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See you in spring: overwinter survival is higher than post summer in the Alpine marmot

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Highlights

This study provides evidence of a higher survival in hibernating mammals of the Alpine ecosystem, the Alpine marmot, compared to the survival of individuals during the summer season, providing a first evidence of different seasonal survival in this species.

High overwinter survival in Alpine marmot

Animal species living in highly seasonal environments developed different strategies to cope with the periodical drastic change of environmental conditions. Hibernating mammals survive the winter season by reducing their activity and metabolism, and by centering their activities during the favorable season. Thus, the demography of these species depends upon both hibernating and active periods. In this study, we explored the apparent survival of Alpine marmots monitored between 2007 and 2018 in the North-Western Italian Alps. We fit Cormack-Jolly-Seber (CJS) models to quantify changes in the apparent survival and capture probability of marmots, after the hibernation

phase and at the end of the summer. Apparent survival after winter almost reached 100% and it was higher than post summer survival. Moreover, while post-summer apparent survival remained almost stable over lifetime, with a slight increase with age, characterized however by wide confidence intervals, overwinter survival decreased with age, especially after 6 years of age. No temporal trends, nor changes between areas at different elevation, were found. We suggest that these results arise from a combination of climatic conditions, predation pressure and social dynamics, which is a pivotal feature of this species and cannot be ignored when considering population dynamics of Alpine marmot.

KEY WORDS: hibernating mammals, survival, overwinter, post-summer, population dynamic, *Marmota marmota*.

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INTRODUCTION

Species living in highly seasonal environments develop physiological and behavioral adaptations to overcome both the periods of scarce food resources and disadvantageous climatic conditions and period of intense engagement in activities like reproduction or social interactions (Kourkgy et al. 2016; Milling et al. 2017; Ma et al. 2021).

A well-known adaptation of mammals to overcome winter is hibernation, a phenomenon characterized by a massive reduction in physiological activity (Geiser & Ruf 1995; Armitage et al. 2003). Hibernation increases the probability of individuals to overcome the harsh season. However, this strategy is advantageous only when individuals manage to accumulate enough fat deposits

during summer, while completing all the other behavioral and physiological activities (i.e. reproduction, interaction with coo-specifics, vigilance against predators, etc.). In fact the energy requirements of hibernating individuals depend upon fat deposits from the active season (Florant & Healy 2012).

Both the hibernating and active phases include mortality risks, influencing a population's survival rate. It has been shown that survival varies according to multiple extrinsic (e.g. climatic, environmental) and intrinsic (e.g. age, sex, reproductive status) factors, which could interact influencing population dynamics (Paniw et al. 2020). For example, Turbill et al. (2011) showed that small mammals have 5 times more chance to die during active months than during hibernation due to the increased risk of being predated. On the contrary, other studies indicate hibernation as the period with higher mortality in all age classes (Cordes et al. 2020; Johnston et al. 2021). This heterogeneity in overwintering and between-winter survival can also generate ambiguous patterns in overall year-to-year survival and its drivers, in case these two types of survival are not disentangled (Rézouki et al. 2016).

Factors affecting survival may also vary seasonally during the year, resulting in different rates between winter and spring-summer seasons (Cordes et al. 2020; Paniw et al. 2020). As Yoccoz (2020) pointed out, analysis of seasonal survival can be highly relevant when considering the effect of climate change on species adapted to the seasonal habitat. Interestingly, the effects of seasonality may vary among similar species inhabiting different areas (Yoccoz 2020).

Most research on population dynamics has focused on the annual cycle or it was restricted to a fixed period, resulting in a bias towards the reproductive season in studies of animal ecology (Marra et al. 2015). Fewer, but increasing, studies have disentangled the contribution of overwintering and between-winter survival in hibernating mammals (Reusch et al. 2019). This gap has happened for multiple reasons, mostly connected with practical difficulties at following the fate of individuals during the whole year. This practice requires, for example, tagging individuals with VHF transmitters (Bryant & Page 2005) or extensive mark-resight schemes possible only with long term

and intense monitoring throughout the whole season, from the emerging to the immersion in hibernation (Clutton-Brock & Sheldon 2010).

