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ORIGINAL PAPER

Heritable variation in the timing of emergence from hibernation

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Abstract

Global climate change is shifting many species' phenology and has created a number of key mismatches that threaten population persistence. Phenotypically plastic individuals have the ability to adjust their behaviour in response to environmental change. While phenotypic plasticity may serve as a buffer, it is generally not known whether in case this plasticity is insufficient there is additive genetic variation in the phenological trait so that populations' may also show an evolutionary response. We show that hibernation emergence date of yellow-bellied marmots (*Marmota flaviventer*), a trait that has been significantly advancing in recent years and is associated with increased spring temperature, is phenotypically plastic. Furthermore, we used the quantitative genetic 'animal model' to decompose variation in emergence date and show there is significant heritable variation. We infer that so far phenotypic plasticity has allowed marmots to track the environmental changes leading to earlier emergence and suggest that in the short run, marmots may be able to continue to plastically respond to environmental change and thus that this trait potentially can evolve when the plasticity no longer buffers the selection for earlier emergence.

Keywords Hibernation · Phenology · Mismatch · Heritability · Global change biology

Introduction

Climate change is altering many species' phenology—the seasonal timing of life cycle events. Examples are seen in earlier arrival dates of migratory birds (Visser et al. 2015), earlier flowering in various plant species (Wadgymar et al. 2018), and advanced butterfly emergence dates (Polgar et al. 2013). This creates potential mismatches that can be costly for many species. Mismatches can create asynchronies in important biotic and abiotic relationships that influence the outcomes of phenological events. Furthermore, phenological variation is amplified both at higher latitudes and higher altitude

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than lower ones causing additional stress on species at high latitude and high elevations (Post et al. 2018), which are regions experiencing the greatest climate change. The implications of phenological mismatches on species have been well documented in bird and plant systems, specifically between egg laying date of birds and their food source (Both and Visser 2001; Reed et al. 2013) and plants and their pollinators (Kudo 2014; Gezon et al. 2016). Birds that lay their eggs too early may experience periods where food is not readily available for newly hatched young. Similarly, in seasonal environments, plants that flower earlier may find that the timing of pollinator activity no longer matches peak reproduction time. Studies of mismatch in general focus on identifying phenological changes and the environmental plasticity of species, but not understanding the mechanisms underlying these differences. Notable exceptions include: genetic variation of fitness-related traits in blue tits (*Cyanistes caeruleus*) at different habitat locations (Blondel et al. 2006), heritable phenotypic plasticity in great tit's (*Parus major*) egg laying date (Nussey et al. 2005), genetic change in the egg hatching date of a winter moth (Van Asch et al. 2013), and an adaptive response to longer growing seasons by genetically altering critical photoperiods in pitcher plant mosquitos (Bradshaw and Holzapfel 2001). Phenotypic plasticity is assumed to be essential to respond to environmental variation and reduce phenological mismatch and mistiming (Visser and Gienapp 2019). However, for a population's phenotype to evolve and respond to selection due to mismatches and mistiming, traits must be heritable. Therefore, it is important to quantify the genetic variation underlining phenotypic differences.

Numerous species have evolved unique adaptations to harsh winter environments including seasonal color change and hibernation. Asynchrony between these phenological events and seasonal timing can have severe consequences. A variety of molting species, including Arctic foxes (*Vulpes lagopus*) (Zimova et al. 2018), weasels (*Mustela nivalis*) (Atmeh et al. 2018), rock ptarmigans (*Lagopus mutus*) (Imperio et al. 2013; Zimova et al. 2018), and snowshoe hares (*Lepus americanus*) (Mills et al. 2013; Zimova et al. 2016) are experiencing mismatches in the timing and rate of seasonal molting compared to the timing and rate of snowmelt; leaving white animals increasingly vulnerable against their now snow-free background. Some species have an ability to maintain crypsis by changing behaviour to match the background environment, as seen in male ptarmigans soiling their white plumage to be more cryptic when snow is absent and they have not molted before snowmelt (Montgomerie 2001).

