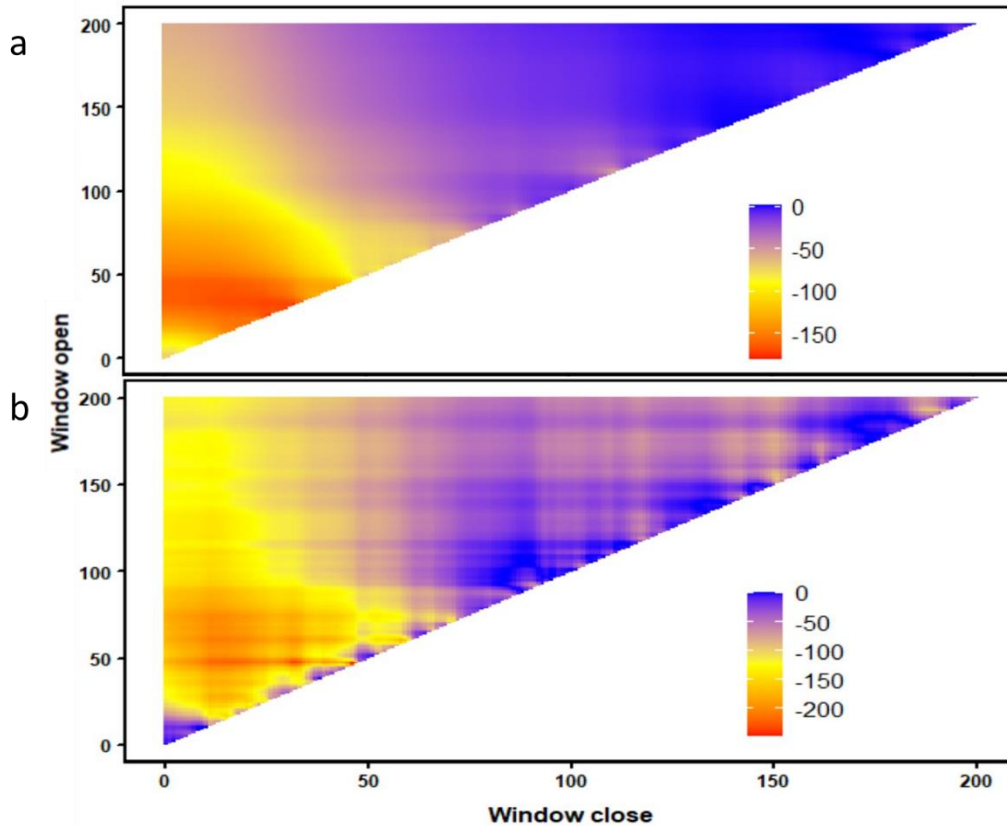


Figure 3. Output from climwin model on the association of a) average snowpack (cm) and b) average temperature ($^{\circ}\text{C}$) with pup emergence date. We allowed our sliding window to vary by day starting at June 1st until 200 days before. Numbers on the axes represent days before June 1st with day 0 being June 1st and day 200 being 200 days before June 1st (November 13th on average). This figure depicts the delta AICs compared between a model with no climate variables and models with different lengths of windows. The lower delta AICs, depicted in red, indicate models with the best fits.

Average spring snowpack was positively related to pup emergence date, but average spring temperature was not (Table 2, Figure 4). Pup emergence date was also affected by valley with pups emerging later in the up-valley compared to the down-valley (Table 2).

Table 2. Univariate animal model (number of females = 184; number of litters = 425, mean number of observations per female = 2.3, range of observations per female = 1-9) to analyze the association of changing average spring snowpack and temperature with pup emergence date. Reference category is down-valley for valley. Pup emergence date was scaled and mean-centered.

