

7-6-2020

Contrasting Effects of Climate Change on Seasonal Survival of a Hibernating Mammal

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26

27 Competing interest statement: The authors declare no competing interests.

28

29 **Keywords**

30 *Marmota flaviventer*, demography, environmental conditions, mark-recapture, individual-
31 based.

32

33 **Author Contributions**

34 Line S Cordes: Lead author. Made substantial contributions to conception, design,
35 acquisition of data, analysis, figures and interpretation of data; drafted and revised the
36 manuscript.

37 Kenneth B Armitage: Provided fundamental insight and knowledge on the study species and
38 system. Involved in revising the manuscript for important intellectual content.

39 Daniel T Blumstein: Provided fundamental insight and knowledge on the study species and
40 system. Substantial contribution to the conception and design; involved in revising the
41 manuscript for important intellectual content.

42 Paul CaraDonna: Provided fundamental insight and knowledge on the study system.
43 Substantial contribution to the development and design of key figures; involved in revising
44 the manuscript for important intellectual content.

45 Dylan Z Childs: Substantial contribution to the analysis and interpretation of data; involved in
46 revising the manuscript for important intellectual content.

47 Brian D Gerber: Substantial contribution to the analysis and interpretation of data; involved in
48 revising the manuscript for important intellectual content.

49 Julien GA Martin: Contribution to collation of data. Involved in revising the manuscript for
50 important intellectual content.

51 Madan Oli: Involved in revising the manuscript for important intellectual content.

52 Arpat Ozgul: Substantial contribution to the conception, design, analysis and interpretation of
53 data; involved in revising the manuscript for important intellectual content.

54

55

56

57 **Abstract**

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

73

74 **Significance statement**

75 Climate change is altering the seasonal environmental conditions to which animals have
76 adapted, but the outcome may differ between seasons for a particular species. Demographic
77 responses therefore need disentangling on a seasonal basis to make accurate forecasts.
78 Our study shows that climate change is causing seasonally divergent demographic
79 responses in a hibernating mammal. Continued climate change will likely have a positive
80 effect on summer survival, but a negative effect on winter survival. This potentially has wide

81 ranging consequences across other species occupying temperate to more extreme arctic
82 and alpine habitats, which is also where the most rapid changes in climate are observed.

83

84 **Introduction**

85 Seasonality is a fundamental driver of ecosystem structure and function (1), and plays a
86 dynamic role in shaping the behaviour and life history of many species (e.g., 2, 3). Animals
87 occupying temperate, arctic and alpine environments experience distinct cyclic variation in
88 biotic and abiotic factors, and have evolved seasonal life-history strategies for coping with
89 the changing conditions. This includes short but mild summers characterised by peaks in
90 resource availability where animals give birth to young and forage to gain fitness, and long
91 often harsh winters with food shortages where animals largely depend on fat reserves for
92 energy and in extreme cases go into hibernation (4, 5). However, climate change is altering
93 the seasonal conditions to which plants and animals are accustomed (e.g., 1, 6).

94 Temperatures are increasing, winter snowfall is declining, snow is melting earlier, growing
95 seasons are extending, and the frequency of extreme events (e.g., droughts) are on the rise
96 (7-11, 6). This has resulted in advancing phenologies (including earlier flowering of plants
97 and earlier emergence of hibernating animals; 12), range shifts (13), and changes to species
98 interactions and communities (14). Less well known, but of critical importance, are the direct
99 demographic consequences of a changing climate (e.g., changes in age-specific survival or
100 fecundity).

101 Animals most likely to be affected by climate change include high latitude and high
102 elevation species which experience distinct seasonal phases but which are restricted by
103 natural boundaries limiting shifts in distribution (horizontal or vertical). While changes in adult
104 survival will likely have the biggest impact on the population dynamics of long-lived
105 mammals, this life history stage also appears more robust to environmental perturbations,
106 whereas survival of younger age classes may be more sensitive and immediate indicators of
107 the effects of climate change (15, 16). However, long-term individual-based data are
108 required over multiple decades to detect trends in survival in response to climate change.

109 Furthermore, long-term data on individual fitness-related traits (such as body mass) are
110 essential because such traits are closely linked with environmental conditions and act as a
111 proxy for an individual's collective past experience (both environmental and social; 17).
112 Species occupying extreme and highly seasonal environments can undergo significant
113 fluctuations in body mass (e.g., 18- 21).

