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# Coping with seasonality: dynamics of adult body mass and survival in an alpine hibernator

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Alpine mammals are highly vulnerable to current and projected climate change because they are confined to a certain elevation range. Physiological and behavioural adaptations in burrowing species, such as finding shelter in burrows when the summer conditions are unfavorable and hibernating in winter during the stressful period of resource shortage, could partly buffer the negative impacts of these forecasted changes. We studied the links between environmental factors and annual variations in adult mass and survival over 14 years in hoary marmots. We hypothesized that annual variation in seasonal environmental factors determines individual mass and survival through direct effects on food quality and availability, expecting greater survival when marmots reach higher mass before hibernation. We found that harsh winters decreased mass at emergence from hibernation by 47% compared with mild winters. Nonetheless, adult marmots had a greater mass gain in summers following harsh winters and reached a similar mass at the end of the summer compared with summers following mild winters. This suggests individuals can adopt a resource allocation strategy that allows maximizing summer mass gain to survive hibernation. Earlier springs also increased summer mass gain by 15 g $day^{-1}$, and tended to increase apparent adult survival by 23%, compared with late springs. While these findings suggest a warming climate could have positive effects on summer mass gain and survival, survival also tended to decrease by 24% in summers with more precipitation. This suggests the forecasted changes in precipitation extremes could also trigger considerable negative effects on the demography of burrowing species in the long term. Our study shows that, although burrowing and hibernating behaviours could buffer responses to environmental changes, these behaviours are not an indefectible shield against climate change.

Keywords: alpine climate, body mass, burrowing, hibernation, hoary marmots, survival

## Introduction

At high altitudes, increased annual minimal temperatures and the occurrence of extreme events, such as warmer and drier summers and winters, have led to widespread

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concerns about the long-term viability of animal populations exposed to climate change in these regions (Beniston et al. 1997, Parmesan and Yohe 2003, Littell et al. 2011). Several species restricted to the highest elevations are already near their climatic and geographic limits and warming temperatures have led to drastic range collapses (Dirnböck et al. 2011, McCain and King 2014). Reduction of suitable habitat has also led to local extinctions for some alpine-dwelling species (Beever et al. 2010). Furthermore, the pace of climate change may exceed the capacity of many species to adapt to the altered climate (Parmesan 2006). The sensitivity, level of exposure, phenotypic plasticity and adaptive capacity to climatic changes vary greatly among species (Foden et al. 2013, McCain and King 2014, Valladares et al. 2014). Therefore, studies assessing species-specific responses to annual fluctuations in environmental and weather conditions are essential to understand, predict and mitigate the impacts of climate change in high altitude ecosystems.

Among alpine herbivores, several species of ground-dwelling squirrels spend numerous months hibernating in burrows (Buck and Barnes 1999). By hibernating underground, individuals benefit from both warmer and more stable temperatures and an extremely low metabolic rate, which allow them to survive on their fat energy stores during the period of food shortage (Buck and Barnes 1999, Nikol'skii 2009). During the summer active period, ground-dwelling squirrels often hide in burrows to avoid unfavorable conditions (Reichman and Smith 1990, Young 1990). They also spend much of their time moving on the surface, which includes mostly foraging activity but also searching for reproductive partners in spring, establishing their home range, defending territory and regulating their body temperature (Festa-Bianchet and Boag 1982, Murie and Harris 1982, Türk and Arnold 1988). The ability for individuals to both isolate themselves in shelters and decrease their metabolic rate allows them to reduce their exposure to environmental stress associated with cold temperatures, food shortage, predation risk and unfavorable weather conditions. Burrowing and hibernating are thus behavioural and physiological adaptations assumed to buffer the negative response that ground-dwelling squirrels face with climate change (Liow et al. 2009, Pike and Mitchell 2013).

Although hibernating species of squirrels have access to shelters and have the ability to hibernate, a growing number of studies are starting to highlight the effects of variation in environmental conditions on different life-history traits and population dynamics in these species (Humphries et al. 2002, Lane et al. 2012). For instance, alpine marmots *Marmota marmota* grew larger and heavier following earlier spring onsets, whereas more arid summers and deeper snow conditions reduced their mass (Canale et al. 2016). Winter conditions may directly influence the metabolic rate and fat depletion of hibernating individuals because a thick snow cover insulates their hibernacula from cold and variable temperatures (Inouye et al. 2000, Tafani et al. 2013). Nevertheless, persistent snow cover in spring limits forage availability and shortens the growing season (Van Vuren and Armitage 1991). This lower food availability at emergence could indirectly impair both survival at emergence and summer mass gain because it could force individuals to subsist on stored fat until vegetation growth begins.

Increased summer temperatures and precipitation during the active season may directly impose thermoregulatory stress and energetic constraints on ground-dwelling squirrels, both of which can negatively affect body mass (Türk and Arnold 1988, Ebensperger and Bozinovic 2000). Increased summer rainfall and temperatures may decrease forage availability and quality as well as limit activity (Armitage 2014, Williams et al. 2016). Increased summer temperatures can accelerate vegetation growth and plant lignification (Doiron et al. 2013), thus reducing forage digestibility. Temperatures over a critical thermal threshold and heavy precipitation decrease activity, time spent above ground and the frequency of foraging bouts (Melcher et al. 1990, Williams et al. 2016). Additionally, heavy summer rainfall may increase soil compaction, burdening individuals with greater energy expenditure to maintain their burrow system (Ebensperger and Bozinovic 2000).

The relationships between seasonal variations of environmental variables and life-history traits of ground-dwelling squirrels are expected to have strong demographic consequences (Van Horne 2007, Armitage 2014). They can provide relevant insight to disentangle the prevalent environmental factors driving the population dynamics of mammals that use burrows and hibernate underground. In the context of climatic changes, more long-term studies are needed to understand the influence of variations in environmental conditions on both body mass and demographic components like survival in hibernating species. Here, we evaluated the influence of winter, spring and summer conditions on adult body mass and adult survival in a population of hoary marmots monitored for 14 years in the foothills of the Canadian Rocky Mountains.

The hoary marmot *Marmota caligata* is the largest species of ground-dwelling squirrels in north-western America and is almost exclusively found in high alpine meadows (Braun et al. 2011). Despite their wide distribution, knowledge about their population dynamics is scarce (Patil et al. 2013). With their relatively long lifespan, hibernating behaviour and high altitudinal distribution, they are a relevant model species to investigate the effects of interannual variations in environmental conditions. The body mass of marmots is directly linked to their energy stored in body reserves and their structural growth (Inouye et al. 2000, Armitage 2014, Supporting information), and these traits are strongly related to an individual's reproductive success (Canale et al. 2016). Adult survival is a crucial demographic parameter in marmots (Ozgul et al. 2010) and body reserves are key to winter survival because marmots rely uniquely on fat reserves during hibernation (Humphries et al. 2003).

Our first objective was to identify environmental factors determining body mass at emergence, a proxy for structural size and energy stored, and summer mass gain, a proxy for structural growth and energy gain. First, we hypothesized that winter conditions were a key determinant of mass following hibernation, predicting that years with a thick layer of isolating snow would reduce thermoregulatory costs and lead to higher mass at emergence (Patil et al. 2013, Rézouki et al. 2016). Second, we hypothesised that access to high-quality forage during the active period would increase mass gain in summer because high-quality forage better fulfills the energetic demands associated with growth and energy storage (Canale et al. 2016). We predicted a greater mass gain in years with a more gradual vegetation growth, mild temperatures and early snowmelt. Because drought lowers forage nutritional value (Van Horne et al. 1997) and increases thermoregulatory stress (Melcher et al. 1990), we predicted that years with hot and dry summers would reduce summer mass gain.