Hibernating mammals are also experiencing changes in the timing of their phenological events. Yellow-bellied marmots (*Marmota flaviventer*) have been emerging earlier from their 7–8 months long hibernation and this is thought to be driven by earlier spring air temperatures (Inouye et al. 2000). Earlier emergence, but constant date of snowmelt makes these hibernating mammals go longer periods without food and cut into fat reserves in order to make it to growing season (Van Vuren and Armitage 1991). By contrast, late emergence from hibernation creates less time for hibernating mammals to gain the appropriate body mass needed for hibernation and reproduction, with juveniles having the least amount of time to gain sufficient body mass to survive hibernation (Armitage et al. 1976; Körtner and Geiser 2000). An example of this is seen in Columbian ground squirrels (*Urocitellus columbianus*) that have been emerging later out of hibernation causing decreased individual fitness (Lane et al. 2019).

Yellow-bellied marmots have a relatively large geographic and elevational range and live in a variety of environments that are characterised by different phenologies (Floyd 2004). Marmots modify the timing of their seasonal cycle to adjust to local environmental conditions (Armitage 2014) and much is known about the importance of phenotypic plasticity in response to environmental changes. Yellow-bellied marmots exhibit plastic responses for many phenotypic traits, such as body mass, reproductive success, and sociality (Maldonado-Chaparro et al. 2015, 2017).

Individuals that are able to change their behaviour in response to environmental change will potentially fare better than those who are not able to. However, phenotypic plasticity may not be sufficient to keep up with the environmental change (Visser 2008), and genetic variation is then necessary for a trait to change in response to selection. Without genetic variation a population cannot evolve by natural selection in response to environmental change and the long-term survival of the population may be at risk. The genetic factors that influence hibernating systems, and specifically hibernation linked to the timing of breeding, have been neglected with the exception of a quantitative genetics analysis in Columbian ground squirrels hibernation emergence date (Lane et al. 2011).

We studied yellow-bellied marmots located in the Colorado Rocky Mountains, where they have been emerging from hibernation earlier in recent years (Inouye et al. 2000). Marmots at this site are an ideal system to study the genetics of hibernation phenology for a number of reasons. First, we have 14 years of emergence date data, combined with detailed spring weather data, along with a molecular genealogy for the animals we study. Second, in addition to annual variation in weather, and hence to some degree, emergence, we study marmots along an elevational gradient and have seen that marmots emerge later at higher elevations (Blumstein et al. 2004), which provides more environmental variation upon which we can use to tease apart environmental and genetic effects.

Studies of marmots at many locations have shown phenotypic plasticity in a number of behavioral traits and we expected to find a substantial amount of plasticity in the emergence date of yellow-bellied marmots in response to environmental factors. We further aimed to quantify genetic variation in emergence date, which if present, would indicate that the population had evolutionary potential to respond to earlier snowmelt dates.

Materials and methods

Study site and subjects

Marmots have been studied around the Rocky Mountain Biological Laboratory (RMBL) located in the East Valley of Gunnison County, Colorado, USA since 1962 (Blumstein 2013; Armitage 2014). Colonies are distributed along a 5 km elevational gradient with a natural break in the marmot population that divides colonies into two valley positions, up valley and down valley. Elevations range between 2700 and 3100 m.a.s.l. Marmots are regularly live trapped during their summer active season and are marked with unique ear tags and their dorsal pelage is dyed with unique marks to permit identification from afar (Schwartz et al. 1998). While trapping we collect hair, which is used for the genetic assignment of maternity and paternity (Blumstein et al. 2010).

