Contrasting effects of climate change on seasonal survival of a hibernating mammal

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Seasonal environmental conditions shape the behavior and life history of virtually all organisms. Climate change is modifying these seasonal environmental conditions, which threatens to disrupt population dynamics. It is conceivable that climatic changes may be beneficial in one season but result in detrimental conditions in another because life-history strategies vary between these time periods. We analyzed the temporal trends in seasonal survival of yellow-bellied marmots (*Marmota flaviventer*) and explored the environmental drivers using a 40-y dataset from the Colorado Rocky Mountains (USA). Trends in survival revealed divergent seasonal patterns, which were similar across age-classes. Marmot survival declined during winter but generally increased during summer. Interestingly, different environmental factors appeared to drive survival trends across age-classes. Winter survival was largely driven by conditions during the preceding summer and the effect of continued climate change was likely to be mainly negative, whereas the likely outcome of continued climate change on summer survival was generally positive. This study illustrates that seasonal demographic responses need disentangling to accurately forecast the impacts of climate change on animal population dynamics.

Marmota flaviventer | demography | environmental conditions | mark–recapture | individual-based

Seasonality is a fundamental driver of ecosystem structure and function (1), and plays a dynamic role in shaping the behavior and life history of many species (e.g., refs. 2, 3). Animals occupying temperate, arctic, and alpine environments experience distinct cyclic variation in biotic and abiotic factors, and have evolved seasonal life-history strategies for coping with the changing conditions. This includes short but mild summers characterized by peaks in resource availability where animals give birth to young and forage to gain fitness, and long often-harsh winters with food shortages where animals largely depend on fat reserves for energy and in extreme cases go into hibernation (4, 5). However, climate change is altering the seasonal conditions to which plants and animals are accustomed (e.g., refs. 1, 6). Temperatures are increasing, winter snowfall is declining, snow is melting earlier, growing seasons are extending, and the frequency of extreme events (e.g., droughts) is on the rise (6–11). This has resulted in advancing phenologies [including earlier flowering of plants and earlier emergence of hibernating animals (12)], range shifts (13), and changes to species interactions and communities (14). Less well known, but of critical importance, are the direct demographic consequences of a changing climate (e.g., changes in age-specific survival or fecundity).

Animals most likely to be affected by climate change include high-latitude and high-elevation species which experience distinct seasonal phases but which are restricted by natural boundaries limiting shifts in distribution (horizontal or vertical). While changes in adult survival will likely have the biggest impact on the population dynamics of long-lived mammals, this life-history stage also appears more robust to environmental perturbations, whereas survival of younger age-classes may be more sensitive and immediate indicators of the effects of climate change (15, 16). However, long-term individual-based data are required over multiple decades to detect trends in survival in response to climate change. Furthermore, long-term data on individual fitness-related traits (such as body mass) are essential because such traits are closely linked with environmental conditions and act as a proxy for an individual's collective past experience [both environmental and social (17)]. Species occupying extreme and highly seasonal environments can undergo significant fluctuations in body mass (e.g., refs. 18–21).

Climate change could conceivably result in seasonally variable demographic responses (1). For example, increasing temperatures may reduce foraging time for certain species in summer to avoid overheating (e.g., refs. 22–24) but may improve survival during winter in harsh environments. A reduction in precipitation

Significance

Climate change is altering the seasonal environmental conditions to which animals have adapted, but the outcome may differ between seasons for a particular species. Demographic responses therefore need disentangling on a seasonal basis to make accurate forecasts. Our study shows that climate change is causing seasonally divergent demographic responses in a hibernating mammal. Continued climate change will likely have a positive effect on summer survival but a negative effect on winter survival. This potentially has wide-ranging consequences across other species occupying temperate to more extreme arctic and alpine habitats, which are also where the most rapid changes in climate are observed.

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Data deposition: The capture histories including age and body mass as time-varying individual covariates and a separate data file including growing season length have been deposited in the Dryad Digital Repository at https://doi.org/10.5061/dryad.ht76hdrcd.

See online for related content such as Commentaries.

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will increase the frequency of summer droughts (11), reducing forage availability for herbivores, whereas a reduction in snowfall during winter could lower locomotion costs and improve forage accessibility (25). Paradoxically, for species that are highly adapted to harsh environments, warmer winter and spring temperatures and a reduction in snowpack could result in animals freezing to death due to a lack of insulation (26). Warming temperatures have caused species-specific shifts in plant phenology resulting in an extended growing season (7, 27, 28). This may allow herbivores more time to gain weight before winter, potentially resulting in demographic or fitness-related benefits.

Due to its distinct circannual life history, highly seasonal montane habitat, and sensitivity to seasonal environmental conditions, yellow-bellied marmots (*Marmota flaviventer*) are a sentinel species for disentangling the seasonal impacts of climate change on demography. Marmots are too small to store sufficient fat to remain active during winter, and therefore hibernate for about 8 mo during this long period of food scarcity relying solely on fat reserves for energy (4, 29). Nevertheless, marmots go through distinct seasonal body mass cycles where adults can lose nearly 40% of weight from peak to minimal mass (30). Yellow-bellied marmots are found in western North America, where climate change is more evident than anywhere else on the continent [apart from the Arctic (11)]. In particular, there has been a significant reduction in late-season snowpack, a rise in temperatures, an increase in precipitation intensity, an increase in the severity of droughts, and pervasive plant mortality (10, 11). Marmots have shown a temporal increase in body mass and a subsequent increase in adult survival, which was hypothesized to be caused by an extended foraging season (31). However, the mechanistic link between seasonal survival, body size, and environmental change has not yet been directly evaluated.

A growing literature has identified the importance of seasonally different demographic responses to climatic conditions [birds (32, 33), fish (34), plants (35), and mammals (20, 36, 37)]. Here we analyzed the temporal trends in seasonal survival and explored the environmental drivers of patterns in survival. We used long-term data (1979 to 2018) collected from a population of yellow-bellied marmots living in the Colorado Rocky Mountains, USA, to investigate three questions: 1) Are phenomenological trends in animal survival consistent across seasons (i.e., winter and summer); 2) are these trends in animal survival consistent across different age-classes (i.e., pup, subadult, and adult); and 3) what are the underlying mechanistic drivers (i.e., environmental conditions) of any such variation in seasonal survival responses? Recognizing seasonal demographic responses to climate change improves our understanding of population dynamics and is crucial for accurately forecasting population change and conserving biodiversity.