Our second objective was to determine whether environmental factors and body mass near immergence affect the survival of adult marmots. We hypothesized that mass at immergence prior to hibernation and winter conditions were the main determinants of annual survival (i.e. from emergence at year t to emergence at year $t+1$; Ozgul et al. 2010, Turbill et al. 2011, Patil et al. 2013, Rézouki et al. 2016). We expected positive effects of higher mass at immergence on annual survival. We also expected that snowier winter would improve annual survival because a thick layer of isolating snow would reduce thermoregulatory costs during hibernation. We also expected survival to be affected by spring and summer conditions preceding hibernation because access to higher quality forage before hibernation should have a positive effect on summer mass gain, and hence on the accumulation of energy reserves essential to survive over winter (Ebensperger and Bozinovic 2000, Pettorelli et al. 2007).

## Material and methods

### Study area and captures

We studied hoary marmots at Caw Ridge (54°N, 119°W), in the foothills of the Rocky Mountains in west-central Alberta, Canada. The landscape includes a few cliffs and is mainly composed of steep grassy slopes and rocky hills. Marmots are located at altitudes varying from the tree line (ca 1900 m a.s.l.) up to the rocky ridges (2100 m a.s.l.). They feed on grassy slopes and often use rocky ridgelines. The alpine environment they inhabit is characterized by an arctic-subarctic climate, with rapidly changing weather. Winters are long (> 200 days, Supporting information) and harsh, with temperatures reaching below −40°C (Festa-Bianchet and Côté 2008).

We captured hoary marmots annually from 2004 to 2017, using Tomahawk and Havahart live traps baited with human urine (Taulman 1989). The capture/recapture period started in late May (around emergence; Fig. 1) and lasted until early September (around immergence; Fig. 1). We manipulated captured individuals in restraining bags, enabling us to mark and measure them. We identified every individual with numbered ear-tags to which we attached color-coded wires for identification from a distance. In addition, we subcutaneously implanted a Passive Integrated Transponder, PIT tag (Avid Identification Systems, Inc. California, USA), providing reliable long-term identification with a unique barcode for each marmot. We measured body mass (± 0.05 kg) with scales, the zygomatic arch width (± 0.1 mm) with calipers, and total body length with a measuring tape (± 0.5 cm). We verified the log–log relationship between the two skeletal measurements and body mass and did not detect any outliers (Supporting information).

All analyses focused on mass and survival of individuals aged two years and older because we had limited sample sizes for pups (< 1 year old) and yearlings. Sex and reproductive status (breeder versus non-breeder) were determined by observing the genitalia and lactation marks in females. Reproductive males have scrotal testes and reproductive females have nipples swollen with milk, surrounded by patches of flattened hairs. We collected DNA samples to validate sex assignments using polymerase chain reaction techniques (PCR; Gorrell et al. 2012). Handling time was on average 15 min (range: 3–40 min). We had a research permit issued by the Alberta Environment and Parks Policy and Planning Division, Fish and Wildlife Policy Branch and our protocols were approved by the animal care committee (CPAUL) at Laval University, Quebec, Canada.

### Environmental conditions

To assess the influence of environmental variation on mass at emergence, summer mass gain and annual survival, we compiled variables describing annual variation in conditions during winter, spring and summer (Fig. 1).

#### *Winter*

As a global index for winter conditions, we used the November–March anomalies of the North Pacific Index (NPI; Trenberth and Hurrell 1994). At Caw Ridge, NPI is negatively correlated with local temperatures and positively correlated with local precipitation (Hamel et al. 2009a). Winters with high NPI values are therefore snowier and colder than winters with low NPI values.

#### *Spring*

Spring conditions could be defined by three variables: percent snow cover at emergence, cumulative spring temperatures and the rate of spring green-up (Fig. 1). Snow cover was estimated based on satellite data from the National Snow and Ice Data Center and the MODIS/Terra Snow Cover 8-Day L3 Global 500m Grid product (MOD10A2; Hall and Riggs 2016). Images were available every eight days with a spatial resolution of 500 m. The area occupied by marmots included 42 pixels (representing 10.5 km$^2$) and we used the maximum extent of snow cover during an eight-day period by coding 1 if a pixel was covered by snow and 0 if not (using the central date of the eight-day interval). We computed the percentage of pixels with a value of 1 on 16 May as a measure of snow persistence around emergence because hoary marmots generally emerge from hibernation in early to mid-May (Braun et al.