This study aimed to unbundle overwinter from post-summer survival in a long-term monitored population of Alpine marmot (*Marmota marmota*) to verify if these demographic traits vary between the two periods and in which direction. The Alpine marmot is a medium-size hibernating rodent, widely distributed in the Alps and characterized by high sociality (Allainé et al. 1994). Cumulative survival for this species decreases with age, with a critical point among 5-7 years, depending on the dominance status of the individual (Berger et al. 2016; Ferrari et al. 2022a).

Although survival dynamics on an annual basis have been investigated in this species, no analysis of variation between overwintering and post-summer survival has been considered before. On the contrary this aspect has been investigated in a cousin species, the yellow-bellied marmot (*Marmota flaviventris*), resulting in a divergent response of the population related to the season analyzed: overall, winter survival was mainly negative, and it was driven by the environmental condition experienced in the previous summer (Cordes et al. 2020). Summer survival was generally positive, likely due to the variation in environmental conditions related to climate changes.

Here we analyze data from a population marked and monitored for multiple years (from 2007 to 2018) and run Cormack-Jolly-Seber models (CJS, Williams et al. 2002) to compare apparent survival after the hibernation (overwintering) and the active (post-summer) seasons. We expect a differential survival rate in the 2 seasons. More specifically, considering the effect of climate change on the winter characteristics and its consequences on the Alpine marmot (Tafari et al. 2013b), we predict that overwinter survival will be lower than post-summer survival (Hypothesis 1, hereinafter H_1). We also expect that (Hypothesis 2, hereinafter H_2) adult and young survival will follow different trends based on the social dynamics of this species (Sendor & Simon 2003). In detail, we expect (Hypothesis 3, hereinafter H_3) a lower post-summer than overwintering survival in young, the age class affected more frequently by social dynamics generated by the dominants or the intruders (Arnold 1990; Panaccio et al. 2021). We also expect that (Hypothesis 4, hereinafter H_4)

adult overwinter survival decreases after the age of 5 (Berger et al. 2012), while adult post-summer survival should increase with age and remain stable around 6-7 years old, when a marmot should be well integrated into its family. Based on a previous study in the same area (Ferrari et al. 2022a), we expect (Hypothesis 5, hereinafter H₅) higher post-summer survival in marmots inhabiting a site with lower densities and close to the forest than an open site where more families live.

MATERIAL AND METHODS

Study species

The Alpine marmot characterizes the high-altitude open habitats from 1,500 to 3,000 m (Allainè et al. 1994; Ferrari et al. 2022a). This medium-sized rodent lives in families of up to 20 individuals (Arnold & Dittami 1997) playing a relevant role in the Alpine prairies since it lives in burrow systems (i.e. holes in the ground) disseminated all over the territory, and it forages on vegetation during the entire, short, vegetative season of the Alps (Ferrari et al. 2022b). Sociality is a pivotal trait of this species, where the dominant pair of a family reproduces once a year (pups are born underground in May and emerge at the end of June/July; Hackländer & Arnold 1999). During the winter marmots hibernate socially, i.e. all family members hibernate together in the winter burrow (Arnold et al. 1991). During the active season, marmots spend most of their time foraging and avoid intense activity during high heat or low visibility hours (Ferrari et al. 2022b). During most of the season the family hierarchy is maintained through aggression and affiliative interaction (Panaccio et al. 2021), and subordinates are tolerated until 3 years old, then forced to leave the natal territory (Arnold 1990).