114 Climate change could conceivably result in seasonally variable demographic
115 responses (see 1). For example, increasing temperatures may reduce foraging time for
116 certain species in summer to avoid overheating (e.g., 22-24), but may improve survival
117 during winter in harsh environments. A reduction in precipitation will increase the frequency
118 of summer droughts (11), reducing forage availability for herbivores, whereas a reduction in
119 snowfall during winter could lower locomotion costs and improve forage accessibility (25).
120 Paradoxically, for species that are highly adapted to harsh environments, warmer winter and
121 spring temperatures, and a reduction in snowpack could result in animals freezing to death
122 due to a lack of insulation (26). Warming temperatures have caused species-specific shifts in
123 plant phenology resulting in an extended growing season (7, 27-28). This may allow
124 herbivores more time to gain weight before winter, potentially resulting in demographic or
125 fitness related benefits. Due to its distinct circannual life history, highly seasonal montane
126 habitat, and sensitivity to seasonal environmental conditions, yellow-bellied marmots
127 (*Marmota flaviventer*) are a sentinel species for disentangling the seasonal impacts of
128 climate change on demography. Marmots are too small to store sufficient fat to remain active
129 during winter and therefore hibernate for about 8 months during this long period of food
130 scarcity relying solely on fat reserves for energy (4, 29). Nevertheless, marmots go through
131 distinct seasonal body mass cycles where adults can lose nearly 40% of weight from peak to
132 minimal mass (30). Yellow-bellied marmots are found in western North America where
133 climate change is more evident than anywhere else on the continent (apart from the Arctic;
134 11). In particular, there has been a significant reduction in late-season snowpack, a rise in
135 temperatures, an increase in precipitation intensity, an increase in the severity of droughts,
136 and pervasive plant mortality (10-11). Marmots have shown a temporal increase in body

137 mass and a subsequent increase in adult survival, which was hypothesized to be caused by
138 an extended foraging season (31). However, the mechanistic link between seasonal survival,
139 body size and environmental change has not yet been directly evaluated.

140 A growing literature has identified the importance of seasonally different demographic
141 responses to climatic conditions (birds: 32, 33; fish: 34; plants: 35; mammals: 36-38). Here
142 we analyzed the temporal trends in seasonal survival and explored the environmental drivers
143 of patterns in survival. We use long-term data (1979-2018) collected from a population of
144 yellow-bellied marmots living in the Colorado Rocky Mountains, USA, to investigate three
145 questions: (1) are phenomenological trends in animal survival consistent across seasons
146 (i.e., winter and summer); (2) are these trends in animal survival consistent across different
147 age classes (i.e., pup, sub-adult, adult); and (3) what are the underlying mechanistic drivers
148 (i.e., environmental conditions) of any such variation in survival responses. Understanding
149 seasonal demographic responses to climate change improves our understanding of
150 population dynamics and is crucial for accurately forecasting population change and
151 conserving biodiversity.

152

153 **Results**

154 **Phenomenological trends in survival**

155 Across age-classes temporal trends in seasonal survival were generally increasing in
156 summer and declining in winter (Fig. 1). This was more pronounced for the younger age-
157 classes, namely pups and yearlings. Pup summer survival showed a convex trend in survival
158 with 95% confidence limits just overlapping zero. Winter pup survival showed a significant
159 convex trend, although survival mainly declined from the middle of the study period (which
160 may explain the highly significant negative linear term). Yearling summer survival displayed
161 a significant convex trend (and a significant positive linear term). There was no significant
162 change in yearling winter survival, although survival did appear to decline in more recent
163 years. Trends in adult summer and winter survival were not significant although confidence
164 limits only just overlapped zero. Summer survival increased, while winter survival declined

165 (see SI Appendix, Fig. S3). Model selection revealed a single top model accounting for >
166 0.78 of the AICc weight (for full model comparison see SI Appendix, Table S1). The top
167 model included a linear temporal trend for all season and state combinations, as well as a
168 quadratic trend for pup and yearling summer and winter survival. Pup and yearling summer
169 survival showed the biggest change increasing by 9 and 20%, respectively, while pup winter
170 survival showed the biggest decline of 8%. Despite the divergent seasonal trends, the net
171 change in survival across the study period was only slightly negative for pups (-3%) and
172 positive for yearlings (7%), whereas for adults there was no discernible change. Although
173 there was substantial monthly variation, the mean monthly recapture rate was 0.87 (SD =
174 0.16) for pups, 0.60 (SD = 0.20) for yearlings, and 0.49 (SD = 0.16) for adults (see SI
175 Appendix, Fig. S4).