Results

Phenomenological Trends in Survival. Across age-classes, temporal trends in seasonal survival were generally increasing in summer and declining in winter (Fig. 1). This was more pronounced for the younger age-classes, namely pups and yearlings. Pup summer survival showed a convex trend in survival with 95% confidence interval just overlapping zero. Winter pup survival showed a significant convex trend, although survival mainly declined from the middle of the study period (which may explain the highly significant negative linear term). Yearling summer survival displayed a significant convex trend (and a significant positive linear term). There was no significant change in yearling winter survival, although survival did appear to decline in more recent years. Trends in adult summer and winter survival were not significant although confidence intervals only just overlapped zero. Summer survival increased, while winter survival declined (*SI Appendix*, Fig. S3). Model selection revealed a single top model accounting for 0.78 of the Akaike's information criterion corrected for small sample size (AICc) weight (for a full model comparison, see *SI Appendix*, Table S1). The top model included a linear temporal trend for all season and state combinations, as well as a quadratic trend for pup and yearling summer and winter survival. Pup and yearling summer survival showed the biggest change, increasing by 9 and 20%, respectively, while pup winter survival showed the biggest decline, of 8%. Despite the divergent seasonal trends, the net change in survival across the study period was only slightly negative for pups (−3%) and positive for yearlings (7%), whereas for adults there was no discernible change. Although there was substantial monthly variation, the mean monthly recapture rate was 0.87 (SD 0.16) for pups, 0.60 (SD 0.20) for yearlings, and 0.49 (SD 0.16) for adults (*SI Appendix*, Fig. S4).

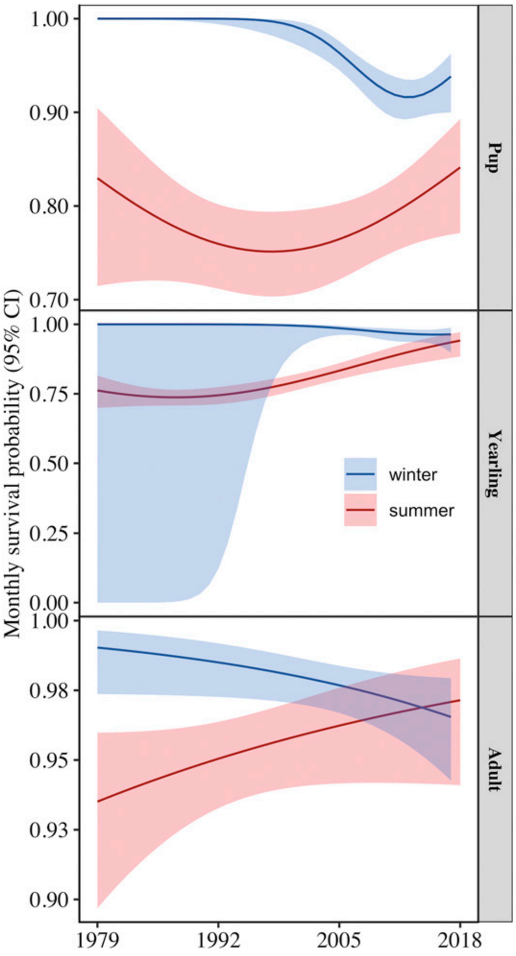

Fig. 1. Estimated trends in summer and winter monthly survival from the phenomenological model.

Change in Environmental Conditions over the Study Period. Environmental conditions within our study area have changed significantly over the past 40 y in accordance with climate change predictions (Fig. 2). The smoothing terms from the generalized additive models (GAMs) were significant for all environmental covariates, except snowmelt date, total snowfall, and drought severity, which all showed significant linear trends (*SI Appendix*, Table S2). Specifically, according to model predictions, mean minimum winter and mean maximum summer temperatures have both increased by 2 °C (although winter temperatures were at one point 4 °C warmer compared with the start of the study period); summers have become drier with a change in the drought severity

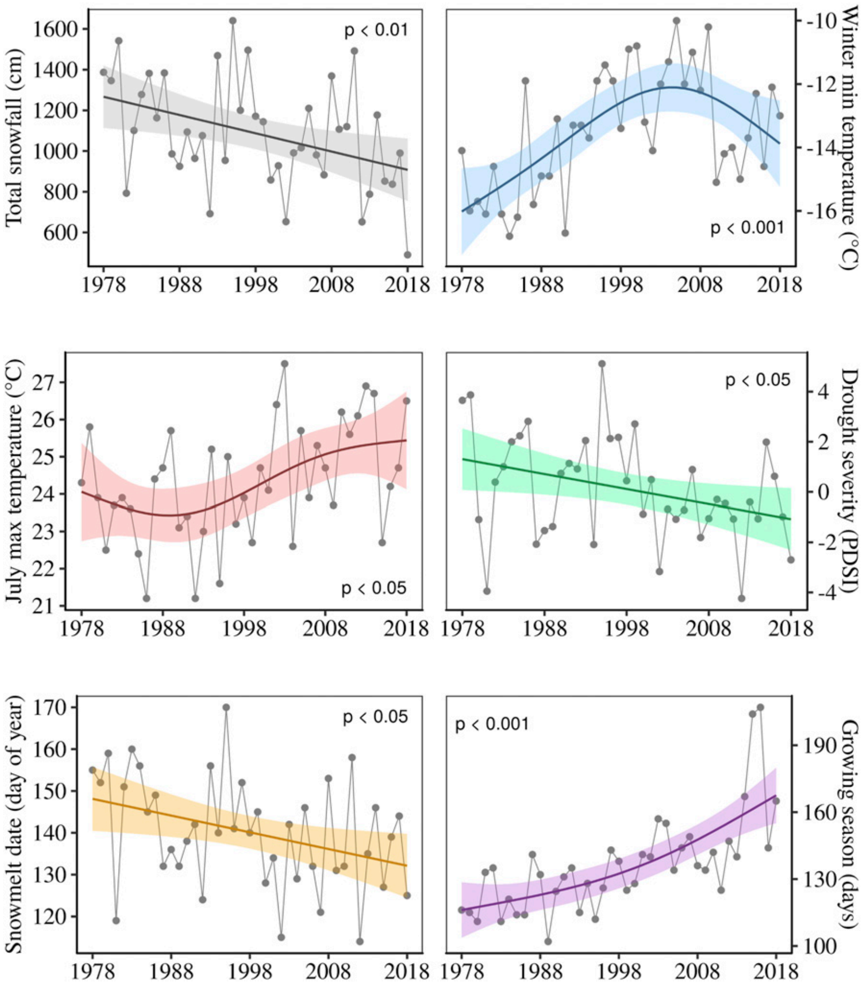

Fig. 2. Temporal variation in environmental variables between 1979 and 2018. Gray dots and lines represent raw data, whereas the colored lines and shaded areas are the predicted relationships and 95% confidence intervals from the GAMs (see also *SI Appendix*, Table S2). For season length, there were no data for 1990 and 1994. The data points for these years are the predicted values.

index from predominantly wet summers (1.3) to mainly dry summers (−1.1), and the growing season has extended by as much as 50 d. Although total winter snowfall shows significant annual variation, there has been a significant decline in predicted snowfall of 3.5 m over the years, and snow is also melting about 16 d earlier in spring.