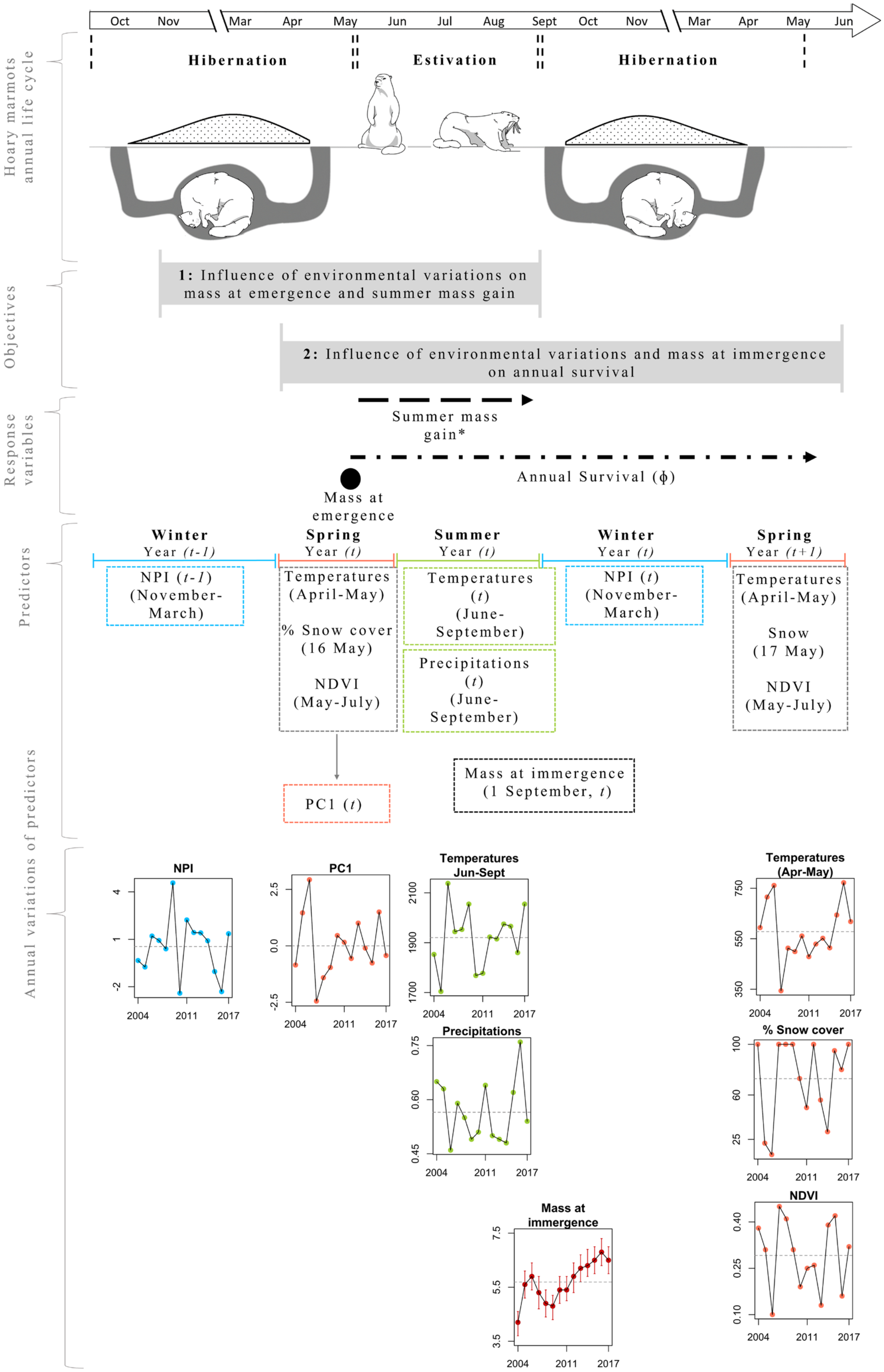

Figure 1. Graphical representation of the study, with a timeline illustrating hoary marmots' life cycle, the research objectives, the dependent and independent variables measured and the annual variation for each independent variable (see Material and methods for specifications – NPI: North Pacific Index, NDVI: normalized difference vegetation index, PC1: scores of the first principal component analysis on spring conditions, masses at immergence: predicted mass for non-breeding females).

2011). Higher percentage values indicate a larger area covered by snow. The percentages of snow on the ground estimated with satellite images were highly consistent with those observed directly in the field during the 2006–2017 period (Supporting information).

To contrast colder versus warmer springs, and as an index of spring phenology, we estimated cumulative temperatures from 1 April to 31 May with data obtained from the Hendrickson Creek meteorological station (53°48'N, 118°30'W, 1448 m a.s.l.), which is the nearest Environment Canada meteorological station to Caw Ridge (20 km). We used data from the meteorological station rather than data collected directly in the field because field work only started in mid-May and temperatures at Hendrickson Creek were highly correlated with temperatures at Caw Ridge (Supporting information). We included April in the spring index because the number of arousal events increases during the last weeks of hibernation (French 1990). Thus, temperature conditions during these awakening moments may affect their timing of emergence (Inouye et al. 2000). Moreover, we could not simply sum maximum temperatures because data were missing on some days each year. Instead, we calculated the area under the curve for the maximum daily temperatures (°C) between 1 April and 31 May, estimated with the *auc* function of the 'flux' package (Jurasinski et al. 2014) in R (<www.r-project.org>).

To estimate the rate of spring green-up, we used the normalized difference vegetation index (NDVI) computed from images of the MODIS satellite (MOD13Q1; Didan 2015). Images were available every 16 days with a spatial resolution of 250 m. For each year, we computed the rate of spring green-up as the maximum slope between two consecutive NDVI values between 9 May and the date at which the maximum value of NDVI was recorded (Pettorelli et al. 2007). Higher slope values indicate faster changes in vegetation growth associated with a shorter period when high-quality forage is available. This NDVI metric predicts annual variation in the timing of spring green-up in the study area (Hamel et al. 2009b).

#### Summer

We defined summer conditions using cumulative summer temperatures and precipitation (Fig. 1). To estimate cumulative summer temperatures, we used the area under the curve for the maximum temperatures (°C) between 1 June and 15 September recorded at Hendrickson Creek (Supporting information). For cumulative summer precipitation (rain and snow), we did not use data from the meteorological station because precipitation can be very localised in mountains (Supporting information). Instead, we used the qualitative data collected locally each day in four categories: no rain, light rain, heavy rain and snow. We defined a precipitation index as the ratio of the number of days of rain or snow (categories light rain, heavy rain and snow) on the total number of days local precipitation was recorded in the field. Therefore, summers with low precipitation ratios were drier than summers with high ratios.

### Statistical analyses

#### Body mass

To assess the effects of winter, spring and summer conditions on summer body mass (Fig. 1), we performed a robust linear mixed model (LMM) with the *robustlmer* function of the R package 'robustlmm' (Koller 2015). We opted for a robust LMM to control for the heavy-tail distribution in the model residuals (Jacqmin-Gabba et al. 2007). The total number of captures over the 14 years of the study is 420, with an annual average number of recaptures of 12 (range: 4–24), for a total of 165 repeated measurements (i.e. recapture of individuals within the same year). We therefore included individual identity nested within year as a random intercept, as well as sex (males: n = 163; females: n = 237) and reproductive status (non-breeders: n = 320; breeders: n = 80) as fixed covariates. Individuals for whom reproductive status was uncertain were not included in the analysis (n = 28).

We included four explanatory environmental variables: winter NPI, cumulative summer temperatures, summer precipitation index and an index of spring conditions. The latter was based on a principal component analysis (PCA) including percent snow cover at emergence, cumulative spring temperatures and rate of spring green-up. We used the scores of the first principal component (PC1), which explained ~64% of the variance, as a global index of spring conditions. Higher PC1 scores described early springs, with high April–May temperatures, less snow cover at emergence and a slower rate of spring green-up (Supporting information). PCA is a variable reduction method that allowed us to produce a global index of spring conditions while limiting the number of variables included in the model, and hence avoiding overparameterization. The main risk when using a variable reduction method like PCA is that we might not fully represent the effect of each variable independently (Freckleton 2011). To explore this eventuality, we fitted three different models with each of the variables described by PC1 included separately and we also presented these individual estimates in Table 1.

Furthermore, because we measured body mass throughout the summer (24 May–5 September), we included date of capture (in Julian days starting on 31 May each year) as a fixed effect and its interactions with the four explanatory environmental variables, as well as with sex and reproductive status (Table 1). Therefore, the influence of an explanatory variable as a main effect represents its influence on the intercept, which means on body mass around emergence at the end of May (Julian day 0), whereas its interaction with Julian days represents its influence on the slope of body mass with time, which means on summer mass gain. In the results, we present the partial residuals (R package 'visreg'; Breheny and Burchett 2017) to show the relationship between the independent variable of interest and body mass while controlling for the effects of the other independent variables included in the model. All variables included in the model had variance inflation factors < 2.4.

We performed all analyses on body mass measurements rather than deriving a measure of body condition index

Table 1. Influence of environmental conditions (defined in Fig. 1), sex and reproductive status on body mass near emergence (main effects) and summer mass gain (interactions with Julian days) of adult hoary marmots at Caw Ridge, Alberta (2004–2017). Parameters with a confidence interval (CI) excluding zero are highlighted in bold. In grey, we present the estimates for the individual effects of the variables described by PC1 that were fitted in three separate models.