	Solution	Standard Error	Z Ratio	P-value
Intercept	-0.473	0.098	-4.853	0.819
Average Spring Snowpack (cm)	0.249	0.068	3.682	0.001
Average Spring Temperature (C)	0.048	0.066	0.728	0.471
Female's Age	0.018	0.048	0.388	0.698
Female's Mass in June	-0.102	0.061	-1.687	0.092
Valley_uv	0.955	0.125	7.665	0.000

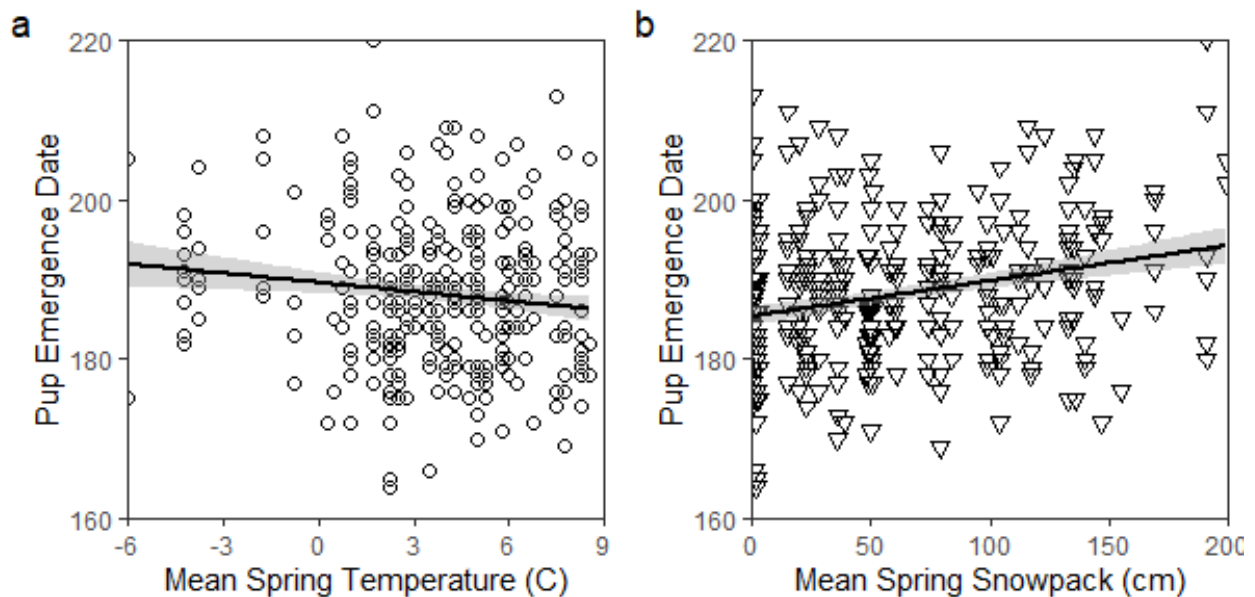


Figure 4. Relationships between climate variables (a mean spring temperature (°C); b mean spring snowpack (cm)) and pup emergence date. (number of females = 192; number of litters = 461).

Heritability was very low for this trait at approximately 8%, as was the additive genetic variance (Table 3). We also report significant inter-annual and inter-individual variation in the date of pup emergence (Table 3).

Table 3. Variance components and ratios for colony, year, additive genetic, and permanent environment from the univariate animal model analyzing the association of changing average spring snowpack and temperature with pup emergence date. (number of females = 184; number of litters = 425).