Mechanistic Drivers of Survival. We compared the top phenomenological model with models including linear and quadratic effects of age on adult survival, and model selection revealed two top models, each accounting for 0.30 of the AICc weight; the top model included a linear effect of age on adult summer survival, and the second top model included a linear effect of age on both adult summer and winter survival. We used the simpler top model with just a linear effect of age on adult summer survival as our baseline model for exploring environmental drivers of trends in survival. Our mechanistic models revealed that different environmental factors appear to drive survival trends in the three age-classes (Fig. 3). More specifically, pup summer survival was largely driven by total winter snowfall, where survival was higher in years of reduced snowfall ($\beta_{\text{snowfall}} = -0.39$; 95% CI = −0.55, −0.22; see also *SI Appendix*, Fig. S5). Although the top model accounted for nearly all of the AICc weight, there was some indication of a relationship between pup summer survival and snowmelt date ($\beta_{\text{snowmelt date}} = -0.28$; 95% CI = −0.45, −0.11). In contrast, pup winter survival was largely driven by drought severity and the length of the growing season, where survival was higher following shorter wetter summers ($\beta_{\text{drought}} = 0.31$; 95% CI = 0.13, 0.50; $\beta_{\text{growing season}} = -0.29$; 95% CI = −0.42, −0.16). Although the model did not account for much of the weight, there was also an indication that pup winter survival was higher during colder winters ($\beta_{\text{winter temp}} = -0.25$; 95% CI = −0.42, −0.08). Yearling summer survival was driven by summer conditions including mean maximum temperatures and the length of the growing season, where survival was higher during warmer longer summers ($\beta_{\text{summer temp}} = 0.23$; 95% CI = 0.11, 0.35; $\beta_{\text{growing season}} = 0.13$; 95% CI = −0.002, 0.25). There was no change in yearling winter survival over the course of the study and no clear relationship with environmental factors, most likely due to the large confidence intervals during the first half of the study. There was a significant negative relationship between adult summer survival and age ($\beta_{\text{age}} = -0.18$; 95% CI = −0.28, −0.09). None of the environmental covariates were significant, although the confidence intervals for winter mean minimum and summer mean maximum temperatures only just overlapped 0, indicating weak positive relationships with higher survival following a warmer winter ($\beta_{\text{winter temp}} = 0.16$; 95% CI = −0.07, 0.39) and during a warmer summer ($\beta_{\text{summer temp}} = 0.19$; 95% CI = −0.08, 0.45). Adult winter survival was largely driven by drought severity and perhaps also the date of snowmelt (although the confidence interval slightly overlapped 0), where survival was higher following a wetter summer ($\beta_{\text{drought}} = 0.38$; 95% CI = 0.09, 0.67) and spring periods where snow melted later ($\beta_{\text{snowmelt date}} = 0.26$; 95% CI = −0.04, 0.55).

For winter survival the effect of continued climate change was likely to be mainly negative, whereas for summer survival the likely outcome of climate change was generally positive. There were six sets of mechanistic models, one for each combination of age-class and season, separately exploring the relationship between environmental covariates, phenotype, age (adults only), and survival (for model selection results, see *SI Appendix*, Table S3). Across age-classes and seasons there was a significant positive relationship between survival and body mass. Body mass had a stronger influence on pup survival in winter compared with summer. The influence of body mass on yearling summer survival was equal to that of pups, but the effect of body mass on adult survival was strong in both seasons, although there was a lot of variation (*SI Appendix*, Fig. S6).

Discussion

Here we explored seasonal differences in survival trends of a mammal occupying a highly seasonal environment and the likely environmental drivers of variation in survival. Our findings illustrate important contrasting trends in survival between seasons. For winter survival, the trend was generally negative for all three age-classes, whereas summer survival was generally positive. Younger age-classes have shown the biggest net change in survival, whereas adults appear more robust in their response to environmental change. Our mechanistic models revealed that different environmental covariates are driving survival trends across the three age-classes, and that age-classes can respond differently to the same environmental covariate (e.g., length of the growing season) between seasons. Our results indicate that the outcome of climate change can differ between seasons and age-classes, and we suspect that this pattern is likely to be common in such highly seasonal environments. Overall, should the patterns we observed in the selected environmental variables continue, climate change will likely have a positive effect on marmot summer survival but a contrasting negative effect on winter survival. In other words, our findings reveal that marmots are most vulnerable during their long season of hibernation compared with the shorter growing season. During hibernation, marmots depend on energy stores acquired over the summer and particular conditions to remain in deep torpor maintaining a low