| Fixed parameters | Estimates [95% CI] |
|---|---|
| Intercept | 3.12 [2.87; 3.36] |
| **Julian days** | 0.026 [0.024; 0.029] |
| Sex (M) | 0.31 [−0.03; 0.64] |
| **Reproductive status (Yes)$_t$** | 0.99 [0.58; 1.41] |
| **Winter NPI$_{t-1}$** | −0.22 [−0.34; −0.10] |
| PC1$_t$ | 0.07 [−0.06; 0.21] |
| *Cumulated spring temperatures$_t$: 0.05 [−0.15; 0.25]* | |
| *Rate of spring green-up$_t$: −0.05 [−0.22; 0.12]* | |
| *Percent snow cover at emergence$_t$: −0.17 [−0.35; 0.01]* | |
| Cumulated summer temperatures$_t$ | 0.17 [−0.04; 0.37] |
| Summer precipitation index$_t$ | −0.18 [−0.42; 0.05] |
| **Julian days×Sex (M)** | 0.0065 [0.0033; 0.0098] |
| **Julian days×Reproductive status (Yes)** | −0.0084 [−0.0135; −0.0034] |
| **Julian days×Winter NPI$_{t-1}$** | 0.0021 [0.0010; 0.0033] |
| **Julian days×PC1$_t$** | 0.0028 [0.0014; 0.0041] |
| *Julian days×Cumulated spring temperatures$_t$: 0.0031 [0.0008; 0.0053]* | |
| *Julian days×Rate of spring green-up$_t$: −0.064 [−0.006; −0.021]* | |
| *Julian days×Percent snow cover at emergence$_t$: −0.065 [−0.350; 0.010]* | |
| Julian days×Cumulated summer temperatures$_t$ | −0.0020 [−0.0042; 0.0001] |
| Julian days×Ratio of summer precipitation$_t$ | 0.0013 [−0.0008; 0.0034] |
| *Variance of random intercept: – marmot ID nested within year 1.36* | |

M = males, $t-1$ = during hibernation, $t$ = following hibernation, NPI = North Pacific Index, PC1 = scores of the first principal component analysis on spring conditions.

based on body mass and zygomatic arch width. This choice was made because the zygomatic arch width contained missing values since it was not always measured when animals were recaptured within a short period of time during the same summer (body mass: n = 420, zygomatic arch width: n = 273). Furthermore, body mass and zygomatic arch width shared a strong positive correlation (Pearson r: 0.83 [95% CI: 0.79; 0.87], n = 273; Supporting information) in adult marmots, indicating that body mass was a good proxy for representing the combination of the energy stored and structural growth during summer. Nonetheless, we performed the analyses on the reduced data set containing no missing values for the zygomatic arch width, and these analyses provided similar results (Supporting information).

### *Survival*

To identify the principal driver of annual survival (Fig. 1), we evaluated whether apparent survival ($\phi$) was influenced by winter, spring and summer conditions, as well as mass at immergence. We used a Cormack–Jolly–Seber model (CJS; Jolly 1965), which estimates apparent survival at the population level based on encounter histories of marked individuals while accounting for the recapture/resighting probability. The encounter history of an individual is a binomial vector forming a series of 0/1 (individual not seen-captured/seen-captured during a specific year). Our model included encounter histories for a total of 132 adult marmots of known sex (females: n = 69; males: n = 63) over 14 years (k = 14 occasions). The encounter histories included both physical captures/recaptures and visual resighting.

We first evaluated the goodness-of-fit (GOF) of the full time-dependent CJS model using the R package 'R2ucare' (Gimenez et al. 2018). For both sexes, the overall GOF test was not significant (females: $\chi^2 = 27.18$, df = 39, p-value = 0.92; males: $\chi^2 = 23.48$, df = 32, p-value = 0.86), with the 2.Ct test revealing little support for trap-dependence (females: $\chi^2 = 14.99$, df = 11, p-value = 0.18; males: $\chi^2 = 12.54$, df = 8, p-value = 0.13) and the 3.Sr test indicating the absence of transient effects (females: $\chi^2 = 2.36$, df = 12, p-value = 1; males: $\chi^2 = 4.73$, df = 10, p-value = 0.91). Hence, the structure of our data met the assumptions underlying the CJS model.

We then modeled the probability of recapture/resighting (p) and apparent survival ($\phi$) with the package 'RMark' (Laake 2013). We first evaluated whether p was affected by time (year as factor), sex and annual field effort, with all the candidate models including on $\phi$ the additive effects of year (year as factor) and sex (see the Supporting information for details). Annual field effort was defined as the total number of days in a year when marmots were recorded from visual observations or captures. Based on Akaike information criterion corrected for small sample size (AICc; Burnham and Anderson 2002), the best model for the probability of recapture/resighting included an influence of sex and annual field effort (Supporting information). Accordingly, for an average field effort, the probability of recaptures/resighting was 0.62 [95% CI: 0.52; 0.71] for females and 0.42 [95% CI: 0.32; 0.53] for males. This model was used to model p in all candidate models that were then evaluated for the influence of environmental conditions and body mass on $\phi$.

Among the candidate models evaluating $\phi$, we tested whether survival was constant or whether it was affected by sex, year and the additive effects of sex and year. We tested the effect of year both as a continuous variable and as a factor. We also included 10 candidate models for evaluating the influence of winter, spring and summer conditions, as well as mass at immergence (Fig. 1), by including a single explanatory environmental variable at a time (Table 2). We evaluated the direct influence of each of the three spring variables (i.e. percent snow cover at emergence, cumulative spring temperatures and rate of spring green-up). We assessed the effects of spring variables at both year $t$ and $t+1$ because spring conditions before hibernation (year $t$) and at emergence after hibernation (year $t+1$) could both influence survival to emergence (Fig. 1). For instance, adult survival could be affected by the conditions experienced in the spring preceding the summer and winter hibernation (year $t$) because spring conditions can influence summer food availability. Adult survival could also be affected by spring conditions after winter hibernation (year $t+1$) because this is when marmots emerge from their burrows, and it is usually a critical period of food shortage that occurs just before the new capture season. We also evaluated a model including current winter conditions, using NPI values at year $t$. We evaluated the effects of summer conditions preceding hibernation by including two candidate models testing cumulative summer temperatures and summer precipitation index at year $t$.

Moreover, we also included a candidate model evaluating the influence of average mass reached at the end of summer before immergence into hibernation (year $t$). This variable was estimated based on the predictions of a LMM similar to the one described for objective 1, i.e. including both 'sex' and 'reproductive status' in interaction with 'Julian days', but excluding all annual environmental conditions and instead including year as a factor (see the Supporting information for the model details). Including sex and reproductive status as covariates in interaction with Julian days allowed the model to estimate specific slopes, i.e. growth rate, for each category, thereby accounting for the unbalanced recaptures according to sex and reproductive status across years. We then predicted mass on 1 September for each year for the category 'non-breeding females', which we used to represent the average annual mass at the end of the summer at the population scale. We used an annual population average rather than individual masses because body mass is a continuous time-varying intrinsic variable that can only be observed for an individual when it is captured, resulting in a very large proportion of unknown values in the analysis (e.g. an animal captured in year $t+1$ but not in year $t$ has survived from $t$ to $t+1$ but its mass in year $t$ is unknown). Such variables are thus very challenging to model (Bonner et al. 2010) and instead we used the average mass at the end of the active season at the population level as an index of the environmental conditions experienced by the individuals during the summer rather than using mass as an index of individual heterogeneity.