We recorded each marmot's age, sex, and body mass when trapped. More than 95% of individuals were trapped for the first time as pups or yearlings and thus we know their birth year. Unknown individuals who were > 2 kg when first trapped were considered to be 2 years old at their first capture (Ozgul et al. 2010). We treated age as a factor, assigning individuals to 3 groups (1 year old, 2 years old, and ≥ 3 years old). Yearlings (1 year olds) are individuals born the previous summer who survived their first hibernation. Virtually all males and about half of the females disperse as yearlings. Marmots typically become sexually mature at age 2 years (Armitage 2014), but some females may be reproductively suppressed by dominant breeding females (Armitage 1998, 2003). To account for variation in sexual reproductivity, which may be a primary driver of emergence, we separated 2 year olds and 3 year olds because 2 year olds have a significantly lower chance of breeding and 3 year olds are generally all reproductively active (Armitage 2003; Armitage et al. 2007). Marmots ≥ 3 years are classified as adults in our study.

We collected DNA for each individual in our study from 2003 to 2017. DNA was extracted from hair samples using a QIAamp Mini Kit (Qiagen Inc., Valencia, CA, USA) and allele frequencies were analyzed using GENEMAPPER (Blumstein et al. 2010; Petelle et al. 2015). Parentage was determined using CERVUS 3.0 (Kalinowski et al. 2007) which calculates the likelihood of each mother and father to a given offspring at a 95% confidence level for the trio. Marmots at our study site are routinely trapped and observed. Candidate mothers were selected using nipple and lactation measurements (Blumstein et al. 2010) and by burrow locations for each offspring. Male marmots were grouped by their valley position and offspring from each geographical group were given the same list of potential fathers. We assumed a sampling proportion of 99% for candidate mothers and 96% for candidate fathers. Adult female marmots are philopatric and are potentially highly related, which can make it difficult to assess parentage using CERVUS. Per the guidelines in Jones and Ardren (2003) we calculated the proportion of females related at a level of $R > 0.4$ for each year (Blumstein et al. 2010) and included it as an additional parameter during parentage assignment within CERVUS. The proportion of loci typed was 0.948 and the proportion mistyped was set at 0.01. The pedigree used for this analysis contained only informative individuals and included 564 individuals with 516 (91.5%) maternal links and 479 (84.9%) paternal links (see Appendix Table 3 for details on pedigree structure).

We collected emergence dates for 14 springs between 2003 and 2018 at up to 16 different marmot groups annually. Starting on 19 April each year, colony sites were visited daily, weather permitting. Sites were skied to or scanned with binoculars and spotting scopes. Percentage of snow cover at each colony site was recorded based on the observed home range size from the previous summer. At each visit, we looked for signs of emergence in the snow such as dug out hibernacula and marmot tracks. If marmot activity was detected, we waited for marmots to emerge and identified animals. Unidentified marmots were classified as yearlings or adults. Individuals were not given an emergence date if they were seen for the first time more than 3 weeks after the date that 50% of the group emerged and were considered to have been missed. We estimated 901 emergence dates for 516 individuals over 14 years.

Statistical analysis

We used the animal model to estimate the genetic basis of the emergence date of yellow-bellied marmots. The animal model is a type of mixed model using both fixed and random effects, linked to a pedigree to decompose phenotypic variation into genetic and environmental components (Wilson et al. 2010). For studying natural populations, the animal model is an excellent tool designed to incorporate multigenerational pedigrees and account for incomplete datasets (Kruuk 2004).

Since emergence date is highly variable from year to year we needed to correct for several environmental factors in order to estimate the heritability of emergence date. Since spring air temperatures and snow depth have been shown to impact emergence date (Van Vuren and Armitage 1991; Inouye et al. 2000), we included effect of March mean temperature, snowpack on 1 April (both measured at the RMBL weather station) and date of 50% snowmelt at each marmot colony. We estimated the mean March temperature instead of mean April temperature because marmots emerge throughout April and a mean April temperature would be based on dates following emergence for at least some individuals. To correct for micro-environmental differences between colonies, we included the colony size, the number of adult males within a colony and the date of emergence of 50% of the group. Because sex, age and body mass before hibernation could impact the date of emergence we also included those effects in the model. Using a mixed model, we predicted 15 August body mass the year before emergence and used this in our analyses (Maldonado-Chaparro et al. 2015).