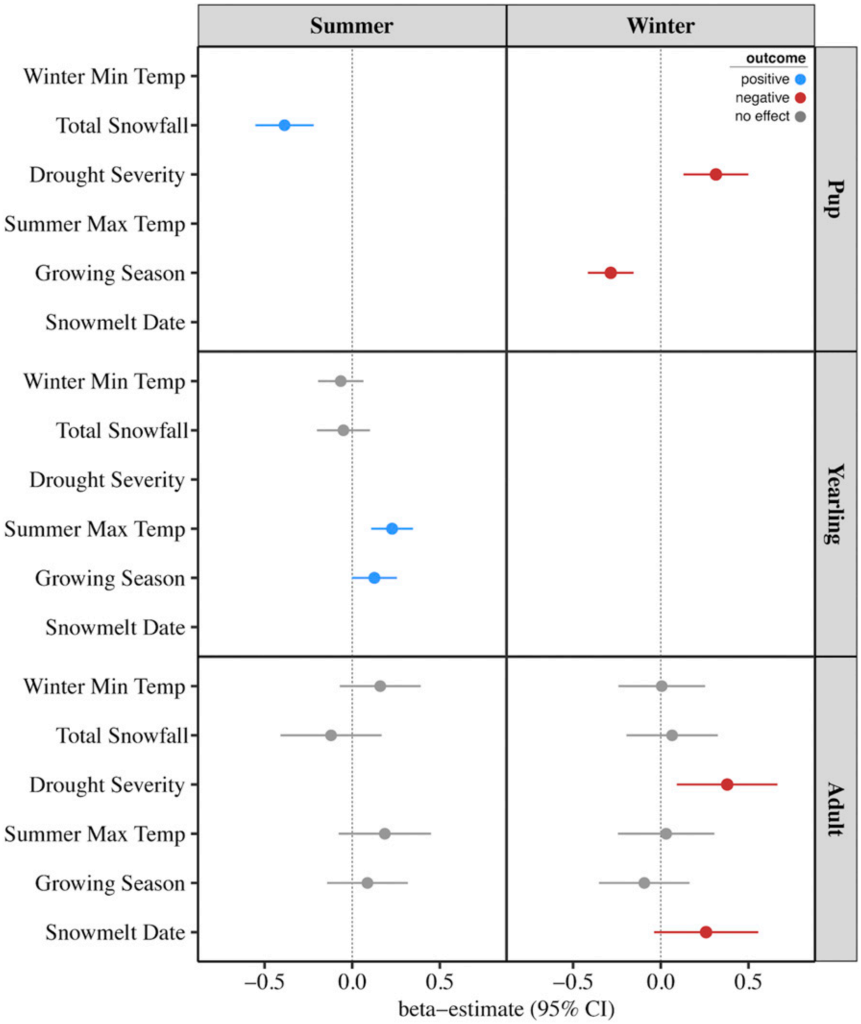

Fig. 3. β-Estimates of top model parameters by season and age-class. "Significant" relationships between survival and the environmental covariates are colored either blue or red (CIs do not overlap 0). Blue indicates that the likely climate change outcome for marmot survival will be positive, whereas red suggests a negative outcome. For example, there is a positive relationship between pup winter survival and drought severity during the previous summer (survival is greater following a wetter summer), and therefore should climate change as predicted result in drier summer conditions, this will have a negative impact on pup winter survival.

metabolic rate (29, 38). Interestingly, trends in winter survival were driven by conditions during the preceding summer, likely impacting individual fitness prior to hibernation, whereas for summer survival environmental conditions during both seasons influenced the probability of survival.

More specifically, regarding the likely outcome of continued climate change, pup summer survival would benefit from reduced winter snowfall (and early snowmelt), probably as a result of reproductive females being in better condition. Extended growing seasons and increased drought severity impacting food and water availability would be detrimental to pup winter survival. A long-term study of alpine marmots found a significant decline in annual pup survival in response to colder and dryer winters reducing the insulating effect of snow and thereby increasing energetic costs of hibernation (39). This is different from our study system, where although snowfall has declined, winters have generally become warmer. The negative relationship between survival and the length of the growing season observed here is notable given that Ozgul et al. (31) proposed that the increase in marmot body mass and hence survival observed in their study was likely the result of the extended growing season and time for marmots to gain weight before hibernation. However, CaraDonna et al. (7) showed that while the growing season has significantly extended, total floral abundance across the season has remained the same, suggesting that, functionally, there may not be more forage available for herbivores. Ultimately, shorter growing seasons where food is compressed may be more beneficial. Aldridge et al. (40) highlighted that shifts in species-level flowering phenology have resulted in a much more distinct bimodal distribution of flower abundance with a midseason period of low abundance. This midseason low may well coincide with the time when pups emerge from the burrows to forage on plants, explaining why they show the strongest response to changes in the length of the growing season. Lastly, longer growing seasons may also leave young marmots more vulnerable to late-season predation.

Unexpectedly, yearling summer survival benefitted from warmer summers. However, we suspect this will change as summers are predicted to continue to warm and become drier, as this would ultimately impact the water content and persistence of food plants (41–43). Furthermore, no marmot population is found in persistently warm or dry natural environments (4). Whether this result is an artifact of changes in permanent emigration during hot summers is unknown, although similar findings were presented in a long-term study of alpine marmots (39). Nonetheless, yearlings with their smaller body size may not be as vulnerable to heat stress compared with adults (4). In contrast to pups, yearling summer survival seemed to benefit from a longer growing season.

There was no significant change in adult summer survival and no significant relationships with any of the environmental variables. Similar to pups, adult winter survival was negatively impacted by increased drought severity during the preceding summer. Earlier work by Inouye et al. (12) showed that marmots are emerging earlier from hibernation in response to warming springs (38 d earlier between 1976 and 1999). The date of snowmelt has advanced over the time period (~16 d) although not as significantly as emergence dates, leading to a potential mismatch between marmot emergence and appearance of forage plants. If marmots are timing their emergence according to temperature cues but having to then wait for snow to melt before forage plants can emerge, this mismatch may have a negative impact on their fitness and hence survival. Unexpectedly, our results indicate that adult winter survival was higher when snow melted later. It is possible that early snowmelt allows predators, such as coyotes, access to colonies, as shown in studies of Olympic marmots where mortality increased significantly when snowpack was low (4). Conversely, it may also be that predation risk is higher when snow melts later as escape burrows remain covered for longer. Group size has been shown to be important for survival in other species either through reducing predation risk (44) or thermoregulatory benefits of social hibernation (45). However, previous work on yellow-bellied marmots revealed a nonlinear relationship between matriline size and survivorship (46), and that the strength of the social relationship was more important than group size, but this depended on the age and sex of the individual (47). Furthermore, colony size within our study population is quite dynamic as a result of births, deaths, and dispersal and therefore difficult to integrate accurately. Because of this, we decided not to include density dependence in our already-complex models.

Our results illustrate disparate seasonal demographic responses to climate change, suggesting that seasonal survival responses need disentangling to fully understand the impact of climate change on the dynamics of animal populations. Critically, our findings highlight the care that should be taken in drawing conclusions from annual survival responses to climate change, as this may be a misinterpretation, simplification, or even underestimation of the actual more complex responses that can differ dramatically at different times of the year. For yellow-bellied marmots, longer summers and shorter winters were expected to be beneficial; however, these relationships are clearly more complex, with contrasting seasonal responses. Given the fact that marmot survival was generally declining during winter in response to summer conditions, this study suggests that continued climate change could tip the energy balance for this species. Small mammals have generally been considered less vulnerable to extinctions compared with medium-sized and larger mammals (48–50). One explanation is that many small mammals reduce their energy expenditure when conditions are poor (e.g., low temperatures or food shortages) either using daily torpor or multiday hibernation, which are the most effective ways to conserve energy (51). Torpor is utilized by mammals from more than half of the mammalian orders spread across all climate zones, including the tropics (52–54). Of the mammals that have gone extinct in recent times, only a small percentage were heterothermic species that used torpor to some extent (51). It now seems that climate-induced environmental changes, particularly during this crucial period of hibernation, may make hibernators, which are also often restricted to mountain tops limiting distribution shifts, more vulnerable. As well as the direct impacts, warming may also permit earlier or increased access by homeotherms elevating levels of competition and predation (5). Social, burrowing, herbivorous mammals, like marmots, play an important role in ecosystem function and the loss or decline of these species could have wider-reaching implications for biodiversity (55). Climate change is pervasive and species all over the world face changes in seasonal conditions, emphasizing the importance of disentangling seasonal demographic responses.