Lastly, we assessed support for these candidate models evaluating $\phi$ based on ΔAICc values and AICc weights (Table 2), considering models with ΔAICc < 2 as equivalent (Burnham and Anderson 2002). Because there was no strong support for most explanatory variables compared with the constant model (Table 2, 3), we did not evaluate models with additive environmental effects. For simplicity, we present results based on a model assuming no difference in survival with respect to reproductive status. These results are equivalent to those obtained based on multistate models accounting by bootstrapping for the effect of reproductive status and its uncertainty (Supporting information). Field effort, the population index of body mass at immergence and

Table 2. Candidate models evaluated for identifying the variables (defined in Fig. 1) affecting apparent annual survival ($\phi$) in adult hoary marmots at Caw Ridge, Alberta (2004–2017).

| Candidate models | *K* | AICc | ΔAICc | AICc weight |
|---|---|---|---|---|
| $\phi$(~Rate of spring green-up$_t$) | 5 | 691.14 | 0 | 0.20 |
| $\phi$(~Summer precipitation index$_t$) | 5 | 691.52 | 0.38 | 0.17 |
| $\phi$(~.) | 4 | 692.23 | 1.09 | 0.12 |
| $\phi$(~Percent snow cover at emergence$_{t+1}$) | 5 | 692.98 | 1.84 | 0.08 |
| $\phi$(~Cumulated spring temperatures$_{t+1}$) | 5 | 693.90 | 2.76 | 0.05 |
| $\phi$(~Year) | 5 | 693.98 | 2.84 | 0.05 |
| $\phi$(~Winter NPI$_t$) | 5 | 694.00 | 2.86 | 0.05 |
| $\phi$(~Sex) | 5 | 694.03 | 2.89 | 0.05 |
| $\phi$(~Rate of spring green–up$_{t+1}$) | 5 | 694.11 | 2.97 | 0.05 |
| $\phi$(~Percent snow cover at emergence$_t$) | 5 | 694.24 | 3.10 | 0.04 |
| $\phi$(~Cumulated spring temperatures$_t$) | 5 | 649.28 | 3.14 | 0.04 |
| $\phi$(~Cumulated summer temperatures$_t$) | 5 | 694.29 | 3.15 | 0.04 |
| $\phi$(~Mass at immergence$_t$) | 5 | 694.29 | 3.15 | 0.04 |
| $\phi$(~Year + Sex) | 6 | 695.80 | 4.66 | 0.02 |
| $\phi$(~year) | 15 | 702.73 | 11.59 | 0.00 |
| $\phi$(~year + Sex) | 16 | 704.38 | 13.24 | 0.00 |
| *All the candidate models above included:* $p$(~Capture effort$_{t+1}$ + Sex) | | | | |

$K$ = the number of identifiable parameters, AICc = Akaike information criterion corrected for small sample size, ΔAICc = delta AICc, AICc weight = Akaike weights, $t$ = preceding/during hibernation, $t+1$ = following hibernation, Year = year as a continuous variable, year = year as factor (n = 14), NPI = North Pacific Index, $p$ = probability of recapture/resighting.

Table 3. Estimates (logit scale) and 95% confidence intervals (CI) for the parameters included in the two most supported models describing annual apparent survival ($\phi$) and the probability of recapture/resighting (p) in adult hoary marmots, at Caw Ridge, Alberta (2004–2017).

| Parameters | Estimate [95% CI] |
|---|---|
| Rate of spring green-up$_t$ | |
| Annual survival ($\phi$) | |
| Intercept | 1.25 [0.97; 1.54] |
| Rate of spring green-up$_t$ | −0.38 [−0.82, 0.06] |
| Probability of recapture/resighting (p) | |
| Intercept | 0.57 [0.19; 0.94] |
| Sex (M) | −0.84 [−1.39; −0.28] |
| Field effort$_t$ | 0.45 [0.19; 0.70] |
| Summer precipitation index$_t$ | |
| Annual survival ($\phi$) | |
| Intercept | 1.20 [0.95; 1.46] |
| Summer precipitation index$_t$ | −0.30 [−0.63, 0.04] |
| Probability of recapture/resighting (p) | |
| Intercept | 0.62 [0.24; 1.01] |
| Sex (M) | −0.89 [−1.45; −0.33] |
| Field effort$_t$ | 0.45 [0.19; 0.71] |

all environmental variables were standardized. NPI values are standardized anomalies and thus did not require further standardization.

## Results

### Body mass

Winter conditions affected body mass near emergence and body mass gain during summer, while spring conditions only affected summer mass gain (Table 1). Marmots experiencing the coldest and snowiest winters (i.e. high NPI values) weighed 1.65 kg [95% confidence interval (CI): 1.53; 1.77] (~47%) less at emergence than marmots experiencing the warmest and driest winters (Fig. 2A). Nevertheless, individuals had a greater mass gain during the summer following coldest and snowiest winters and hence had compensated mass loss by the end of the summer. After colder and snowier winters, body mass gain during the summer was 35.9 g day$^{-1}$ [95% CI: 35.6; 36.2], whereas it was 21.1 g day$^{-1}$ [95% CI: 20.9; 21.2] during the summer following warmer and drier winters (Fig. 2A). Early springs were associated with a greater body mass gain during summer (Table 1). Individuals experiencing early springs, that is warmer and drier springs with low snow cover and more gradual rate of spring green-up (higher PC1 values), gained 34.3 g day$^{-1}$ [95% CI: 34.2; 34.6], whereas individuals experiencing delayed springs with rapid green-up gained 19.4 g day$^{-1}$ [95% CI: 18.9; 19.9] (Fig. 2B).

Males and females weighed nearly the same around emergence (estimate [95% CI]: females = 3.18 kg [2.94; 3.42]; males = 3.47 kg [3.20; 3.74]), but mass gain in males was ~21% higher than in females (estimate [95% CI]: females = 24.9 g day$^{-1}$ [24.7; 25.2]; males = 31.9 g day$^{-1}$ [31.6; 32.2]), and thereby males reached a 14% higher body mass at immergence into hibernation than females (Fig. 3A, Table 1). Breeding individuals were about 1.06 kg heavier than non-breeding ones around emergence (estimate [95% CI]: breeding individuals = 3.99 kg [3.57; 4.40]; non-breeding individuals = 2.93 kg [2.68; 3.18]), but their mass gain (estimate [95% CI]: 17.7 g day$^{-1}$ [17.6; 17.9]) was ~33% lower than non-breeding individuals (estimate [95% CI]: 26.3 g day$^{-1}$ [26.0; 26.4]; Fig. 3B).

### Survival

For apparent annual survival $\phi$, the constant model was the most parsimonious (lower number of parameters) among the equivalent models ($\Delta$AICc < 2, Table 2). This result, along with the low support for models including year, suggests little variation in the survival probability among years. The annual survival estimate [95% CI] obtained by the constant model is 0.77 [0.72; 0.81]. Still, the candidate model with the lowest AICc included the rate of spring green-up during the spring preceding hibernation (Table 2). This model had about twice higher support (as measured by AICc weight, Table 2) than the constant model. Average survival probability tended to increase with shallower slopes in NDVI, that is with gradual and slower vegetation growth (Table 3). When the rate of spring green-up was the fastest, the probability of annual survival was 0.67, whereas it was 0.87 when spring green-up was slowest (Fig. 4A). Although this effect is a considerable biological difference for a fitness component known to be highly buffered against temporal variability in long-lived species (Gaillard and Yoccoz 2003), the uncertainty was very large (Table 3).

The summer precipitation index preceding hibernation was also included among the set of equivalent models ($\Delta$AICc < 2) and had slightly more support than the constant model (Table 2). This effect was also uncertain (Table 3) but suggested that average survival probability tended to be lower when there were more days with precipitation during the summer (Fig. 4B). This relationship was mainly driven by an unusual summer that had twice more rainy days than the second rainiest summer (Fig. 4B), which resulted in a decrease on average of 24% in survival rate compared to the complete study period. Furthermore, the model including mass was not supported (estimate [95% CI]: −0.01 [−0.32; 0.30]).

