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28

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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.

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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 ($\beta_{snowfall}$=-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 ($\beta_{snowmelt\ date}$=-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   ($\beta_{drought}$=0.31; 95% CI=0.13, 0.50; $\beta_{growing\ season}$=-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 ($\beta_{winter\ temp}$=-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   ($\beta_{summer\ temp}$=0.22; 95% CI=0.11, 0.35; $\beta_{growing\ season}$=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 (β_{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 ($\beta_{winter\ temp}$=0.16;

218   95% CI=-0.07, 0.39) and during a warmer summer ($\beta_{summer\ temp}$=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 ($\beta_{drought}$=0.38; 95% CI=0.09, 0.67) and spring periods where snow

222 melted later ($\beta_{snowmelt}$ 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

Environmental data

We include six environmental variables namely (i) winter snowfall (cm), (ii) winter temperature (mean minimum temperature (°C) between November and March), (iii) summer temperature (mean maximum July temperature (°C)), (iv) snowmelt date (bare ground) in spring, and (v) length of the growing season (days), data for which have been collected at RMBL for the entire period. We include (vi) 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 RMBL, which was collected from the National Centres 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 zero centred 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 (58), 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

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 (≥ 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

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 [$year_{rescaled} =$

458    $(year - year_{avg}) / year_{sd}$], which allowed β-estimates for the linear and quadratic terms to be

459   similar in magnitude.

460

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

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

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.

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Figures

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

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

Figure 3. β-estimates of top model parameters by season and age-class. 'Significant' relationships between survival and the environmental covariates are coloured either blue or red (confidence intervals do not overlap zero). 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.

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