Variables	Variance Component (Estimate \pm SE)	Variance Ratio (Estimate \pm SE)	LRT	p-value
Colony	0.000 \pm NA	0.000 \pm 0.000	0.000	1
Year	0.083 \pm 0.034	0.119 \pm 0.045	19.083	< 0.001
Additive Genetic	0.054 \pm 0.061	0.077 \pm 0.086	0.856	0.355
Permanent Environment	0.167 \pm 0.066	0.241 \pm 0.092	7.458	0.006
Residual Variance	0.39 \pm 0.037			

There was no statistically significant inter-individual variation in the degree of plasticity nor covariation between the intercept and the slope for either spring snowpack (Slope Variance \pm SE = 0.39 \pm 1.68, Intercept/Slope Covariance \pm SE = 1.07 \pm 1.69, $LRT_2 = 0.40$, p-value = 0.82) or spring temperature (Slope Variance \pm SE = 0.02 \pm 1.45, Intercept/Slope Covariance \pm SE = 0.27 \pm 1.69, $LRT_2 = -0.01$, p-value = 1) (Figure 5).

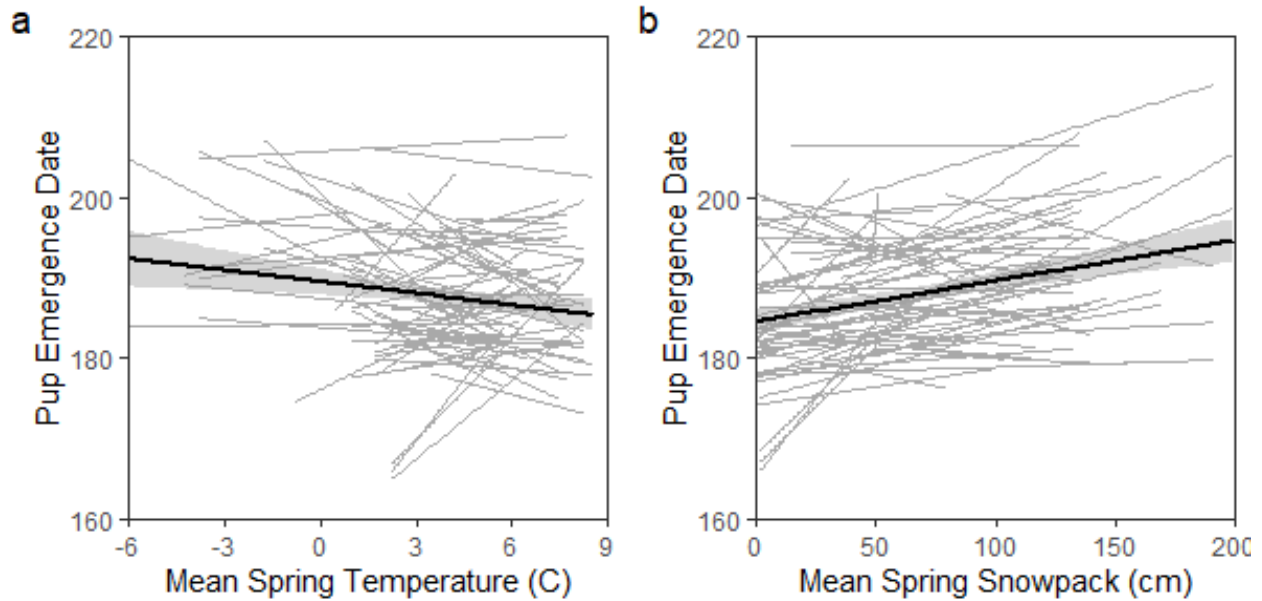


Figure 5. Relationships between climate variables (a mean spring temperature ($^{\circ}\text{C}$); b mean spring snowpack (cm)) and pup emergence date. The black, bold line represents the average individual response. Each thin grey line represents a unique female, the length of line showing the range of weather conditions measured for that female. Plot has been filtered to include only those females with 3 or more litters. (number of females = 73; number of litters = 303).

For litter size, we found only a positive effect of the mother's mass in June and no effect of pup emergence date (neither linear nor quadratic) (Table 4). For the proportion of pups in a litter surviving to one year old, we found only a negative linear effect of pup emergence date (Table 4, Figure 6a). For the total number of pups in a litter surviving to one year old, we found a positive effect of maternal mass in June and a negative linear effect of pup emergence date (Table 4, Figure 6b). In addition, we found an effect of valley with more pups surviving to one year old in the up-valley compared to in the down-valley (Table 4).