## Discussion

We observed that winter conditions determined mass at emergence and summer mass gain for adult hoary marmots. Spring conditions also influenced summer mass gain, with earlier springs leading to faster growth rates. Surprisingly, annual survival was relatively stable among years and was not directly affected by mass reached at the end of summer at a population level, even though this latter trait showed large inter-annual variations. Still, our results suggest a potentially

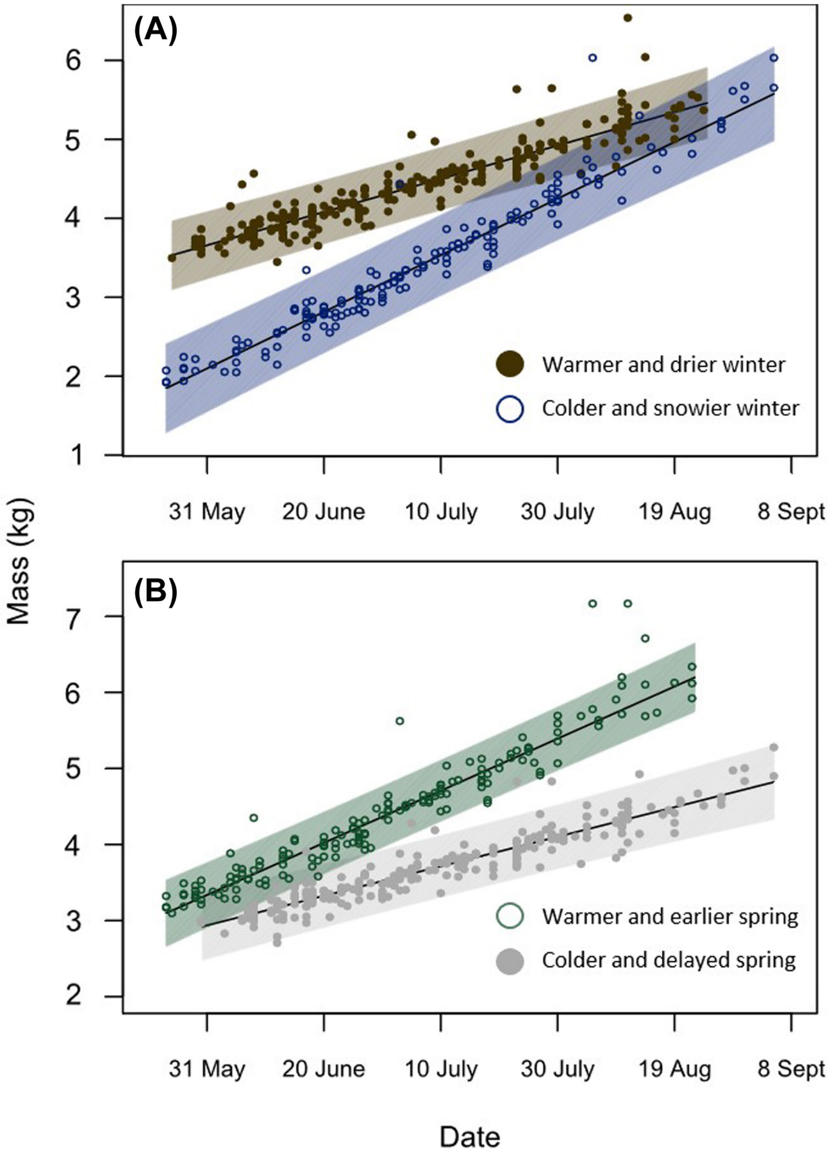

Figure 2. Effects of environmental variations in winter (A) and spring (B) on changes in body mass during summer, for adult hoary marmots at Caw Ridge, Alberta, Canada (2004–2017, n = 420). (A) Influence of North Pacific Index winter anomalies prior to emergence (NPI *t* − 1; Fig. 1), illustrating the predictions for the lowest NPI year (warmer and drier winter) and the highest NPI year (colder and snowier winter) between 2004 and 2017. (B) Influence of the first component of a principal component analysis on spring conditions at emergence (PC1 *t*; Fig. 1, Supporting information), illustrating the predictions for the year with the highest PC1 score (warmer and earlier spring) and the lowest PC1 score (colder and delayed spring) between 2004 and 2017. Solid lines and the shaded areas are the predictions and 95% confidence intervals accounting for covariates. Dots are the partial residuals accounting for the effects of the other variables in the model.

marked reduction in annual survival in years when hibernation was preceded by a late spring and high summer precipitation. Our study underlines the need to consider the effects of environmental factors throughout the annual cycle to fully assess how they affect fundamental life-history traits of burrowing and hibernating species.

Lower temperatures combined with greater snow precipitation in winter resulted in a lower body mass at emergence. At first glance, these results seemed counter-intuitive because the insulation properties provided by a thick snow cover should increase mass at emergence and temper the negative effects of outer temperatures, as previously observed in alpine marmots (Tafani et al. 2013). The latter study, however, differs from ours on two key aspects. First, snowy winters are also warmer in their study area, not colder as in our case. Second, they evaluated the influence of precipitation and temperatures only in April, not during the entire winter, and therefore showed that springs with warmer temperatures and greater precipitation resulted in higher mass at emergence. Consequently, two mechanisms likely explain the negative influence of snowier but colder winters on body mass at emergence in our study.