Study area

We collected data from summer 2007 to summer 2018, in the study area of Orvieilles located in Valsavarenche (Gran Paradiso National Park, North-western Italian Alps, 45°34'N; 7°11'E). The study area includes two sites: a Low Site, located at 2100 m asl defined as marginal habitat and characterized by a higher survival probability (Ferrari et al. 2022b); a High Site, located at 2300 m

asl, an open meadow with wide visibility and far from forest edges. In both areas, the main predators of Alpine marmots are red foxes (*Vulpes vulpes*) and golden eagles (*Aquila chrysaetos*).

Capture and individual marking

Marmots inhabiting the study area were captured using Tomahawk live traps (150 × 30 × 30 cm, Tomahawk Live Traps, Hazelhurst, WI, USA) from late April to the beginning of July every summer. For more information on the capture protocol, refer to Ferrari et al. (2013). Marmots were marked with an intraskin transponder (Bayer Animal Coder, Bayer SpA, Milan, Italy) and coloured plastic ear tags for visual recognition from a distance (Minirotag, 5 cm length, Ghislandi and Ghislandi, Bergamo, Italy). During the first capture, we assigned sex and age to each individual: marmots were classified as a pup of the year, yearling or adult. Subsequently, individuals were re-sighted during ongoing monitoring campaigns and behavioral observations in the field area between July and September.

Statistical analysis

Each year there was an initial capture session at the beginning of the summer period, and a second and third capture session in the middle and the end of the summer period. We modeled our data through the Cormack-Jolly-Seber model (CJS, Williams et al. 2002) using the package “marked” (Laake et al. 2013) in the R programming environment (R Core Team 2021), by considering only the trapping sessions in June and September. Based on our experience from the study area, we used our monthly re-sight sessions as trapping occasions, in the CJS, as the assumption of a static population was respected. Moreover, to avoid censoring and data truncation (Colchero et al. 2012), we considered only those marmots that had been captured in their 1st year of age ($n = 159$). By doing so, we were able to model apparent survival (ϕ) and capture probabilities (P) in function of the age of each individual. In this study, we were interested only in the estimation of apparent survival during each summer (post summer) and between consecutive summer (overwinter) survivals. Therefore, sessions in June and September were treated as a dichotomous covariate. We also indicated the site where animals were observed, distinguishing between one site at 2000 m asl

and a second site, at 2200 m asl (Ferrari et al. 2022a). For all tested CJS models, the variance covariance matrix was computed as Hessian.

We selected the best fitting model based on the Akaike's Information Criterion (Symonds & Moussalli 2011). Capture probability (P) was modeled in function of: sex of individuals (sex); the site of their colony (site); a dummy variable indicating whether individuals had been captured at the beginning or at the end of the summer (postwinter); the year (year); the age of each individual in years (age); an interaction term between the age of each individual and the month of each trapping session (postwinter:age), which tested for the hypotheses that older marmots were less susceptible to being captured at the beginning of summer, due to previous experience. We also included a variable (td) to account for temporal dependence between consecutive trapping sessions, to quantify the effect of capture histories over parameter estimation (Laake et al. 2013).

Apparent survival (Φ) was modeled in function of sex; site; age; year; postwinter; an interaction term between the sex and age of each individual (sex:age), to model age-specific differences in survival between the two sexes (e.g. due to different costs related to dispersal or maternity); an interaction term between age and the site (age:site), to account for different age trajectories of survival between different environmental conditions; an interaction term between site and postwinter (site:postwinter); an interaction term between year and the age of animals (year:age); an interaction term between year and the time of the capture session during summer (year:postwinter); an interaction term between year and the site of each colony (year:site) and an interaction between the age of each individual and the time of the capture session during summer (age:postwinter).

All data are available in Mendeley Data, V1 (doi:10.17632/g4rm72w8rz.1).

RESULTS

Between 2007 and 2018, 249 marmots were trapped in Orvieilles but given the decision to include only individuals captured from their 1st year onwards, we modeled 22 trapping sessions that involved 151 individuals on 11 consecutive years. Of these 151, from the High Site, there were 32 females and 45 males; from the Low Site, 33 were females and 41 were males.