Table 4. GLMM (number of females = 176; number of litters = 417) determining the association of pup emergence date with the weighted proportion of pups surviving their first winter (binomial distribution), the total number of pups surviving their first winter (Poisson distribution), and litter size (Poisson distribution). Reference category is down-valley for valley. Pup emergence date was fitted using orthogonal polynomials.

	Weighted Proportion				Total Pups				Litter Size			
	Estimate	Standard Error	Z-Value	P-Value	Estimate	Standard Error	Z-value	P-value	Estimate	Standard Error	Z-value	P-value
Intercept	-0.209	0.239	-0.874	0.382	0.583	0.093	6.297	<0.001	1.51	0.055	27.693	<0.001
Female's Mass in June	0.149	0.109	1.367	0.172	0.189	0.059	3.208	0.001	0.134	0.035	3.803	<0.001
Female's Age	-0.034	0.086	-0.4	0.689	-0.02	0.046	-0.44	0.66	-0.047	0.03	-1.578	0.114
Valley_uv	0.528	0.294	1.793	0.073	0.238	0.104	2.281	0.023	-0.022	0.08	-0.277	0.782
Average Spring Snowpack (cm)	0.19	0.173	1.097	0.272	0.112	0.081	1.381	0.167	0.039	0.038	1.029	0.304
Average Spring Temperature (C)	-0.072	0.172	-0.419	0.675	0.02	0.079	0.258	0.796	0.03	0.035	0.838	0.402
Pup Emergence Date	-5.58	1.846	-3.022	0.003	-2.402	0.979	-2.454	0.014	-0.799	0.619	-1.292	0.196
Pup Emergence Date ^ 2	0.075	1.389	0.054	0.957	0.161	0.778	0.206	0.837	-0.242	0.495	-0.49	0.624