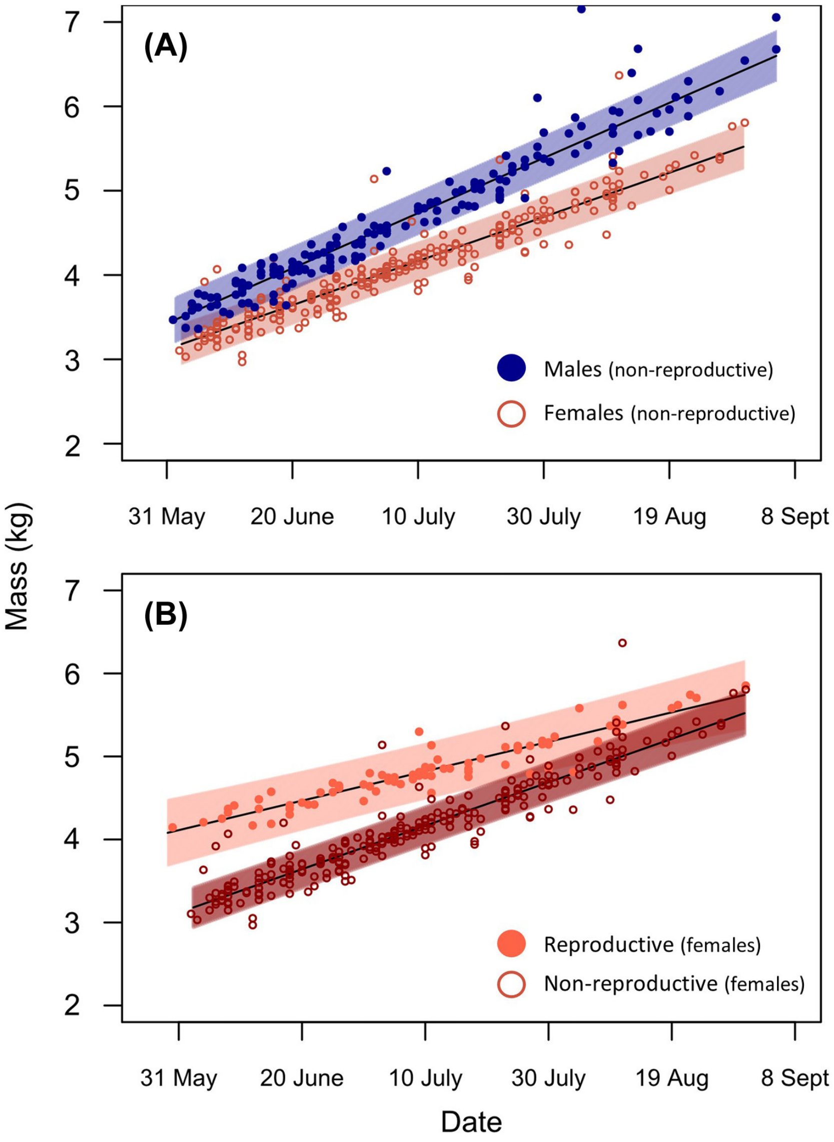

Figure 3. Changes in marmot mass during summer according to sex (A) and reproductive status (B), for adult hoary marmots at Caw Ridge, Alberta, Canada (2004–2017, n = 420). Solid lines and the shaded areas are the predictions and 95% confidence intervals accounting for covariates. Dots are the partial residuals accounting for the effects of the other variables in the model.

First, outer temperatures during the snow-free period following immergence between September and November (Supporting information) are frequently below the freezing point. Indeed, mean temperature at Hendrickson Creek from September to the end of November was 0°C between 2004 and 2017, with average minimal temperatures of −7°C (range of daily minimum temperatures: −45.2 to 14°C). Because the temperature in burrows depends mostly on the temperature of surrounding soils (Nikol'skii 2009), a very thin or absent snow cover during this period exposes marmots to cold temperatures increasing their metabolic activity. In fact, the minimal metabolic expenditure for marmots is reached at 5°C, with metabolic expenditures increasing linearly with decreasing temperatures (Arnold et al. 1991).

Second, Tafani et al. (2013) have shown that during periods when temperatures are greater than −10°C, only shallow snow depth (~1 m) is required to buffer large-scale temperature oscillations. Their results, however, also demonstrated that when the outside temperatures decreased below −10°C, the temperature inside the borrow reached −5°C for several days in row even with a deep snow layer (> 1 m, see Appendix D of Tafani et al. 2013). This latter scenario is likely to occur often during the winter in our study area because the climate is rather dry, with a low mean annual precipitation of 620 mm, and winter temperatures that can drop below −40°C. Therefore, even though burrows can buffer cold temperatures to a certain extent during part of hibernation, the temperature in winter is a critical component that can lower body mass around emergence.

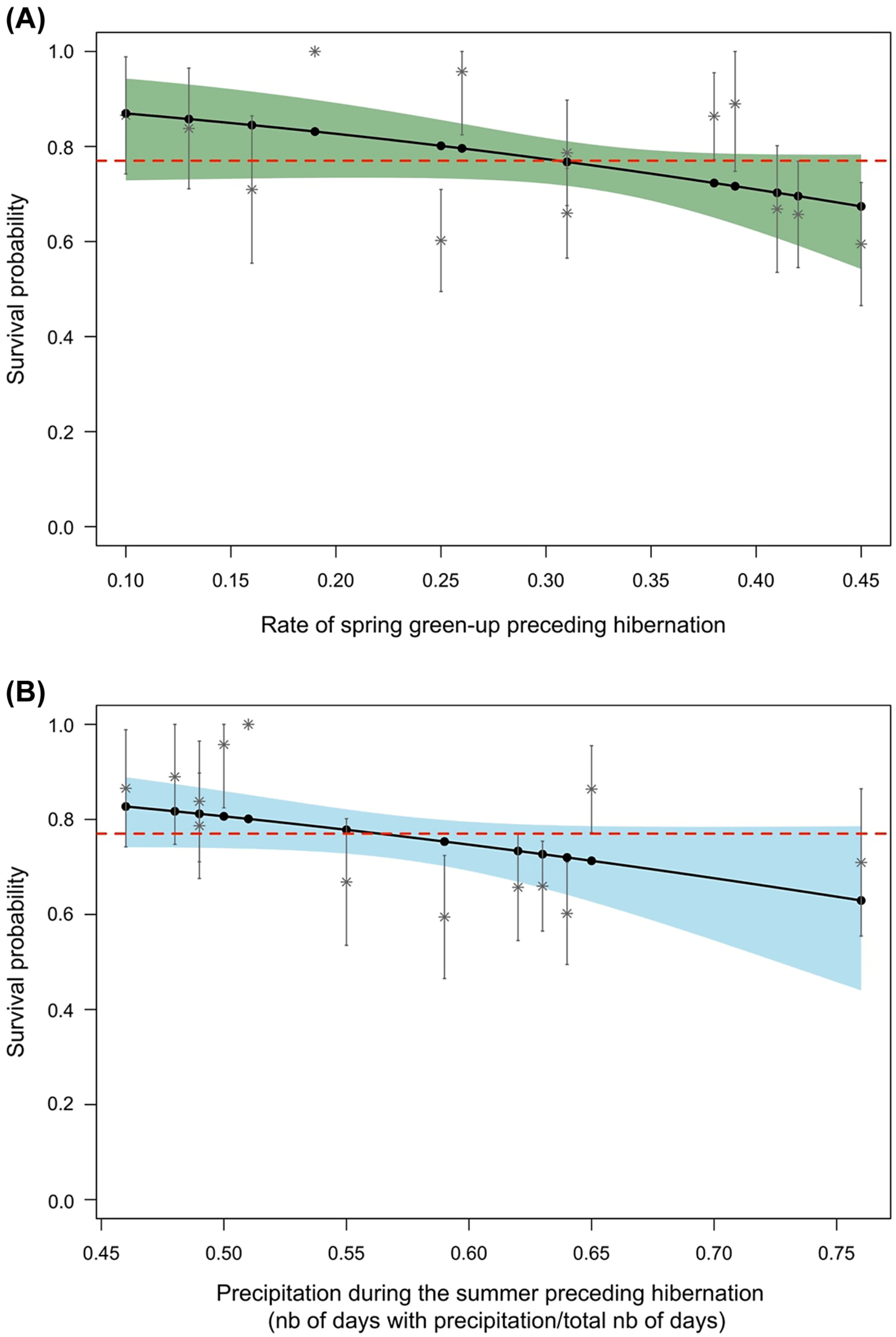

Figure 4. Changes in annual survival probability in relation with the rate of spring green-up preceding hibernation (A: normalized difference vegetation index NDVI *t*) and the summer precipitation index preceding hibernation (B: number of days with precipitation (rain or snow) on the total number of days *t*), for adult hoary marmots at Caw ridge, Alberta, Canada (2004–2017, n = 132; see Fig. 1 for parameter definition). The black lines are the predictions from the best model for each covariate (Table 2, 3), the colored polygons delimit the 95% confidence intervals (CI) and the black dots are the predictions for each specific value of either spring green-up (A) or summer precipitation index (B) measured in the study (n = 13 annual values). Asterisks and error bars are the mean survival and standard error predicted for each year based on a full time-dependent model (i.e. model ϕ(~year) in Table 2). The red dotted lines represent the average survival probability predicted for the whole study period (i.e. model ϕ(~.) in Table 2).