176

177 **Change in environmental conditions over the study period**

178 Environmental conditions within our study area have changed significantly over the past 40
179 years in accordance with climate change predictions (Fig. 2). The smoothing terms from the
180 GAMs were significant for all environmental covariates, except snowmelt date, total snowfall
181 and drought severity, which all showed significant linear trends (see SI Appendix, Table S2).
182 Specifically, according to model predictions, mean minimum winter and mean maximum
183 summer temperatures have both increased by 2°C (although winter temperatures were at
184 one point 4°C warmer compared to the start of the study period); summers have become
185 drier with a change in the drought severity index from predominantly wet summers (1.3) to
186 mainly dry summers (-1.1), and the growing season has extended by as much as 50 days.
187 Although total winter snowfall shows significant annual variation, there has been a significant
188 decline in predicted snowfall of 3.5 m over the years, and snow is also melting about 16 days
189 earlier in spring.

190

191 **Mechanistic drivers of survival**

192 We compared the top phenomenological model to the models including linear and quadratic
193 effects of age on adult survival, and model selection revealed two top models, each
194 accounting for 0.30 of the AICc weight; the top model included a linear effect of age on adult
195 summer survival, and the second top model included a linear effect of age on both adult
196 summer and winter survival. We used the simpler top model with just a linear effect of age
197 on adult summer survival as our baseline model for exploring environmental drivers of trends
198 in survival. Our mechanistic models revealed that different environmental factors appear to
199 drive survival trends in the three age classes (Fig. 3). More specifically, pup summer survival
200 was largely driven by total winter snowfall, where survival was higher in years of reduced
201 snowfall ($\beta_{\text{snowfall}}=-0.39$; 95% CI=-0.55, -0.22; see also SI Appendix Fig. S5). Although the
202 top model accounted for nearly all the AICc weight, there was some indication of a
203 relationship between pup summer survival and snowmelt date ($\beta_{\text{snowmelt date}}=-0.28$; 95% CI=-
204 0.45, -0.11). In contrast, pup winter survival was largely driven by drought severity and the
205 length of the growing season, where survival was higher following shorter wetter summers
206 ($\beta_{\text{drought}}=0.31$; 95% CI=0.13, 0.50; $\beta_{\text{growing season}}=-0.28$; 95% CI=-0.42, -0.16). Although the
207 model did not account for much of the weight there was also an indication that pup winter
208 survival was higher during colder winters ($\beta_{\text{winter temp}}=-0.25$; 95% CI=-0.42, -0.08). Yearling
209 summer survival was driven by summer conditions including maximum temperatures and the
210 length of the growing season, where survival was higher during warmer longer summers
211 ($\beta_{\text{summer temp}}=0.22$; 95% CI=0.11, 0.35; $\beta_{\text{growing season}}=0.13$; 95% CI=-0.002, 0.25). There was no
212 change in yearling winter survival over the course of the study and no clear relationship with
213 environmental factors most likely due to the large variation. There was a significant negative
214 relationship between adult summer survival and age ($\beta_{\text{age}}=-0.18$; 95% CI=-0.28, -0.09).
215 None of the environmental covariates were significant, although the confidence limits for
216 winter minimum and summer maximum temperatures only just overlapped zero indicating
217 weak positive relationships with higher survival following a warmer winter ($\beta_{\text{winter temp}}=0.16$;
218 95% CI=-0.07, 0.39) and during a warmer summer ($\beta_{\text{summer temp}}=0.19$; 95% CI=-0.08, 0.45).
219 Adult winter survival was largely driven by drought severity and perhaps also the date of

220 snowmelt (although confidence limits slightly overlap zero), where survival was higher
221 following a wetter summer ($\beta_{\text{drought}}=0.38$; 95% CI=0.09, 0.67) and spring periods where snow
222 melted later ($\beta_{\text{snowmelt date}}=0.26$; 95% CI=-0.04, 0.55).