Fixed effects (Table 1) included in the model were measured at three different levels: (1) effects estimated at the population level: average temperature in March and 1 April snowpack; (2) effects estimated at the colony level: 50% snowmelt date, valley position, colony size and number of adult males in a colony; and (3) effects estimated at the individual level: sex, age as a factor (1 year, 2 years, 3 years and older) and mass the previous year. Effects were not scaled in order to directly interpret the coefficient in terms of emergence date.

We fitted additive genetic, permanent environment, colony, and year as random effects for our model (Table 1). Since observations of marmot activity started each year at the latest on 19 April (day 109 of the year) for all colonies, in years with early emergence some individuals might have been active before we observed them for the first time. To account for this, we used a left-censored Gaussian distribution on day 110, indicating that any individuals observed for the first time on day 110 might have emerged earlier.

Models were fitted in R 3.6.1 (R Team 2019) using the program MCMCglmm (Hadfield 2010). We used parameter expanded priors ($V=1$, $nu=0.002$. $alpha.mu=0$, $alpha.V=1000$) for all random effects. We used 230,000 iterations including 30,000

Table 1 Definitions of effects used in statistical analysis

	Definition
Fixed effects	
50% snow cover	Recorded date snow melt was 50% at each colony
Number of males	Number of adult males (≥ 3 years old) in each colony
Number of individuals	Total number of individuals living at each colony
Mass the previous year	Estimated Aug 15 body mass the year before emergence
Sex	Marmot sex
Age	Age for each trapped individual; split into three levels: 1 years old, 2 years old, ≥ 3 years old
Valley position	Colony locations split into two categories: up valley and down valley
Average March temperature	Average daily air temperature measured at RMBL weather station
Snow April 1st	Snow depth on 1 April measured at RMBL weather station
Random effects	
Additive genetic variation	Average effect of single alleles for each individual
Permanent environmental variation	Environmental effects on individual's phenotype that are constant across (or common to) repeated measures on that individual (Kruuk and Hadfield 2007)
Colony variation	Environmental effects shared by groups of individuals within a specific colony location
Year variation	Yearly variation in emergence date
Phenotypic variance	Total amount of variation in the emergence date

burn-in iterations and a thinning interval of 200. The autocorrelation for each parameter was below 0.05. For each parameter, we reported the posterior mode with the (lower/upper) 95% highest posterior density intervals (HPDI). A parameter was considered significantly different from zero if its 95% HPDI did not include zero. It should be noted that variance parameters cannot be negative and thus significance was assessed by evaluating the shape of the posterior distribution and how close the lower 95% HPDI was to zero. We estimated the heritability conditioned on the fixed effects as V_a/V_P where V_a and V_P are, respectively, the estimated additive genetic variance and the sum of the variance components associated with the random effects and the residual variance. Since the model included fixed effects capturing environmental variability, it is suggested to also report the observed phenotypic variance (variance in the observations; Wilson 2008). However, since we used a censored-Gaussian distribution, the observed variance might underestimate true trait variance. We instead reran the analysis without the inclusion of weather variables in the model to obtain variance estimates (and ratios) unconditioned on the yearly variation in weather conditions (Appendix Table 4).

Results

We found that emergence date was highly variable in our population. Individuals emerged as early as 12 April and as late as 9 June (range of 58 days), with a median on 7 May over the 14 years studied. Furthermore, average March temperature, 50% snowmelt date at each colony, age, and mass the previous year were all significant (Table 2). Thus, marmots emerged earlier when March was warmer, when snow cover decreased earlier, and when they were bigger. Our findings support our hypothesis of plasticity in the emergence date of our population in response to numerous environmental factors. Individual plasticity was previously tested for and shown in other traits including body mass and reproductive success (Maldonado-Chaparro et al. 2015).