Materials and Methods

Study System. Yellow-bellied marmots (*M. flaviventer*) are large (3.4 to 6.4 kg), hibernating subalpine rodents found in western North America (30, 56, 57). These animals go through seasonal cycles of body mass, which for adults can vary by as much as a couple of kilograms [up to ~40% change (30)]. Due to their distinct circannual lifestyle, highly seasonal montane habitat, and sensitivity to environmental conditions, yellow-bellied marmots are an ideal species to explore seasonal responses to climate change. We used data from the population located in the Upper East River Valley, Colorado, in and around the Rocky Mountain Biological Laboratory (RMBL), which has been studied since 1962. The population comprises four main colonies and 12 satellite colonies distributed between 2,700 and 3,100 m above sea level.

Live Trapping. We used live trapping data from 1979 to 2018 (an interval during which we had high-quality environmental data and extensive trapping effort) to construct capture histories for each individual (58). A significant effort was employed to trap all individuals of the population at least once each year between May and September. Between 48 and 332 individual marmots have been trapped annually since 1962. Individuals were marked with both fur dye and permanent ear tags with unique ID numbers (59). Individuals were also weighed during each capture. All research was conducted with ethics approval from the University of Kansas or the University of California Los Angeles and with permits issued by Colorado Parks and Wildlife.

Environmental Data. We include six environmental variables, namely 1) winter snowfall (cm), 2) winter temperature (mean minimum temperature [°C] between November and March), 3) summer temperature (mean maximum July temperature [°C]), 4) snowmelt date (date of bare ground) in spring, and 5) length of the growing season (d), data for which have been collected at the RMBL for the entire study period. We include 6) a measure of drought severity, which was calculated using the Palmer Drought Severity Index (PDSI) using precipitation and temperature data for Crested Butte (and calibrated for the RMBL), which was collected from the National Centers for Environmental Information (NCEI) Climate Data Online; negative PDSI values indicate drier than average conditions while positive values indicate wetter than average conditions. All environmental covariates were 0-centered and thus standardized to compare effect sizes.

These environmental variables have previously been shown to be important for marmot fitness. Adequate winter snowfall is important to keep burrows insulated, allowing marmots to remain in deep torpor while minimizing energy expenditure (60). Years of low snow cover have been shown to increase mortality of marmots (26), most likely as a result of colder temperatures inside the burrow, thereby increasing energy expenditure (60). Marmots use spring temperatures as a cue to emerge from hibernation but, while spring temperatures have warmed and marmots are emerging earlier from hibernation, the average snowmelt date has not advanced as significantly, creating a potential mismatch in phenologies (12). Prolonged snow cover in spring has a negative impact on marmot survival and reproduction (57), and marmots have to wait longer for food plants to appear (61). During the summer, marmots are sensitive to warmer temperatures as a result of having a relatively large body size (4). To avoid thermal stress, they are likely to reduce aboveground activity, which consequently reduces the amount of time spent foraging (4). The growing season has extended as a result of shifts in flowering phenology (7), and Ozgul et al. (31) demonstrated an increase in body size and hence survival of marmots apparently in response to an extended growing season, potentially allowing marmots more time to gain weight before the next winter. The length of the plant growing season was calculated as the number of days between the appearance of first flowers and last flowers (7, 58); community-level flowering onset occurs within a few days of snowmelt and flowering proceeds until the end of the season, terminating with late-summer frost events or significant snowfall. Lastly, marmots obtain water from food plants and droughts can therefore significantly impact their growth and survival (62). This is particularly true for the month of July, which is characterized by a summer monsoon. The level of precipitation during this period will greatly influence plant growth during the latter part of the summer. To explore trends in environmental covariates across the period, we fitted GAMs (*SI Appendix*, Table S2).

Data Analysis. Capture–mark–recapture (CMR) models were constructed in R [v3.6.1 (63)] within the package RMark (64), which fitted the models in MARK v9.0 (65). Model selection was conducted using Akaike's information criterion corrected for small sample size and AICc model weights. Effect sizes of individual parameters were evaluated using β-estimates (slopes) and their 95% CIs.

Multistate Mark–Recapture Models. Capture–mark–recapture data were analyzed using a multistate CMR model, which included the following model parameters: probability of survival (*S*), recapture probability (*p*), and state-transition probability conditional on survival (Ψ). The trapping season (April to August/September), when marmots were active, was split into five monthly primary occasions to limit heterogeneity in the interval between capture occasions, namely the summer occasions, while the rest of the year (September to March) made up the monthly winter occasions, although there were no observations during this time (Fig. 4). Only "known-age females" were used in our analyses (n = 1,506) because males often disperse before the end of their second year, making it difficult to discriminate between survival and dispersal. Individuals were assigned to one of three states based on their age: pup (<1 y old), yearling (1 y old), and adult (≥2 y old). The uneven time intervals between occasions were accounted for within the model whereby the time intervals between the monthly summer occasions were set to 1, while the interval between August and April the following year was set to 8. Furthermore, we wanted the flexibility to separately explore temporal trends in and mechanistic drivers of survival between seasons and age-classes. Therefore, instead of using season and state as design covariates, we decoupled these into six binary indicator variables of "pup summer," "pup winter," "yearling summer," "yearling winter," "adult summer," and "adult winter." Because of the monthly variation in recapture across the trapping season, we created a continuous covariate of capture effort: the ratio of numbers of nonpups captured in a given month relative to the total number of nonpups captured that year. This capture effort effect was added to each state and season binary indicator variable. Because of the very low numbers of individuals trapped in April, we fixed the recapture probability for this month to 0, and for pups we also fixed the