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

233

234 **Discussion**

235 Here we explored seasonal differences in survival trends of a mammal occupying a highly
236 seasonal environment and the likely environmental drivers of variation in survival. Our
237 findings illustrate important contrasting trends in survival between seasons. For winter
238 survival, the trend was generally negative for all three age-classes, whereas summer
239 survival was generally positive. Younger age-classes have shown the biggest net change in
240 survival, whereas adults appear more robust in their response to environmental change. Our
241 mechanistic models revealed that different environmental covariates are driving survival
242 trends across the three age-classes, and that age classes can respond differently to the
243 same environmental covariate (e.g., length of the growing season) between seasons. Our
244 results indicate that the outcome of climate change can differ between seasons and age-
245 classes, and we suspect that this pattern is likely to be common in such highly seasonal
246 environments. Overall, should the patterns we observed in the selected environmental
247 variables continue, climate change will likely have a positive effect on marmot summer

248 survival, but a contrasting negative effect on winter survival. In other words, our findings
249 reveal that marmots are most vulnerable during their long season of hibernation compared to
250 the shorter growing season. During hibernation marmots depend on energy stores acquired
251 over the summer and particular conditions to remain in deep torpor maintaining a low
252 metabolic rate (29, 39). Interestingly, trends in winter survival were driven by conditions
253 during the preceding summer, likely impacting individual fitness prior to hibernation, whereas
254 for summer survival both summer and winter environmental conditions influenced the
255 probability of survival.

256 More specifically, regarding the likely outcome of continued climate change, pup
257 summer survival would benefit from reduced winter snowfall (and early snowmelt), most
258 likely as a result of reproductive females being in better condition. Extended growing
259 seasons and increased drought severity impacting food and water availability would be
260 detrimental to pup winter survival. A long-term study of alpine marmots found a significant
261 decline in annual pup survival in response to colder and dryer winters reducing the insulating
262 effect of snow and thereby increasing energetic costs of hibernation (40). This is different to
263 our study system, where although snowfall has declined, winters have generally become
264 warmer. The negative relationship between survival and the length of the growing season
265 observed here is notable given that Ozgul *et al.* (31) proposed that the increase in marmot
266 body mass and hence survival observed in their study was likely the result of the extended
267 growing season and time for marmots to gain weight before hibernation. However,
268 CaraDonna *et al.* (7) showed that while the growing season has significantly extended, total
269 floral abundance across the season has remained the same, suggesting that functionally,
270 there may not be more forage available for herbivores. Ultimately, shorter growing seasons
271 where food is compressed may be more beneficial for the animals depending on them.
272 Aldridge *et al.* (41) highlighted that shifts in species-level flowering phenology have resulted
273 in a much more distinct bimodal distribution of flower abundance with a mid-season period of
274 low abundance. This mid-season low may well coincide with the time when pups emerge
275 from the burrows to forage on plants explaining why they show the strongest response to

276 changes in the length of the growing season. Lastly, longer growing seasons may also leave
277 young marmots more vulnerable to late season predation.

278 Unexpectedly, yearling summer survival benefits from warmer summers. However,
279 we suspect this will change as summers are predicted to continue to warm and become
280 drier, as this would ultimately impact the water content and persistence of food plants (42-
281 44). Furthermore, no marmot population is found in persistently warm or dry natural
282 environments (4). Whether this result is an artefact of changes in permanent emigration
283 during hot summers is unknown, although similar findings were presented in a long-term
284 study of alpine marmots (40). Nevertheless, yearlings with their smaller body size may not
285 be as vulnerable to heat stress compared to adults (4). In contrast to pups, yearling summer
286 survival seemed to benefit from a longer growing season.

287 There was no significant change in adult summer survival and no significant
288 relationships with any of the environmental variables. Similar to pups, adult winter survival
289 was negatively impacted by increased drought severity during the preceding summer. Earlier
290 work by Inouye *et al.* (12) showed that marmots are emerging earlier from hibernation in
291 response to warming springs (38 days earlier between 1976 and 1999). The date of
292 snowmelt has advanced over the time period (~16 days) although not as significantly as
293 emergence dates, leading to a potential mismatch between marmot emergence and
294 appearance of forage plants. If marmots are timing their emergence according to
295 temperature cues, but having to then wait for snow to melt before forage plants can emerge,
296 this mismatch may have a negative impact on their fitness and hence survival.