We found that for a given body mass, yearlings emerged earlier than adults (2 years old = 6.187; 95% HPDI 3.001/9.309 and ≥ 3 years old = 5.389; 95% HPDI 0.617/8.760 where HPDI is the lower/upper of the highest posterior density interval). The other fixed effects in our models—number of males in a colony, number of individuals in a colony, sex, valley position, and snow depth on 1 April were not significantly different from 0 (Table 2).

We found a significant additive genetic effect (V_a = 22.574; 95% HPDI 12.336/31.307) on emergence date that corresponded to a heritability of $h^2 = 0.16$ (95% HPDI 0.10/0.26; conditioned on weather effects Table 2) and $h^2 = 0.13$ (95% HPDI 0.08/0.22; unconditioned on weather effects Appendix Table 3). We found no permanent environment effects, but colony and year random effects explained 11% and 10% respectively of the variance in emergence date (Table 1). It should be noted that since an individual spends its life in the same colony after settling at age 1 or 2, that permanent environment and colony effects might be confounded.

Table 2 Estimates of effects and variance obtained using the animal model for yellow-bellied marmot emergence date with weather conditioned effects

	Estimate	95% HPD intervals	
		Lower	Upper
Fixed effects			
Intercept	84.408	64.789	98.014
50% snow cover	**0.415**	**0.272**	**0.574**
N males	0.323	– 0.342	0.842
N individuals	– 0.033	– 0.146	0.069
Mass previous year	**– 0.004**	**– 0.006**	**– 0.003**
Sex [M]	0.420	– 0.774	2.075
Age [2]	**6.187**	**3.001**	**9.309**
Age [3+]	**5.389**	**0.617**	**8.760**
Valley [up]	– 1.488	– 8.609	3.361
Av March temp	**– 2.159**	**– 3.652**	**– 0.289**
Snow April 1st	– 0.047	– 0.133	0.008
Variance components			
V_a	**22.574**	**12.336**	**31.307**
V_{pe}	0.024	0.000	3.484
V_{colony}	**6.965**	**2.873**	**32.044**
V_{year}	**10.308**	**4.144**	**32.416**
V_R	66.812	58.406	73.842
V_P	112.39	95.432	145.063
Conditioned variance ratio			
r^2	**0.19**	**0.12**	**0.27**
h^2	**0.16**	**0.10**	**0.26**
pe^2	0.00	0.00	0.03
$colony^2$	**0.11**	**0.03**	**0.24**
$year^2$	**0.10**	**0.04**	**0.24**

Females, yearlings and down-valley were used as reference levels in the analysis. V_a, V_{pe}, V_{colony}, V_{year} and V_R are the additive genetic, permanent environment, colony, year and residual variance respectively. V_P is the sum of the variance components in the model and the residual variance. r^2 is the repeatability measured as $V_a + V_{pe}/V_p$ and h^2 is the heritability. Significant results are indicated in bold

Discussion

We found both significant environmental drivers of marmot emergence date and significant heritability in emergence date. This is one of the first demonstrations of heritable variation in a hibernation trait.

Yearlings emerged earlier than adults for a given mass. This was somewhat unexpected since adults were expected to emerge earlier, especially adult males. Three suggestions may explain this result. First, adults are heavier than yearlings on average (Armitage et al. 1976; Armitage 2014). In our data, yearlings mean August mass the previous year was significantly less than 2 year olds and 3 year olds and older [yearlings = 1465 ± 16 g (standard error), 2 years old = 3158 ± 35 g, ≥ 3 = 3837 ± 40 g with males being heavier than females; Appendix Fig. 1]. Since higher body mass is associated with earlier emergence, heavier adults on average emerge earlier than yearlings. Adult males are known to be the first in their colonies to emerge from hibernation to begin spermatogenesis to ensure reproductive dominance if there are other males around (Blumstein 2009). Importantly, they can afford earlier emergence because their large mass enables them to survive in times of limited food availability after emergence and before snow has fully melted. Adult males (≥ 3 years old = 4901 ± 111 g) are considerably larger than adult females (≥ 3 years old = 3654 ± 30 g; Fig. 1). Second, yearlings are still growing; having an earlier start could increase the length of their active season favoring growth and fat accumulation. Third, adult marmots with smaller body mass are threatened by a variety of environmental factors, and may be killed by predators, deplete their fat reserves and may starve when they emerge before 50% snowmelt date (Van Vuren and Armitage 1991) and should benefit from later emergence. Small adult marmots have less to gain from earlier emergence than yearlings that face the same environmental risks, but need to accumulate more mass (both by skeletal growth and fat accumulation) for hibernation and thus might benefit from earlier emergence.