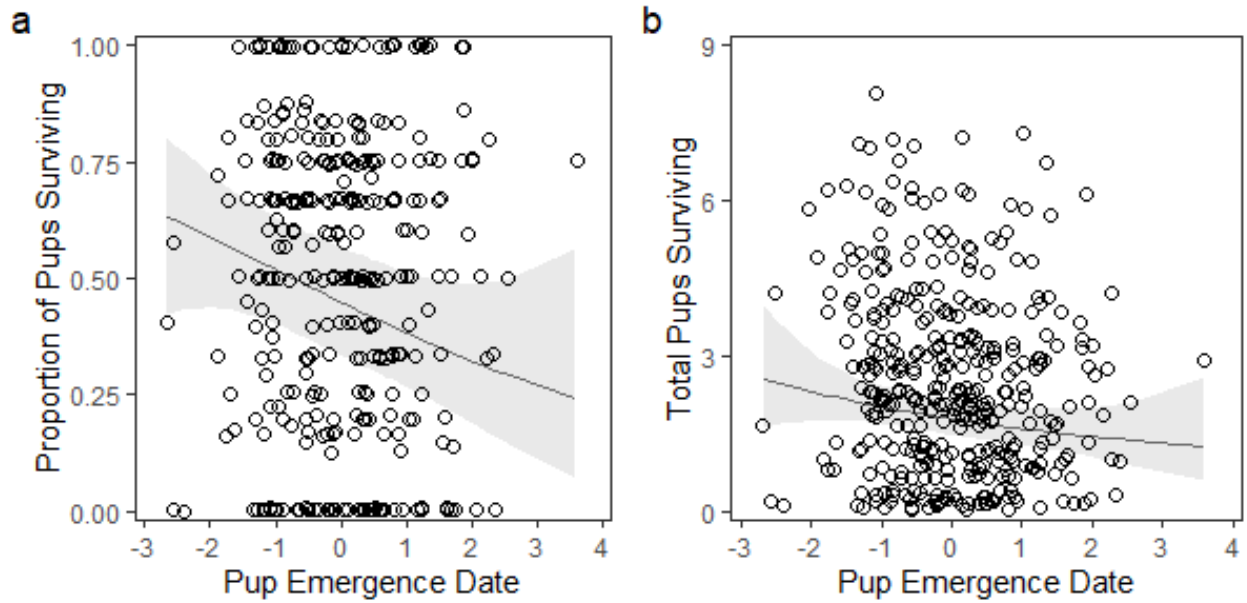


Figure 6. Relationships between pup emergence date and fitness proxies. Panel a presents the output of our selection model examining the relationship between pup emergence date and the weighted proportion of pups surviving their first winter. Panel b presents the output of our selection model examining the association of pup emergence date with the total number of pups surviving their first winter. The black line represents the prediction from the models. The grey shading is the associated confidence intervals. Data points have been jittered to enable clearer visualization (number of females = 176; number of litters = 417).

Discussion:

We found that pup emergence date was weakly linked to female emergence date, with late emerging females mating in their burrow and early emerging females delaying reproduction. We found a positive effect of spring snowpack on the timing of pup emergence, but no effect of spring temperature. We found directional, but not stabilizing selection for pup emergence date, with pups that emerged earlier better surviving their first winter. We additionally found among-individual variation at the female level in pup emergence date, but no additive genetic basis for that variation. While there was population-level plasticity in response to average spring snowpack, there was no inter-individual variation in plasticity for either average spring snowpack or temperature.

We showed a weaker relationship between female and pup emergence date than expected. Indeed, there was substantial variation in pup emergence date, with the earliest pup emerging about a month before and the latest emerging about a month later than expected based on their mother's emergence date (Figure 2). Gestation and lactation length were assumed to have a fixed duration (30 and 25 days respectively), but there might be some among-individual variation in both of their lengths. Yellow-bellied marmots are considered capital breeders and mate when little to no food is available in the environment (Armitage, 2014). Therefore, the body condition of a female might shorten or lengthen gestation by a few days. During lactation, most females have emerged from their burrow and thus both a female's body condition and micro-environmental variation in food availability could lead to inter-individual variation in lactation length before pups are weaned. Again, variation by a few days is expected. Overall, among-individual and environmental variation in gestation and lactation length, would only explain a variation by a few days in the relationship

between pup emergence date and their mother's emergence date. Given that pups could emerge up to a month before and up to a month after expected based on their mother's emergence date, it is clear the females are in some cases delaying reproduction after emerging and in others, able to mate in their burrow before emerging. Females delaying reproduction after emerging might be due to environmental variation, poor body conditions, and/or the absence of a male to mate with. Indeed, our results showed that pup emergence date was related to spring snowpack, with pups emerging later in springs with heavier snow (Table 2). This possibility of delaying reproduction because of spring snowpack may also explain why pup and adult emergence date are not similarly associated with spring temperature. Given that the date of emergence from hibernation of adult marmots is strongly related to spring temperature, (Inoyue *et al.*, 2000; Edic *et al.*, 2020), we would also expect a positive relationship between pup emergence and spring temperatures. Yet, we find no association of spring temperature with pup emergence date (Table 2) and therefore, female marmots may delay their reproduction until there is less snow regardless of spring temperatures.

However, Andersen *et al.* (1976) postulated that delaying reproduction decreased fitness as the growing season was shortened for pups and females. Indeed, we found directional selection for earlier pup emergence even though females are emerging earlier from their hibernacula (Edic *et al.*, 2020) and growing season length has increased (Cordes *et al.*, 2020). To elaborate, litters that emerged earlier had increased probability to survive and increased number of pups surviving to one year old than litters that emerged later, indicative of directional selection (Table 4). This may be a result of increased time during the growing season to forage and gain weight when pups are born earlier in the season (Monclús *et al.*, 2014). Further, earlier born pups tend to be heavier at weaning than later born pups and this weight is positively correlated with overwinter survival