297 Unexpectedly, our results indicate that adult winter survival was higher when snow melted
298 later. It is possible that early snowmelt allows predators, such as coyotes, access to colonies
299 as shown in studies of Olympic marmots where mortality increased significantly when
300 snowpack was low (4). Conversely, it may also be that predation risk is higher when snow
301 melts later as escape burrows are covered. Group size has been shown to be important for
302 survival in other species either through reducing predation risk (45) or thermoregulatory
303 benefits of social hibernation (46). However, previous work on yellow-bellied marmots

304 revealed a non-linear relationship between matriline size and survivorship (47), and that the
305 strength of the social relationship was more important than group size, but this depended on
306 the age and sex of the individual (48). Furthermore, colony size within our study population
307 is quite dynamic as a result of births, deaths, and dispersal and therefore difficult to integrate
308 accurately. Because of this, we decided not to include density dependence in our already
309 complex models.

310 Our results illustrate disparate seasonal demographic responses to climate change,
311 suggesting that seasonal survival responses need disentangling to fully understand the
312 impact of climate change on the dynamics of animal populations. Critically our findings
313 highlight the care that should be taken in drawing conclusions from annual survival
314 responses to climate change, as this may be a misinterpretation, simplification or even
315 underestimate of the actual more complex responses that can differ dramatically at different
316 times of the year. For yellow-bellied marmots, longer summers and shorter winters were
317 expected to be beneficial, however, these relationships are clearly more complex with
318 contrasting seasonal responses. Given the fact that marmot survival was generally declining
319 during winter in response to summer conditions, this study suggests that continued climate
320 change could tip the energy balance for this small mammal. Small mammals have generally
321 been considered less vulnerable to extinctions compared to medium-sized and larger
322 mammals (49-51). One explanation is because many small mammals reduce their energy
323 expenditure when conditions are poor (e.g. low temperatures or food shortages) either using
324 daily torpor or multi-day hibernation which is the most effective way to conserve energy (52).
325 Torpor is utilised by mammals from more than half of the mammalian orders spread across
326 all climate zones, including the tropics (53-55). Of the mammals that have gone extinct in
327 recent times, only a small percentage were heterothermic species that used torpor to some
328 extent (52). It now seems that climate induced environmental changes, particularly during
329 this crucial period of hibernation, may make hibernators, which are also often restricted to
330 mountain tops limiting distribution shifts, more vulnerable. As well as the direct impacts,
331 warming may permit homeotherms to move in increasing competition and predation (5).

332 Social, burrowing, herbivorous mammals, like marmots, play an important role in ecosystem
333 function and the loss or decline of these species would have wider reaching implications for
334 biodiversity (56). Climate change is pervasive and species all over the world face changes in
335 seasonal conditions emphasising the importance of disentangling seasonal demographic
336 responses.

337

338 **Material and Methods**

339 **Study system**

340 Yellow-bellied marmots (*Marmota flaviventer*) are large (3.4-6.4 kg), hibernating subalpine
341 rodents found in western North America (30, 57-58). These animals go through seasonal
342 cycles of body mass, which for adults can vary by as much as a couple of kilograms (up to
343 ~40% change; 30). Due to their distinct circannual lifestyle, highly seasonal montane habitat
344 and sensitivity to environmental conditions, yellow-bellied marmots are an ideal species to
345 explore seasonal responses to climate change. We used data from the population located in
346 the Upper East River Valley, Colorado, in and around the Rocky Mountain Biological
347 Laboratory (RMBL), which has been studied since 1962. The population comprises four
348 main colonies and 12 satellite colonies distributed between 2700-3100 m above sea level.

349

350 **Live trapping**

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

359

360 **Environmental data**

361 We include six environmental variables namely (i) winter snowfall (cm), (ii) winter
362 temperature (mean minimum temperature (°C) between November and March), (iii) summer
363 temperature (mean maximum July temperature (°C)), (iv) snowmelt date (bare ground) in
364 spring, and (v) length of the growing season (days), data for which have been collected at
365 RMBL for the entire period. We include (vi) a measure of drought severity, which was
366 calculated using the Palmer Drought Severity Index (PDSI) using precipitation and
367 temperature data for Crested Butte and calibrated for RMBL, which was collected from the
368 National Centres for Environmental Information (NCEI) Climate Data Online; negative PDSI
369 values indicate drier than average conditions while positive values indicate wetter than
370 average conditions. All environmental covariates were zero centred and thus standardized to
371 compare effect sizes.