Emergence is influenced by reproductive opportunities including, reproductive competition. Male marmots compete for territories inhabited by females and mate with all females in the colony. Early emergence can be a way to guarantee the dominant male is able to mate with females first as they emerge. However, and in contrast to a previous study (Blumstein 2009), our results did not show a significant association between the number of adult males in a colony and the emergence date. This is understandable because the previous analysis was based on a group level emergence date metric whereby the more individuals that emerged early means that 50% emergence was met earlier. By contrast, our current analysis is on the individual level and we find that the number of males did not explain variation in the day on which other individuals emerged.

As was expected given previous analyses (Inouye et al. 2000; Blumstein 2009), two key environmental factors were associated with emergence date. The date of 50% snowmelt was positively correlated with emergence date, suggesting that marmots emerged earlier when the snow melted sooner (Van Vuren and Armitage 1991). Also significant was the average temperature in March; marmots emerged earlier when March was warmer.

In addition to environmental effects on emergence date, we found significant heritability in emergence date in our marmot population (Table 2). This significant variation means that there is an evolutionary potential to adjust hibernation emergence date under directional selection. Such variation may be important in the future if, as predicted, continued global warming systematically shifts snowmelt. Marmots at our study site have been emerging earlier on average for the past 25 years (Inouye et al. 2000). Based on previous studies, it is likely that environmental effects are driving this transformation rather than evolutionary change (Ozgul et al. 2010). Without a selection analysis we cannot infer how the emergence date affects population fitness, however the substantial phenotypic plasticity we have identified has likely buffered the selection pressure for earlier emergence date. The combination of both plasticity and heritability suggests an adaptive response to environmental change despite directional selection (Radchuk et al. 2019) possibly reducing potential phenological mismatch.

A key question in the environmental change literature is whether there is significant variation to respond to directional change (Réale et al. 2003; Boutin and Lane 2014). We have identified both phenotypic plasticity and genetic variation that should permit this population to respond to the directional selection (Inouye et al. 2000) of a warming planet where the snow melts earlier in the Colorado high country. This study has revealed the presence of previously unknown genetic variation in a key life history trait that is often not considered in population dynamics and that is not obviously being selected for due to the plasticity in the trait, but may give marmots the ability to adapt and survive unsuitable climates. Thus it becomes clear that, for hibernating species, hibernation related traits should be better integrated in studies of adaptation to climate change and that we should focus less on active season traits only. Other species may also have undiscovered evolutionary potential for traits that are sensitive to environmental change and critical for population fitness. It would be revealing to study plasticity and heritability in species with more constrained ranges where phenotypic plasticity may be more limited.

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Author contributions JAM and DTB conceived the project, JGAM and DTB collected data, MNE organized and proofed the data, JGAM analyzed the data, all authors discussed results and wrote the MS.

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Data accessibility Data and code are available on the OSF: https://doi.org/10.17605/OSF.IO/924PK.

Compliance with ethical standards

Conflict of interest We declare we have no competing interests.

Ethical standards Marmots were studied under annual permits issued by the Colorado Division of Wildlife (TR-917). All procedures were approved under research protocol ARC 2001-191-01 by the University of California Los Angeles Animal Care Committee on 13 May 2002, and renewed annually.

Appendix

See Tables 3, 4 and Fig. 1.