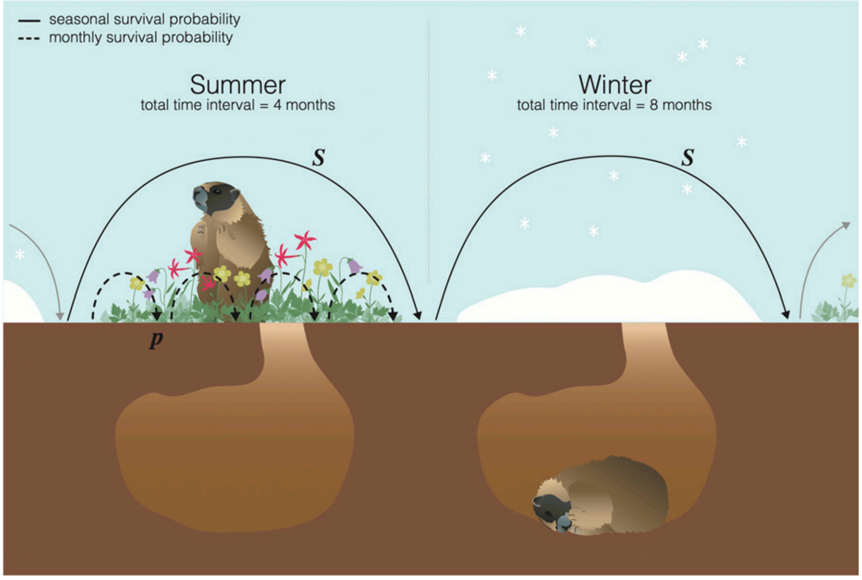

Fig. 4. Model schematic of the seasonal multistate mark–recapture modeling framework showing monthly survival (*S*) and recapture probabilities (*p*) between occasions during the active summer season (dashed arrows), as well as seasonal survival probability across the summer and winter seasons (solid arrows). Transition probabilities between states were not included in the schematic as all transitions were fixed at either 0 or 1. The yellow-bellied marmot image credit: Integration and Application Network, University of Maryland Center for Environmental Science (https://ian.umces.edu/symbols/). All other artwork in the schematic was created by P.J.C.

May recapture probability to 0, as no pups had been trapped during that month. All state-transition probabilities were fixed to either 0 or 1. Infeasible state transitions from pup to adult and from all older to younger age-classes were fixed at 0. State transitions between summer months were fixed to 1, as individuals had to remain in the same age-class. Transitions between years from pup in August to yearling in April, yearling in August to adult in April, and adult in August to adult in April were fixed to 1. Therefore, all models included a constant Ψ. Models were constructed to explore the phenomenological time trends in state-specific survival, the influence of age on adult survival, and the mechanistic influence of the environmental covariates on state-specific survival within each season. We ran goodness-of-fit testing in the program U-CARE for multistate models (JollyMove) including tests for transience, trap dependence, and the complementary tests 3G.SM and M.LTEC (66). The overall $\hat{c}$ (a measure of overdispersion) was calculated by dividing the sum of χ^2 values from all test components with the sum of the degrees of freedom, which indicated there was no evidence of overdispersion ($\hat{c} = 1.02$). Furthermore, we refitted a random selection of models twice using initial values from the original model and compared β-estimates from the refitted models to three decimal places. These refitted models revealed that our models were reaching the global maxima rather than a local maxima, which has been identified as an issue with multistate models.

Phenomenological Trends in Survival. The phenomenological models describe the temporal trends in survival without attempting to explain the underlying biological processes. In order to estimate and compare seasonal trends in monthly survival, we created a year variable, which contained the same value for all five summer occasions and the single winter occasion within a year. We used this new year variable to evaluate time trends (*T*s). This also meant that we only estimated a single (monthly) survival estimate per season per year. We constructed a set of phenomenological models containing either a linear time trend (T) or a quadratic effect (T^2) on the six binary indicator variables described above (for full model syntax, see *SI Appendix*, Table S1). Because of the long time period that the study covered, year was rescaled [$\text{year}_{\text{rescaled}} = (\text{year} - \text{year}_{\text{avg}})/\text{year}_{\text{sd}}$], which allowed β-estimates for the linear and quadratic terms to be similar in magnitude.

Body Mass Imputations. We incorporated body mass (measured in grams) as a time-varying individual covariate in this analysis. To do so, a measure of body mass is required for each primary occasion after the individual is first trapped as a pup until the end of the time series (even though the animal may no longer be present or alive). These time-varying individual covariates are therefore typically restricted to variables such as age that do not require continual capture. However, we were able to impute body mass for each individual twice during each year following their first capture using a similar approach to Ozgul et al. (31) (for more details on the modeling procedure, see *SI Appendix*). Body mass measurements were log-transformed [following Ozgul et al. (31)]. For summer survival, we used body mass imputations from the 15 July for pups as pups only emerge in early summer, and from the 1 June for yearlings and adults. For winter survival, we used body mass imputations for the 31 August for all age-classes.

Mechanistic Drivers of Trends in Survival. Our mechanistic models describe the environmental or phenotypic (i.e., body mass) processes driving the phenomenological patterns in marmot survival. Before exploring environmental drivers of trends in survival, we first tested the effect of age on adult survival (as pup and yearling stages only involved 1 y). We used the top phenomenological model and included a linear effect of age on both summer and winter adult survival, linear effect of age on just summer or winter survival, and finally a quadratic effect of age on both summer and winter adult survival. The top model would become the baseline model from which we constructed our mechanistic models. However, to reduce the number of possible mechanistic models (i.e., given six environmental covariates and six season–state combinations), we explored the influence of environmental covariates on each state–season pair in turn, resulting in six model sets: one for each of the binary indicator variables (i.e., summer pup, winter pup, summer yearling, winter yearling, summer adult, and winter adult survival). For example, when exploring the mechanistic drivers of pup summer survival, the binary indicator variable "pup summer" and the interaction between pup summer and body mass (time-varying individual covariate) formed the basis of the model. Environmental variables (time-varying individual covariates) were included as interactions with pup summer. All other binary indicator variables (state–season combinations) were the same as in the baseline model. For summer pup survival, we only explored the effects of total snowfall (which could indirectly influence fitness of reproductive females as well as green up through snowmelt around the time pups emerge), snowmelt date (i.e., date of bare ground), summer temperature, and drought on their survival. For yearling and adult summer survival, we used the effect of the length of the growing season from the previous summer (i.e., lag growing season), as the growing season likely would not have ended prior to the last sighting of the individual. We constructed models with one, two, or three environmental covariates, which were not collinear.

Data Deposition. The capture histories including age and body mass as time-varying individual covariates and a separate data file including growing season length have been deposited in the Dryad Digital Repository at https://doi.org/10.5061/dryad.ht76hdrcd. The complete flowering phenology dataset used to calculate growing season length is archived at https://osf.io/jt4n5/. RMBL environmental data (including total snowfall, mean minimum monthly temperatures, and snowmelt date) can be downloaded from http://www.gothicwx.org/. The monthly average temperature and total precipitation data for Crested Butte that were used to calculate a calibrated drought severity index for the RMBL were downloaded from the NCEI Climate Data Online (https://www.ncei.noaa.gov/). Code used to run analyses is available upon request.