372 These environmental variables have previously been shown to be important for
373 marmot fitness. Adequate winter snowfall is important to keep burrows insulated allowing
374 marmots to remain in deep torpor while minimizing energy expenditure (60). Years of low
375 snow cover have been shown to increase mortality of marmots (26), most likely as a result of
376 colder temperatures inside the burrow, thereby increasing energy expenditure (60). Marmots
377 use spring temperatures as a cue to emerge from hibernation, but while spring temperatures
378 have warmed and marmots are emerging earlier from hibernation, the average snowmelt
379 date has not advanced as significantly creating a potential mismatch in phenologies (12).
380 Prolonged snow cover in spring has a negative impact on marmot survival and reproduction
381 (58), and marmots have to wait longer for food plants to appear (61). During the summer
382 marmots are sensitive to warmer temperatures as a result of having a relatively large body
383 size (4). To avoid thermal stress, they are likely to reduce aboveground activity, which
384 consequently reduces the amount of time spent foraging (4). The growing season has
385 extended as a result of shifts in flowering phenology (7), and Ozgul *et al.* (31) demonstrated
386 an increase in body size and hence survival of marmots apparently in response to an
387 extended growing season, potentially allowing marmots more time to gain weight before the

388 next winter. The length of the plant growing season was calculated as the number of days
389 between the appearance of first flowers and last flowers (7); community-level flowering onset
390 occurs within a few days of snowmelt and flowering proceeds until the end of the season,
391 terminating with late-summer frost events or significant snowfall. Lastly, marmots obtain
392 water from food plants and droughts can therefore significantly impact their growth and
393 survival (62). This is particularly true for the month of July, which is characterized by a
394 summer monsoon. The level of precipitation during this period will greatly influence plant
395 growth during the latter part of the summer. To explore trends in environmental covariates
396 across the period, we fitted generalised additive models (see SI Appendix, Table S2).

397

398 **Data analysis**

399 Capture-mark-recapture (CMR) models were constructed in R (v3.6.1; 63) within the
400 package RMark (64), which fitted the models in MARK v9.0 (65). Model selection was
401 conducted using Akaike's Information Criterion corrected for small sample size (AICc) and
402 AICc model weights. Effect sizes of individual parameters were evaluated using β -estimates
403 (slopes) and their 95% confidence intervals.

404

405 **Multistate mark-recapture models**

406 Capture-mark-recapture data were analysed using a multistate CMR model, which included
407 the following model parameters: probability of survival (S), recapture probability (p), and
408 state transition probability conditional on survival (Ψ). The trapping season (April–
409 August/September) where marmots were active was split into five monthly primary
410 occasions to limit heterogeneity in the interval between capture occasions, namely the
411 summer occasions, while the rest of the year (September to March) made up the monthly
412 winter occasions, although there were no observations during this time (see Fig. 4). Only
413 “known-age females” were used in our analyses ($n = 1506$) because males often disperse
414 before the end of their second year making it difficult to discriminate between survival and

415 dispersal. Individuals were assigned to one of three states based on their age: pup (< 1 year
416 old), yearling (1 year old), and adult (\geq 2 year old). The uneven time intervals between
417 occasions were accounted for within the model whereby the time intervals between the
418 monthly summer occasions were set to one, while the interval between August and April the
419 following year was set to eight). Furthermore, we wanted the flexibility to separately explore
420 temporal trends in and mechanistic drivers of survival between seasons and age-classes.
421 Therefore, instead of using season and state as design covariates, we decoupled these into
422 six binary indicator variables of 'pup summer', 'pup winter', 'yearling summer', 'yearling
423 winter', 'adult summer', and 'adult winter'. Because of the monthly variation in recapture
424 across the trapping season we created a continuous covariate of capture effort; the ratio of
425 numbers of non-pups captured in a given month relative to the total number of non-pups
426 captured that year. This capture effort effect was added to each state and season binary
427 indicator variable. Because of the very low numbers of individuals trapped in April, we fixed
428 the recapture probability for this month to 0, and for pups we also fixed the May recapture
429 probability to 0 as no pups had been trapped during the month. All state transition
430 probabilities were fixed to either 0 or 1. Infeasible state transitions from pup to adult and from
431 all older to younger age-classes were fixed at 0. State transitions between summer months
432 were fixed to 1 as individuals had to remain in the same age-class. Transitions between
433 years from pup in August to yearling in April, yearling in August to adult in April, and adult in
434 August to adult in April were fixed to 1. Therefore all models included a constant ψ . Models
435 were constructed to explore both the phenomenological time trends in state-specific survival,
436 the influence of age on adult survival, and the mechanistic influence of the environmental
437 covariates on state-specific survival within each season. We ran goodness of fit testing in the
438 program U-CARE for multistate models (JollyMove) including tests for transience, trap-
439 dependence, and the complementary tests 3G.SM and M.LTEC (65). The overall \hat{c} (a
440 measure of overdispersion) was calculated by dividing the sum of X^2 values from all test
441 components with the sum of the degrees of freedom, which indicated there was no evidence