(Monclús *et al.*, 2014). We do not find a similar pattern with litter size (Table 4). Given the selective pressures for earlier births in the marmots, we would predict that females that reproduce later in the season would produce fewer, but heavier pups than those females that reproduce earlier (Stearns, 1992). Indeed, it is predicted that in unfavourable environments, it is advantageous to not reproduce to your full capacity (Monclús *et al.*, 2011). However, in our study, it seems that regardless of the fitness costs associated with giving birth later in the season, females will give birth to the same number of pups regardless of when they will emerge. This may stem from previous stabilizing selection on the number of pups that can be produced. Further, Monclús *et al.*, (2014) report that mothers will not attempt to provide the offspring born later with more resources compared to offspring born earlier to mitigate the effect of being born later. Therefore, even though pups born later in the season will have lower survival, mothers will not invest more resources in them to reduce the fitness costs (Monclús *et al.*, 2014).

Despite these existing directional selection pressures to reproduce early, pup emergence date will not show an evolutionary response because of its low additive genetic variation (Table 3). There are two plausible explanations for this low variation. First, female marmots can re-absorb fetuses if they are not viable. By using pup emergence date as a proxy for the timing of reproduction, we are effectively removing all those females that may have reproduced, but not given birth to any pups. This removes a potentially significant source of variation in the trait and may explain the lack of observable heritability. If females reproducing too early or late tend to reabsorb or abort their pregnancies, this may also decrease variation through stabilizing selection. Secondly, the timing of reproduction is a fitness trait and fitness traits are generally reported to be less heritable compared to other traits (Merilä & Sheldon, 2000). This phenomenon is generally

attributed to Fisher's fundamental theorem (Price & Schluter, 1991) which proposes that there should be strong selection on fitness traits that maximally increase fitness (Merilä & Sheldon, 2000). This reduces the heritability by reducing the amount of variation in the trait – only the variation that provides the greatest fitness benefit will be left in the population following this strong selection (Merilä & Sheldon, 2000). This may explain the pattern we observe here. There may have been strong selection on the timing of pup emergence date to increase fitness, causing a reduction in the amount of additive genetic variance present and as a result lowering the heritability of the trait. However, there have been challenges to this theorem with suggestions that the lower heritability of fitness traits is not due to decreased additive genetic variance, but rather increased residual (Merilä & Sheldon, 2000), or environmental variance (Price & Schluter, 1991). In our model we report both low additive genetic variance and high residual variance.

Past selective pressures may also explain why we found no inter-individual variation in the plasticity of pup emergence date with spring snowpack (Figure 5). Female marmots are responding in the same way to the same changes in average spring snowpack. Inter-individual differences in the intercept in our plasticity model indicated that in the average environment, individuals are reproducing at different times (Nussey *et al.*, 2007). No covariation between the intercept and the slope indicated that there is no relationship between the timing of reproduction in the average environment and how plastic an individual is (Brommer, 2013). The lack of inter-individual variation in the slope in our population indicated that individuals do not differ in their response to changes in the environment. This may be explained by canalization (Stearns, 1982). Marmots are heavily constrained by their climate and have a relatively short period of time to reproduce and gain mass again prior to hibernating. Since there is strong selection to reproduce within a short

window of time where fitness is optimized, and strong selection is expected to decrease the magnitude of inter-individual differences (Westneat *et al.*, 2009), this may explain the lack of IxE in our study population. Predation might also drive the small variation. If females varied substantially in the timing of their reproduction in response to the same environmental conditions, pups would emerge at different times, exposing them to increased predation risk as there are fewer pups available at any given time as prey (Michel *et al.*, 2020).