Model selection indicates that the best candidate model estimates apparent survival and capture probability in function of two covariates: the age of each individual and the timing of each capture session (at the beginning or at the end of each summer), as well as their interaction (Table 1).

Capture probability was also influenced by capture history on previous trapping sessions (Table 1).

Apparent survival varied with the age of Alpine marmot and according to the timing of the capture, if at the beginning or at the end of the summer and their interaction (Table 2). Capture probability model included age of the marmot, the timing of the capture and their interaction (Table 2).

Overwinter survival was high, especially in the 1st years of life, and declined steadily with age, after 5 years of age (Fig. 1). On the contrary, post summer survival was lower with respect to overwinter survival, and relatively stable across an individual lifespan. However, a light increased direction with the age can be noted, but confidence intervals were too wide to get a reliable indication in this sense (Fig. 1).

DISCUSSION

Comparison among overwintering and post summer survival

Our first prediction H_1 was met, suggesting a different trend in survival between the 2 seasons. Still, the direction we got was opposite to the one we expected: according to our results, overwinter survival is high in Alpine marmot populations, nearly reaching 100% in young individuals (Fig. 1), while post-summer survival was lower (almost 75%). As predicted in H_2 , overwinter survival trajectory decreases with age, similar to the one obtained by Berger et al. (2016), characterized by a marked reduction in survival after 5 years old. Likewise, to what was reported by Ferrari et al. (2022b) on survival estimates of the same population, in this study the decline in survival is sweeter without a sharp point of decrease compared to the one resulted in Berger et al. (2016) which was focused on dominant individuals only. We suggest that the overall age-survival trajectory in the population of Alpine marmot as a whole is better described by a slight decrease in survival, which coincides with the age when individuals should have become dominant or dispersed, both events including higher risk of conflicts with conspecifics.

Although previous literature on the genus *Marmota* indicates winter as the main period influencing survival in all age classes (Armitage 2013; Cordes et al. 2020; Johnston et al. 2021), our results confirm those obtained by Bryant and Page (2005) and Turbill et al. (2011) showing that hibernation increase survival in hibernating species compared to active phases characterized by a higher mortality rate. In Vancouver Island marmot (*Marmota vancouverensis*), data from radiotelemetry indicate late summer as the period with the higher mortality rate, compared to a very low mortality in the winter with an almost 100% survival rate after hibernation (Bryant & Page 2005); these results are in line with those presented in our study, and confirm the necessity to continue data collection about population dynamics in hibernating species, especially in relation to the length (in terms of annual series but also of months during the year) of such studies (Yoccoz 2020).

Predation has been suggested as the leading cause of the observed low survival during the active season (Turbill et al. 2011). In Vancouver Island marmot predation could be attributed in the post-mortem studies to the various predators. This made it possible to define predation as the main cause of death in this species (Bryant & Page 2005). In our study, where we don't have telemetry data, it is sporadic to find marmot carcasses, and we seldom observe an attack from fox or eagle, we can only have an indirect estimate of frequency and density of predators, which were estimated to be high in our area (Fasce et al. 2017).

However, we think that social dynamics, and not only predation risks, may explain our lower post summer survival. Observations of infanticide and forced removal of old dominants due to the arrival of new dominant during the active season have been observed in different cases (Coulon 1995; Ferrari et al. 2012), influencing post summer survival of populations. Effectively, the number of neighboring families (and thus a higher probability of intrusion) explains part of the family's stability, an element influencing juvenile survival over the summer (Ferrari et al. 2022a).

Overwinter and post summer survival trend in different age classes

In young, post summer survival is lower than overwinter survival, as we predicted in H₃. However, we didn't get a clear increase of this trait with age, as we would expect. Contrary to our expectation in H₄, post summer survival is nearly stable along an individual lifetime of in our results; just a slightly increasing trend with age can be noted (Fig. 1). Although we acknowledge that this trend is far from being neat, we suggest that this dynamic could be consistent with the social dynamics of this species and related to agonistic interaction, dispersal dynamics and dominance competition (Panaccio et al. 2020). Similarly to work done by Berger et al. (2016), it would be interesting to analyze subordinates and dominant individuals separately to investigate if social dynamics directly affect post summer survival in this species.