Although mass at emergence was lower in springs following cold and snowy winters, marmots had a greater mass gain and managed to reach a similar mass at the end of the summer compared with years following mild winters. A study on golden-mantled ground squirrels *Urocitellus lateralis* showed that individuals that had >50% of their fat reserves surgically extracted completely restored these reserves in approximately eight weeks (Dark et al. 2006). These results suggest that ground-dwelling squirrels can adopt behavioural and physiological strategies to maximize mass gain during the active season, such as modifying their foraging tactics (Armitage et al. 1976, Bachman 1993) or decreasing their metabolic rate during unfavorable conditions (Zervanos and Salsbury 2003). They can also reduce the energy allocated to growth (as suggested by the analysis on zygomatic arch width; Supporting information) and reproduction (Patil et al. 2015, Supporting information). The scarcity of data collected on litter size prevents us from evaluating the tradeoff between maximizing summer mass gain versus reproduction in our study. The existence of such a tradeoff could have a large effect on population dynamics.

We observed a greater summer mass gain after warm and early springs. In our study area, earlier springs were strongly associated with higher temperatures in May, faster snowmelt, and a more gradual vegetation growth. Gradual vegetation growth in early springs influences mass gain in herbivores (Pettorelli et al. 2007, Garel et al. 2011) because it usually provides longer access to highly nutritive forage as plant digestibility is greater during the earlier stages of vegetation growth. Although we have no precise data on timing of emergence, early springs probably triggered marmots to emerge earlier in our study area. Indeed, even though we set the traps at a similar date each year, we started capturing marmots about a week earlier in years when spring arrived early (Fig. 2B). Nonetheless, our results suggest that marmots did not experience a phenological mismatch but rather benefited from earlier access to forage because earlier snowmelt and a more gradual vegetation growth resulted in a greater mass gain.

Furthermore, our results indicate that mass at immergence may not be a major factor affecting survival. The absence of the effect of mass at immergence on apparent survival may be due to potential costs associated with being fatter, including increased locomotory costs and reduced mobility both leading to increased predation risk (Witter and Cuthill 1993, Humphries et al. 2003). Furthermore, Turbill et al. (2011) showed that monthly survival was higher during hibernation compared with the active season among hibernating species and claimed it is probably because inactivity minimizes their exposition to predation (Turbill et al. 2011). Nevertheless, they were able to show that variation in adult annual survival probability among mammal hibernating species were strongly related to body mass (Turbill et al. 2011). We might have been unable to observe an effect of mass at immergence on adult annual survival because we could not consider mass at the individual level. Furthermore, the individual ability to adopt tactics to maximize summer mass gain after harsh winters may allow adult marmots in our population to be in generally good condition prior to hibernation, above the optimal threshold required to survive the winter (Dark et al. 2006, Forger et al. 2008).

The most parsimonious survival model was the constant model that revealed an apparent adult survival of 0.77 [0.72; 0.81]. That survival rate is comparable with the 0.81 ± 0.10 observed for reproductive alpine marmots studied by Rézouki et al. (2016). Still, it is relatively low compared with the survival rate of 0.88 to 0.93 observed in another population of alpine marmots (Stephens et al. 2002) or the rate of 0.87 to 0.91 observed for philopatric individuals within a population of yellow-bellied marmots *Marmota flaviventris* (Van Vuren and Armitage 1994). Our estimate is close to the survival rate of 0.74 (95% CI = [0.65; 0.81]) obtained for individuals followed by telemetry in more precarious populations of Vancouver Island marmots *Marmota vancouverensis* (Bryant and Page 2005). For Vancouver Island marmots, life-table calculations suggested that a survival rate around 80% was necessary to sustain the population (Bryant 1998). Because hoary marmots are close physiologically and biologically to Vancouver Island marmots (Kruckenhauser et al. 1999), and because adult survival is a major determinant of population stability in long-lived species (Gaillard et al. 1998, Gaillard and Yoccoz 2003), the apparent adult survival of 77% could indicate that the Caw Ridge marmot population is stable or perhaps slightly decreasing.

Even though the constant survival model was the most parsimonious, our results suggest that annual survival decreased following summers with faster green-up and higher accumulated precipitation. Even though these effects were weakly supported, apparent survival probability decreased up to 23% and 24% when adult marmots experienced faster green-up rate and rainy summers, respectively. Therefore, although annual survival of adult marmots seemed relatively stable, our results suggest survival was potentially more influenced by spring–summer rather than winter conditions.

Summers with rapid green-up or drought could indirectly impair survival by altering forage quality and availability (Lenihan and Van Vuren 1996, Bennett 1999). Nonetheless, mass at immergence did not seem to be a major driver of annual survival at the population scale, which implies that mechanisms other than energy acquisition alone may affect adult condition and survival. Moreover, contrary to other studies (Van Horne et al. 1997, Armitage 2013), summer drought was not a limiting factor in our study area, as indicated by the high ratio of days with precipitation (from 0.46 to 0.76 among years; Fig. 1, 4B). Frequent rainfall or snow may have reduced forage quality and time spent above ground, in addition to enhance climate-induced stress, as witnessed in Beever et al. (2010). Heavy rainfall could also lead to occasional mortality via hypothermia or to water-saturated soils leading to an increased cost for individuals to maintain their burrow systems (Ebensperger and Bozinovic 2000, Proulx 2012). Our results suggest that marmots could be as vulnerable to frequent precipitation as to drought episodes.

Overall, our study suggests that the predicted rise in temperature for all seasons and the earlier arrival of springs in the Rocky Mountains would not impair hibernating species of ground-dwelling squirrels at high altitude. Combined with the stable survival rate that we observed for adult marmots and the potential positive influence of early spring on survival, higher temperatures in winter and in spring could lead to a sustainable population. Nonetheless, models of climate change also predict increases in snow precipitation during winter and spring, which would delay the timing of snowmelt (Fyfe and Flato 1999) and could eventually counterbalance the benefits of early springs by restricting access to forage. Extreme variations in summer precipitation could also harm populations of hoary marmots, as they seem to negatively respond to frequent precipitation. Sheltering underground and hibernating are not indefectible shields against climate change as our results demonstrate that annual variation in winter and summer conditions also impact life-history traits in species performing these behaviors. Our results suggest that seasonal variations in key traits such as mass and survival in adults are the first step towards a mechanistic understanding of demography in a species inhabiting one of the most vulnerable environments facing climate change.

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## Author contributions

**Béatrice Carrier**: Conceptualization (equal); Data curation (lead); Formal analysis (lead); Funding acquisition (lead); Investigation (lead); Methodology (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (lead). **Steeve D. Côté**: Conceptualization (lead); Funding acquisition (supporting); Investigation (supporting); Methodology (supporting); Project administration (lead); Resources (supporting); Supervision (supporting); Validation (supporting); Writing – original draft (supporting); Writing – review and editing (supporting). **Sandra Hamel**: Conceptualization (equal); Data curation (supporting); Formal analysis (supporting); Investigation (supporting); Methodology (supporting); Supervision (lead); Validation (supporting); Visualization (supporting); Writing – original draft (supporting); Writing – review and editing (supporting). **Mathieu Garel**: Data curation (supporting); Formal analysis (supporting); Methodology (supporting); Software (supporting); Validation (supporting); Visualization (supporting); Writing – original draft (supporting); Writing – review and editing (supporting).

## Data availability statement

The data used for our manuscript and R code are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.ngf1vhhw4> (Carrier et al. 2022).

## Supporting information

The supporting information associated with this article is available from the online version.

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