Significant sources of variation in our animal model were valley, permanent environment, and year (Table 2; Table 3). Pup emergence date is earlier in the down-valley compared to the up-valley. This is to be expected as these two sites differ in elevation by about 200 m, causing a two-week delay in the phenology of the up-valley compared to the down-valley (Monclús *et al.*, 2014). Inter-individual variation in pup emergence date may be due to microenvironmental differences experienced by females such as burrow quality, foraging ability, or differences in environmental conditions experienced (*e.g.*, trees preventing snow melt; van Vuren & Armitage, 1991). Inter-annual variation in pup emergence date may be expected due to yearly variations in environmental conditions such as variation in the number of males present or amount of snow in the area. We find no association of colony area with the date of pup emergence, but this may be because permanent environment effect and colony are correlated as females do not generally leave once they are reproductively mature (Edic *et al.*, 2020). Colony effects that may have been confounded with permanent environment may be the number of individuals present, as marmots can produce more pups when there are fewer individuals in the colony (Maldonado-Chapparro *et al.*, 2015), the number of males present in the colony, or the degree of reproductive suppression present in the colony. These factors could all impact the timing of reproduction in a colony-specific way.

For the model examining the annual number of pups surviving their first winter, we found that more pups survive their first winter in the up-valley compared to the down-valley (Table 4). This is likely due to differing predation rates between the valleys, with higher predation in the down-valley compared to the up-valley. Predation and winter conditions are the main causes of death in marmots, and young marmots are very susceptible to predation (Armitage, 2014). For the models on litter size and annual number of pups surviving, we report a positive effect of a mother's mass in June (Table 4). June body mass of a mother has been reported to have a positive effect on the mass of her offspring, and heavier offspring are expected to have higher chances of overwinter survival (Monclús *et al.*, 2014). Additionally, as marmots are capital breeders, higher body masses are often associated with more resources available for reproduction, potentially explaining larger litter sizes for larger females.

There are some limitations to our dataset that may have impacted our results. First, despite best efforts, we might have some error on emergence date for pups and mothers because we rely on visual observations to determine emergence. While our observation effort is high in this study with colonies observed on a near-daily basis with approximately 1000 hours of observations logged per year, exact emergence dates may still be missed. We additionally tried to control for this by limiting our analyses to only the main colonies as these are observed with a higher frequency than satellite colonies. Therefore, we are less likely to have missed emergence dates in the main colonies compared to the satellite colonies. Further, we are only able to use pup emergence date as our proxy for the timing of reproduction. Being able to see inside burrows and know exactly when pups are born would provide a better estimate of the timing of reproduction in addition to identifying cases when all pups died during lactation. Similarly, being able to know

when a female mated would also provide more information about pregnancy interruption (reabsorption and abortions). Additionally, we unfortunately only have data on female emergence date between 2003-2017. It would have been interesting to analyze pup and female emergence dates for more years. Finally, since we only have one weather station on site, the climate variables used are the same between valleys. In the future it would be interesting to separate weather variables between the valleys since the up-valley environment is harsher and there is phenology delay of about two weeks between the valleys.

Conclusions:

Overall, we report that while marmots are plastically adjusting the timing of pup emergence date in response to changing spring snowpack, individuals do not differ in their plasticity level. Further, pup emergence date is not heritable but there is selection for pups to emerge earlier. This indicates that pup emergence date may not have an optimum time and it is just better to emerge earlier. Without having inter-individual variation in plasticity and without being able to evolve in response to natural selection, this population may be limited in its ability to track optimal environmental conditions for reproduction. If climate continues to change, this may prove problematic. For instance, the length of the active season may change, altering the timing of food availability. If pups do not emerge early enough, they may not be able to gain enough mass prior to hibernation. Similarly, if the mother reproduces too late in the season, she will also be limited in her ability to gain sufficient mass for hibernation. This potential mismatch in the length of the active season and when pups emerge may impact population fitness, causing a decrease in pup and dam survival. Additionally, future research should investigate the discrepancy we report between female and pup emergence to determine the ecology behind this pattern.

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