Variation according to the site

Our last hypothesis (H₅) was not met, as the best-selected model did not include the area among variables, resulting in an equal survival among seasons in the two sites. As we found a different annual survival in a previous study in the same area (Ferrari et al. 2022a), this result is unexpected, and we need further analysis to verify it.

CONCLUSION

We estimate overwinter and post summer survival in the Alpine marmot, a hibernating rodent well distributed in the Alps. Results provide a clear difference between survival in these two periods, with the latter characterized by a lower survival, almost stable during an individual lifetime.

Predation has been documented as a main cause of mortality during the active period in other mammals, while in our cases we are not in the condition to have a precise index of this factor. On the contrary, considering the relevance of sociality for the Alpine marmot, we suggest that social dynamics, and not only predation, may explain this variation. To evaluate the potential effect and the direction of change in the climate, specific data and climatic parameters are needed in future studies on this species.

Overwinter survival is very high, suggesting Alpine marmots are efficient hibernators since their 1st years of age, partially thanks to their social thermoregulation strategy (Allainé & Theuriau 2004).

Literature is accumulating about the differential effect of climate change even on cousin species inhabiting the Alpine environment (Yoccoz 2020), and most authors agree on the necessity to find the best method to monitor and analyze such a complex scenario (Armitage 2013; Paniw et al. 2020; Yoccoz 2020). In social species like marmot, there could be a threshold in the benefits given by sociality, and this threshold itself may be subjected to variation according to external conditions. We thus argue that more effort should be located into recognizing and investigating the link between sociality and environmental changes.

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DISCLOSURE STATEMENT

Authors declare no conflict of interest.

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ETHICAL STANDARDS

All applicable institutional and national guidelines for the care and use of animals were followed.

AUTHOR CONTRIBUTION

C. Ferrari collected the data in the field; C. Ferrari, S. Bertolino, J. Cerri, A. von Hardenberg conceived the idea of the manuscript, J. Cerri analyzed the data, C. Ferrari wrote the manuscript; all authors provided editorial advice.

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DATA ACCESSIBILITY

Data are deposited in Mendeley at 10.17632/g4rm72w8rz.1, code is available from the corresponding author on request.

REFERENCES

Allainé D, Rodrigue I, Le Berre, M, Ramousse R. 1994. Habitat preferences of alpine marmots, *Marmota marmota*. *Can J Zool.* 72:(12) 2193–2198. doi:10.1139/z94-293

Allainé D, Theuriau F. 2004. Is there an optimal number of helpers in Alpine marmot family groups? *Behav Ecol.* 15(6):916–924. doi:10.1093/beheco/arh096

Armitage KB. 2013. Climate change and the conservation of marmots. *Natural Science*, 05(05): 36-43. doi.org/10.4236/ns.2013.55A005

Armitage KB, Blumstein DT, Woods BC. 2003. Energetics of hibernating yellow-bellied marmots (*Marmota flaviventris*). *Comp Biochem Physiol A.* 134(1):101–114. doi:10.1016/S1095-6433(02)00219-2

Arnold W. 1990. The evolution of marmot sociality: II. Costs and benefits of joint hibernation. *Behav Ecol Sociobiol.* 27(4):239-246. doi:10.1007/BF00164895

Arnold W, Dittami J. 1997. Reproductive suppression in male alpine marmots. *Anim Behav.* 53(1):53–66. doi:10.1006/anbe.1996.0277

Arnold W, Heldmaier G, Ortmann S, Pohl H, Ruf T, Steinlechner S. 1991. Ambient temperatures in hibernacula and their energetic consequences for alpine marmots *Marmota marmota*. *J Thermal Biol.* 16(4):223–226.