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1. J. G. Ernakovich *et al*., Predicted responses of arctic and alpine ecosystems to altered seasonality under climate change. *Glob. Change Biol.* **20**, 3256–3269 (2014).
2. M. S. Boyce, Seasonality and patterns of natural selection for life histories. *Am. Nat.* **114**, 569–583 (1979).
3. Ø. Varpe, Life history adaptations to seasonality. *Integr. Comp. Biol.* **57**, 943–960 (2017).
4. K. B. Armitage, Climate change and the conservation of marmots. *Nat. Sci.* **5**, 36–43 (2013).
5. F. Geiser, Hibernation. *Curr. Biol.* **23**, R188–R193 (2013).
6. H. Steltzer, E. Post, Ecology. Seasons and life cycles. *Science* **324**, 886–887 (2009).
7. P. J. CaraDonna, A. M. Iler, D. W. Inouye, Shifts in flowering phenology reshape a subalpine plant community. *Proc. Natl. Acad. Sci. U.S.A.* **11**, 4916–4921 (2014).
8. Intergovernmental Panel on Climate Change (IPCC), *Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*, R. K. Pachauri, L. A. Meyer; Core Writing Team, Eds. (IPCC, Geneva, Switzerland, 2014).
9. IPCC, "Summary for policymakers" in *Global Warming of 1.5°C. An IPCC Special Report on the Impacts of Global Warming of 1.5°C above Pre-Industrial Levels and Related Global Greenhouse Gas Emission Pathways, in the Context of Strengthening the Global Response to the Threat of Climate Change, Sustainable Development, and Efforts to Eradicate Poverty*, (World Meteorological Organization, Geneva, Switzerland, 2018).
10. P. W. Mote, A. F. Hamlet, M. P. Clark, D. P. Lettenmaier, Declining mountain snowpack in western North America. *Bull. Am. Meteorol. Soc.* **86**, 39–50 (2005).
11. J. Overpeck, B. Udall, Climate change. Dry times ahead. *Science* **328**, 1642–1643 (2010).
12. D. W. Inouye, B. Barr, K. B. Armitage, B. D. Inouye, Climate change is affecting altitudinal migrants and hibernating species. *Proc. Natl. Acad. Sci. U.S.A.* **97**, 1630–1633 (2000).