Table 3 Pedigree statistics used in the analysis, which contained only informative individuals

	Count
N individuals	564
N maternal links	516
N paternal links	479
N full sibs	1172
N maternal sibs	2014
N maternal half sibs	842
N paternal sibs	5907
N paternal half sibs	4735
N maternal grandmothers	443
N maternal grandfathers	298
N paternal grandmothers	224
N paternal grandfathers	197
Maximum depth (N generations)	10
Founders	45
N inbred individuals (non-zero F)	160
N F > 0.125	95

Table 4 Estimates of effects and variance obtained using the animal model for yellow-bellied marmot emergence date without yearly weather conditions

	Estimate	95% HPD intervals	
		Lower	Upper
Fixed effects			
Intercept	131.63	126.15	137.81
50% snow cover	–	–	–
N males	0.0146	−0.559	0.632
N individuals	0.0097	−0.091	0.123
Mass previous year	**−0.0034**	**−0.0055**	**−0.0034**
Sex [M]	0.701	−0.883	2.230
Age [2]	**6.031**	**3.166**	**9.825**
Age [3+]	**4.777**	**0.272**	**8.938**
Valley [up]	2.441	−1.953	8.618
Av March temp	–	–	–
Snow April 1st	–	–	–
Variance components			
V_a	**19.850**	**11.088**	**30.841**
V_{pe}	0.017	0.000	3.714
V_{colony}	**9.266**	**3.126**	**33.816**
V_{year}	**26.309**	**15.362**	**82.747**
V_R	69.612	60.478	76.854
V_P	138.13	113.72	192.71
Conditioned variance ratio			
r^2	**0.15**	**0.07**	**0.22**
h^2	**0.13**	**0.08**	**0.22**
pe^2	0.00	0.00	0.03
$colony^2$	**0.08**	**0.03**	**0.22**
$year^2$	**0.25**	**0.12**	**0.44**

Weather variables not fitted in this restricted model are indicated by "–". Females, yearlings and down-valley were used as reference levels in the analysis. V_a, V_{pe}, V_{colony}, V_{year} and V_R are the additive genetic, permanent environment, colony, year and residual variance respectively. V_P is the sum of the variance components in the model and the residual variance. r^2 is the repeatability measured as $V_a + V_{pe}/V_p$ and h^2 is the heritability. Significant results are indicated in bold

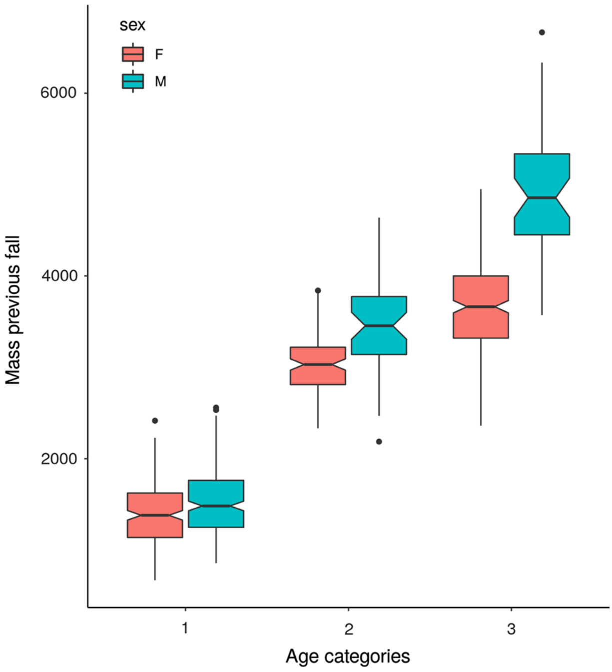

Fig. 1 Boxplot of the mass the previous August as a function of age and sex categories in yellow-bellied marmots using 901 mass measurements from 516 individuals. The bold horizontal lines and notches represent the median and 95% confidence interval around the median. The top and bottom of the boxes are the 25% and 75% quartiles. The whiskers extend to 1.5 the interquartile range and points are potential outliers

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