Berger V, Lemaître J-F, Dupont P, Allainé D, Gaillard J-M, Cohas A. 2016. Age-specific survival in the socially monogamous alpine marmot (*Marmota marmota*). *J Mammal.* 97(3):992–1000.

Bryant AA, Page RE. 2005. Timing and causes of mortality in the endangered Vancouver Island marmot (*Marmota vancouverensis*). *Can J Zool.* 83(5):674–682. doi:10.1139/Z05-055

Clutton-Brock T, Sheldon BC. 2010. Individuals and populations: the role of long-term, individual-based studies of animals in ecology and evolutionary biology. *Trends Ecol Evol.* 25(10):562–573. doi:10.1016/j.tree.2010.08.002

Colchero F, Jones OR, Rebke M. 2012. BaSTA: an R package for Bayesian estimation of age-specific survival from incomplete mark–recapture/recovery data with covariates. *Methods Ecol Evol.* 3(3):466-470. doi:10.1111/j.2041-210X.2012.00186.x

Cordes LS, Blumstein DT, Armitage KB, CaraDonna PJ, Childs DZ, Gerber BD, Ozgul A. 2020. Contrasting effects of climate change on seasonal survival of a hibernating mammal. *Proc Natl Acad Sci USA.* 117(30):18119–18126.

Coulon J. 1995. Infanticide in the Alpine marmot (*Marmota marmota*). *Ethol Ecol Evol.* 7(2):191–194. doi:10.1080/08927014.1995.9522965

Fasce P, Fasce L, Bergese F. 2017. Status of the golden eagle (*Aquila chrysaetos*) in the Western Alps. *Avocetta*. 41:35-38.

Ferrari C, Pasquaretta C, Caprio E, Ranghetti L, Bogliani G, Rolando A, Bertolino S, Bassano B von Hardenberg A. 2022a. Extrinsic and intrinsic factors affecting the activity budget of alpine marmots (*Marmota marmota*). *Mamm Res*. 64(1):64-67. doi:10.1007/s13364-022-00623-9

Ferrari C, Pasquaretta C, Carere C, Cavallone E, von Hardenberg A, Réale D. 2013. Testing for the presence of coping styles in a wild mammal. *Anim Behav*. 85(6):1385–1396.

[doi:10.1016/j.anbehav.2013.03.030](https://doi.org/10.1016/j.anbehav.2013.03.030)

Ferrari C, Pasquaretta C, von Hardenberg A, Bassano B. 2012. Intraspecific killing and cannibalism in adult alpine marmots *Marmota marmota*. *Ethol Ecol Evol* 24:388-394. doi: 10.1080/03949370.2012.683454

Ferrari C, Zanet S, Rolando A, Bertolino S, Bassano B, von Hardenberg A. 2022b. Marginal habitats provide unexpected survival benefits to the alpine marmot. *Pop Ecol*. 64(1):64–77.

[doi:10.1002/1438-390X.12104](https://doi.org/10.1002/1438-390X.12104)

Florant GL, Healy JE. 2012. The regulation of food intake in mammalian hibernators: a review. *J Comp Physiol B*. 182(4):451–467. doi:10.1007/s00360-011-0630-y

Geiser F, Ruf T. 1995. Hibernation versus daily torpor in mammals and birds: physiological variables and classification of torpor patterns. *Physiol Zool*. 68(6):935–966

Hackländer K, Arnold W. 1999. Male-caused failure of female reproduction and its adaptive value in alpine marmots (*Marmota marmota*). *Behav Ecol*. 10(5):592–597. doi:10.1093/beheco/10.5.592

Johnston AN, Christophersen RG, Beaver EA, Ransom JJ. 2021. Freezing in a warming climate: Marked declines of a subnivean hibernator after a snow drought. *Ecol Evol*. 11(3):1264–1279. doi:10.1002/ece3.7126