442 of overdispersion ($\hat{c} = 1.02$). Furthermore, we refitted a random selection of models twice
443 using initial values from the original model and compared β -estimates from the refitted
444 models to 3 decimal places. These refitted models revealed that our models were reaching
445 the global maxima rather than a local maxima, which has been identified as an issue with
446 multistate models.

447

448 **Phenomenological trends in survival**

449 The phenomenological models describe the temporal trends in survival without attempting to
450 explain the underlying biological processes. In order to estimate and compare seasonal
451 trends in monthly survival, we created a year variable, which contained the same value for
452 all six summer occasions and the single winter occasion within a year. We used this new
453 year variable to evaluate time trends (T). This also meant that we only estimated a single
454 (monthly) survival estimate per season per year. We constructed a set of phenomenological
455 models containing either a linear time trend (T) or a quadratic effect (T^2) on the six binary
456 indicator variables described above (for full model syntax see SI Appendix, Table S1).

457 Because of the long time-period that the study covered, year was rescaled [$\text{year}_{\text{rescaled}} =$
458 $(\text{year} - \text{year}_{\text{avg}}) / \text{year}_{\text{sd}}$], which allowed β -estimates for the linear and quadratic terms to be
459 similar in magnitude.

460

461 **Body mass imputations**

462 We incorporated body mass (measured in grams) as a time-varying individual covariate in
463 this analysis. To do so a measure of body mass is required for each primary occasion after
464 the individual is first trapped as a pup until the end of the time series (even though the
465 animal may no longer be present or alive). These time-varying individual covariates are
466 therefore typically restricted to variables such as age that do not require continual capture.
467 However, we were able to impute body mass for each individual twice during each year
468 following their first capture using a similar approach to Ozgul *et al.* (31) (for more details on
469 the modelling procedure see SI Appendix). Body mass measurements were log transformed

470 (following Ozgul *et al.* (31)). For summer survival, we used body mass imputations from the
471 15 July for pups as pups only emerge early summer, and from the 1 June for yearlings and
472 adults. For winter survival, we used body mass imputations for the 31 August for all age-
473 classes.

474

475 **Mechanistic drivers of trends in survival**

476 Our mechanistic models describe the environmental or phenotypic (i.e. body mass)
477 processes driving the phenomenological patterns in marmot survival. Before exploring
478 environmental drivers of trends in survival, we first tested the effect of age on adult survival
479 (as pup and yearling stages only involved one year). We used the top phenomenological
480 model and included a linear effect of age on both summer and winter adult survival, linear
481 effect of age on just summer or winter survival, and finally a quadratic effect of age on both
482 summer and winter adult survival. The top model would become the baseline model from
483 which we constructed our mechanistic models. However, to reduce the number of possible
484 mechanistic models (i.e., given six environmental covariates and six season-state
485 combinations), we explored the influence of environmental covariates on each state-season
486 pair in turn, resulting in six model sets; one for each of the binary indicator variables (i.e.,
487 summer pup, winter pup, summer yearling, winter yearling, summer adult, and winter adult
488 survival). For example, when exploring the mechanistic drivers of pup summer survival, the
489 binary indicator variable 'pup summer', and the interaction between 'pup summer' and body
490 mass (time varying individual covariate) formed the basis of the model. Environmental
491 variables (time varying individual covariates) were included as interactions with 'pup
492 summer'. All other binary indicator variables (state-season combinations) were the same as
493 in the baseline model. For summer pup survival, we only explored the effects of total
494 snowfall (could indirectly influence fitness of reproductive females, as well as green up
495 through snowmelt around the time pups emerge), snowmelt date (i.e., date of bare ground),
496 summer temperature, and drought on their survival. For yearling and adult summer survival,
497 we used the effect of the length of the growing season from the previous summer (i.e. lag

498 growing season), as the growing season likely would not have ended prior to the last
499 sighting of the individual. We constructed models with one, two or three environmental
500 covariates, which were not collinear.