13. M. M. Humphries, D. W. Thomas, J. R. Speakman, Climate-mediated energetic constraints on the distribution of hibernating mammals. *Nature* **418**, 313–316 (2002).
14. G. R. Walther *et al*., Ecological responses to recent climate change. *Nature* **416**, 389–395 (2002).
15. J.-M. Gaillard, N. G. Yoccoz, Temporal variation in survival of mammals: A case of environmental canalization? *Ecology* **84**, 3294–3306 (2003).
16. B.-E. Sæther, Ø. Bakke, Avian life history variation and contribution of demographic traits to the population growth rate. *Ecology* **81**, 642–653 (2000).
17. A. Ozgul, A. W. Bateman, S. English, T. Coulson, T. H. Clutton-Brock, Linking body mass and group dynamics in an obligate cooperative breeder. *J. Anim. Ecol.* **83**, 1357–1366 (2014).
18. S. N. Atkinson, M. A. Ramsay, The effects of prolonged fasting of the body composition and reproductive success of female polar bears (*Ursus maritimus*). *Funct. Ecol.* **9**, 559–567 (1995).
19. C. L. Buck, B. M. Barnes, Annual cycle of body composition and hibernation in free-living arctic ground squirrels. *J. Mammal.* **80**, 430–442 (1999).
20. M. Douhard, S. Guillemette, M. Festa-Bianchet, F. Pelletier, Drivers and demographic consequences of seasonal mass changes in an alpine ungulate. *Ecology* **99**, 724–734 (2018).
21. J. Dark, Annual lipid cycles in hibernators: Integration of physiology and behavior. *Annu. Rev. Nutr.* **25**, 469–497 (2005).
22. J. F. Aublet, M. Festa-Bianchet, D. Bergero, B. Bassano, Temperature constraints on foraging behaviour of male alpine ibex (*Capra ibex*) in summer. *Oecologia* **159**, 237–247 (2009).
23. K. Krajick, Climate change. All downhill from here? *Science* **303**, 1600–1602 (2004).
24. J. C. Melcher, K. B. Armitage, W. P. Porter, Thermal influences on the activity and energetics of yellow-bellied marmots (*Marmota flaviventris*). *Physiol. Zool.* **63**, 803–820 (1990).
25. C. Bellard, C. Bertelsmeier, P. Leadley, W. Thuiller, F. Courchamp, Impacts of climate change on the future of biodiversity. *Ecol. Lett.* **15**, 365–377 (2012).
26. D. P. Barash, The social biology of the Olympic marmot. *Anim. Behav. Monogr.* **6**, 171–245 (1973).
27. T. T. Høye, E. Post, H. Meltofte, N. M. Schmidt, M. C. Forchhammer, Rapid advancement of spring in the high Arctic. *Curr. Biol.* **17**, R449–R451 (2007).
28. A. M. Iler, T. T. Høye, D. W. Inouye, N. M. Schmidt, Nonlinear flowering responses to climate: Are species approaching their limits of phenological change? *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **368**, 20120489 (2013).
29. K. B. Armitage, D. T. Blumstein, B. C. Woods, Energetics of hibernating yellow-bellied marmots (*Marmota flaviventris*). *Comp. Biochem. Physiol. A Mol. Integr. Physiol.* **134**, 101–114 (2003).
30. K. B. Armitage, D. T. Blumstein, "Body-mass diversity in marmots" in *Holarctic Marmots as a Factor of Biodiversity*, K. B. Armitage, V. Yu. Rumiantsev, Eds. (ABF Publishing House, Moscow, Russia, 2002), pp. 22–32.
31. A. Ozgul *et al*., Coupled dynamics of body mass and population growth in response to environmental change. *Nature* **466**, 482–485 (2010).
32. J. M. Cushing, S. M. Henson, Periodic matrix models for seasonal dynamics of structured populations with application to a seabird population. *J. Math. Biol.* **77**, 1689–1720 (2018).
33. J. A. Hostetler, T. S. Sillett, P. P. Marra, Full-annual-cycle population models for migratory birds. *Auk* **132**, 433–449 (2015).
34. R. D. Bassar, B. H. Letcher, K. H. Nislow, A. R. Whiteley, Changes in seasonal climate outpace compensatory density-dependence in eastern brook trout. *Glob. Change Biol.* **22**, 577–593 (2016).
35. R. Salguero-Gómez, W. Siewert, B. B. Casper, K. Tielbörger, A demographic approach to study effects of climate change in desert plants. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **367**, 3100–3114 (2012).
36. M. Paniw, N. Maag, G. Cozzi, T. Clutton-Brock, A. Ozgul, Life history responses of meerkats to seasonal changes in extreme environments. *Science* **363**, 631–635 (2019).
37. N. G. Yoccoz, R. A. Ims, Demography of small mammal in cold regions: The importance of environmental variability. *Ecol. Bull.* **47**, 137–144 (1999).
38. S. L. Lindstedt, M. S. Boyce, Seasonality, fasting endurance, and body size in mammals. *Am. Nat.* **125**, 873–878 (1985).
39. C. Rézouki *et al*., Socially mediated effects of climate change decrease survival of hibernating alpine marmots. *J. Anim. Ecol.* **85**, 761–773 (2016).
40. G. Aldridge, D. W. Inouye, J. R. Forrest, W. A. Barr, A. J. Miller-Rushing, Emergence of a mid-season period of low floral resources in a montane meadow ecosystem associated with climate change. *J. Ecol.* **99**, 905–913 (2011).
41. M. Farooq, A. Wahid, N. Kobayashi, D. Fujita, S. M. A. Basra, "Plant drought stress: Effects, mechanisms and management" in *Sustainable Agriculture*, E. Lichtfouse, M. Navarrete, P. Debaeke, S. Véronique, C. Alberola, Eds. (Springer, Dordrecht, The Netherlands, 2009), pp. 153–188.
42. D. R. Campbell, Early snowmelt projected to cause population decline in a subalpine plant. *Proc. Natl. Acad. Sci. U.S.A.* **116**, 12901–12906 (2019).
43. A. M. Iler *et al*., Reproductive losses due to climate change-induced earlier flowering are not the primary threat to plant population viability in a perennial herb. *J. Ecol.* **107**, 1931–1943 (2019).
44. E. Sorato, P. R. Gullett, S. C. Griffith, A. F. Russell, Effects of predation risk on foraging behaviour and group size: Adaptations in a social cooperative species. *Anim. Behav.* **84**, 823–834 (2012).
45. W. Arnold, Social thermoregulation during hibernation in alpine marmots (*Marmota marmota*). *J. Comp. Physiol. B* **158**, 151–156 (1988).
46. K. B. Armitage, O. A. Schwartz, Social enhancement of fitness in yellow-bellied marmots. *Proc. Natl. Acad. Sci. U.S.A.* **97**, 12149–12152 (2000).
47. A. P. Montero, D. M. Williams, J. G. Martin, D. T. Blumstein, More social female yellow-bellied marmots, *Marmota flaviventer*, have enhanced summer survival. *Anim. Behav.* **160**, 113–119 (2020).
48. M. Cardillo, Biological determinants of extinction risk: Why are smaller species less vulnerable? *Anim. Conserv.* **6**, 63–69 (2003).
49. M. Cardillo *et al*., Multiple causes of high extinction risk in large mammal species. *Science* **309**, 1239–1241 (2005).
50. R. Dirzo *et al*., Defaunation in the Anthropocene. *Science* **345**, 401–406 (2014).
51. F. Geiser, C. Turbill, Hibernation and daily torpor minimize mammalian extinctions. *Naturwissenschaften* **96**, 1235–1240 (2009).
52. F. Geiser, Metabolic rate and body temperature reduction during hibernation and daily torpor. *Annu. Rev. Physiol.* **66**, 239–274 (2004).
53. J. Schmid, J. U. Ganzhorn, Optional strategies for reduced metabolism in gray mouse lemurs. *Naturwissenschaften* **96**, 737–741 (2009).
54. C. Stawski, C. Turbill, F. Geiser, Hibernation by a free-ranging subtropical bat (*Nyctophilus bifax*). *J. Comp. Physiol. B* **179**, 433–441 (2009).
55. A. D. Davidson, J. K. Detling, J. H. Brown, Ecological roles and conservation challenges of social, burrowing, herbivorous mammals in the world's grasslands. *Front. Ecol. Environ.* **10**, 477–486 (2012).
56. B. A. Frase, R. S. Hoffmann, *Marmota flaviventris*. *Mamm. Species* **135**, 1–8 (1980).
57. K. B. Armitage, "Recovery of a yellow-bellied marmot population following a weather-induced decline" in *Adaptive Strategies and Diversity in Marmots*, R. Ramousse, D. Allainé, M. Le Berre, Eds. (International Marmot Network, Lyon, France, 2003), pp. 217–224.
58. L. S. Cordes *et al*, Marmot capture history data and growing season length data. Dryad. https://doi.org/10.5061/dryad.ht76hdrcd. Deposited 16 June 2020.
59. K. B. Armitage, "Yellow-bellied marmot" in *CRC Handbook of Census Methods for Terrestrial Vertebrates*, D. E. Davis, Ed. (CRC Press, Boca Raton, FL, 1982), pp. 148–149.
60. W. Arnold *et al*., Ambient temperatures in hibernacula and their energetic consequences for alpine marmots *Marmota marmota*. *J. Therm. Biol.* **16**, 223–226 (1991).
61. D. Van Vuren, K. B. Armitage, Duration of snow cover and its influence on life-history variation in yellow-bellied marmots. *Can. J. Zool.* **69**, 1755–1758 (1991).
62. K. B. Armitage, "Unusual mortality in a yellow-bellied marmot population" in *Actual Problems of Marmots Investigation*, V. Yu. Rumiantsev, Ed. (ABF Publishing House, Moscow, Russia, 1994), pp. 5–13.
63. R Core Team, R: A Language and Environment for Statistical Computing (Version v3.6.1, R Foundation for Statistical Computing, Vienna, Austria, 2019). https://www.R-project.org/. Accessed 23 June 2020.
64. J. L. Laake, RMark: An R Interface for Analysis of Capture-Recapture Data with MARK (AFSC Processed Rep. 2013-01, Alaska Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, Seattle WA, 2013).
65. G. C. White, K. P. Burnham, Program MARK: Survival estimation from populations of marked animals. *Bird Study* **46**, 120–139 (1999).
66. R. Choquet, J. D. Lebreton, O. Gimenez, A. M. Reboulet, R. Pradel, U-CARE: Utilities for performing goodness of fit tests and manipulating CApture–REcapture data. *Ecography* **32**, 1071–1074 (2009).