501

502 **Data deposition**

503 The capture histories including age and body mass as time-varying individual covariates and
504 a separate data file including growing season length have been deposited in the Dryad
505 Digital Repository: <insert link>. The complete flowering phenology dataset used to calculate
506 growing season length is archived here: <https://osf.io/jt4n5/>. RMBL environmental data
507 (including total snowfall, mean minimum monthly temperatures, and snowmelt date) can be
508 downloaded from: <http://www.gothicwx.org/>. The monthly average temperature and total
509 precipitation data for Crested Butte that was used to calculate a calibrated drought severity
510 index for RMBL was downloaded from the National Centres for Environmental Information
511 (NCEI) Climate Data Online (<https://www.ncei.noaa.gov/>). Code used to run analyses is
512 available upon request.

513

514 **Acknowledgements**

515 Marmots were studied under annual permits issued by the Colorado Parks and Wildlife
516 (most recently via TR-917). All procedures were approved under research protocols
517 approved by the University of Kansas and more recently by ARC 2001-191-01 approved by
518 the University of California Los Angeles Animal Care Committee on May 13, 2002, and
519 renewed annually. Line Cordes and Arpat Ozigul were supported by the Swiss National
520 Science Foundation (31003A_182286 and 31003A_182286). Dan Blumstein was supported
521 by the National Geographic Society, UCLA (Faculty Senate and the Division of Life
522 Sciences), a Rocky Mountain Biological Laboratory research fellowship, and by the NSF
523 (IDBR-0754247, and DEB-1119660 and 1557130 to D.T.B., as well as DBI 0242960,
524 0731346, and 1226713 to the Rocky Mountain Biological Laboratory). We thank all the

525 marmoteers who helped in data collection as well as Billy Barr and the Rocky Mountain
526 Biological Laboratory for the long-term collection of local environmental data. Installation,
527 maintenance and publication of data from the RMBL weather stations has been supported
528 by NSF award (MRI- 0821369) and DOE funding as well as ongoing operational support
529 from RMBL, the Upper Gunnison River Water Conservancy District and the LBNL Science
530 Focus Area 2.0 project. We would also like to thank David Inouye and Nora Underwood for
531 providing access to the flowering phenology data. Brian Gerber was supported by the USDA
532 National Institute of Food and Agriculture, Hatch Formula project 1017848. Yellow-bellied
533 marmot symbol in the model schematic was provided courtesy of the Integration and
534 Application Network, University of Maryland Center for Environmental Science
535 (ian.umces.edu/symbols/). A special thanks to the Department of Fish, Wildlife, and
536 Conservation Biology at Colorado State University for hosting Line Cordes as a research
537 scientist.

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721 **Figures**

722

723 Figure 1. Estimated trends in summer and winter monthly survival from the
724 phenomenological model.

725

726 Figure 2. Temporal variation in environmental variables between 1979-2018. Grey dots and
727 line represent raw data, whereas the coloured line and shaded area is the predicted
728 relationship and 95% confidence limits from the GAMs (see also SI Appendix, Table S2). For
729 season length, there were no data from 1990 and 1994. The data points for these years are
730 the predicted values.

731

732 Figure 3. β -estimates of top model parameters by season and age-class. 'Significant'
733 relationships between survival and the environmental covariates are coloured either blue or
734 red (confidence intervals do not overlap zero). Blue indicates that the likely climate change
735 outcome for marmot survival will be positive, whereas red suggests a negative outcome. For
736 example, there is a positive relationship between pup winter survival and drought severity
737 during the previous summer (survival is greater following a wetter summer), and therefore
738 should climate change as predicted result in drier summer conditions this will have a
739 negative impact on pup winter survival.

740

741 Figure 4. Model schematic of the seasonal multistate mark-recapture modelling framework
742 showing monthly survival and recapture probabilities between occasions during the active
743 summer season (dashed line arrows), as well as seasonal survival probability (S) across the
744 summer and winter seasons (solid line arrows). Transition probabilities between states were
745 not included on schematic as all transitions were fixed to either 0 or 1.

746