Kourkgy C, Garel M, Appolinaire J, Loison A, Toïgo C. 2016. Onset of autumn shapes the timing of birth in Pyrenean chamois more than onset of spring. *J Anim Ecol*. 85(2):581–590. doi:10.1111/1365-2656.12463

Laake JL, Johnson DS, Conn PB. 2013. marked: an R package for maximum likelihood and Markov Chain Monte Carlo analysis of capture–recapture data. *Methods Ecol Evol*. 4(9):885-890. doi:10.1111/2041-210X.12065

Ma Y, Wang M, Wei F, Nie Y. 2021. Geographic distributions shape the functional traits in a large mammalian family. *Ecol Evol*. 11(19):13175–13185. doi:10.1002/ece3.8039

Marra PP, Cohen EB, Loss SR, Rutter JE, Tonra CM. 2015. A call for full annual cycle research in animal ecology. *Biol Lett*. 11(8):20150552. doi:https://doi.org/10.1098/rsbl.2015.0552

Milling CR, Rachlow JL, Johnson TR, Forbey JS, Shipley LA. 2017. Seasonal variation in behavioral thermoregulation and predator avoidance in a small mammal. *Behav Ecol*. 28(5):1236–1247. doi:10.1093/beheco/axx084

Panaccio M, Ferrari C, Bassano B, Stanley CR, von Hardenberg A. (2021). Social network analysis of small social groups: Application of a hurdle GLMM approach in the Alpine marmot (*Marmota marmota*). *Ethol.* 127(6), 453–464. <https://doi.org/10.1111/eth.13151>

Paniw M, Childs DZ, Armitage KB, Blumstein DT, Martin JGA, Oli MK, Ozgul A. 2020. Assessing seasonal demographic covariation to understand environmental-change impacts on a hibernating mammal. *Ecol Lett.* 23(4):588–597. doi:10.1111/ele.13459

R Core Team. 2021. R: A language and environment for statistical computing. Vienna (Austria): R Foundation for Statistical Computing. Available from: <https://www.R-project.org/> [Accessed 2021].

Reusch C, Gampe J, Scheuerlein A, Meier F, Grosche L, Kerth G. 2019. Differences in seasonal survival suggest species-specific reactions to climate change in two sympatric bat species. *Ecol Evol.* 9(14):7957–7965. doi:<https://doi.org/10.1002/ece3.5292>

Rézouki, C., Tafani, M., Cohas, A., Loison, A., Gaillard, J.-M., Allainé, D., & Bonenfant, C. (2016). Socially mediated effects of climate change decrease survival of hibernating Alpine marmots. *J Animal Ecol.* 85(3), 761–773. <https://doi.org/10.1111/1365-2656.12507>

Sendor T, Simon M . 2003. Population dynamics of the pipistrelle bat: Effects of sex, age and winter weather on seasonal survival. *J Anim Ecol.* 72(2):308–320.
doi:10.1046/j.1365-2656.2003.00702.x

Symonds MRE, Moussalli A. 2011. A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. *Behav Ecol Sociobiol.* 65(1):13–21. [doi:10.1007/s00265-010-1037-6](https://doi.org/10.1007/s00265-010-1037-6)

Tafari M, Cochas A, Bonenfant C, Gaillard JM, Lardy S, Allainé D. 2013. Sex-specific senescence in body mass of a monogamous and monomorphic mammal: The case of Alpine marmots. *Oecologia.* 172(2):427–436. [doi:10.1007/s00442-012-2499-1](https://doi.org/10.1007/s00442-012-2499-1)

Turbill C, Bieber C, Ruf T. 2011. Hibernation is associated with increased survival and the evolution of slow life histories among mammals. *Proc R Soc Lond B.* 278(1723):3355–3363. [doi:10.1098/rspb.2011.0190](https://doi.org/10.1098/rspb.2011.0190)

Williams BK, Nichols JD, Conroy MJ. 2002. Chapter 17. Estimating survival, movement, and other state transitions with mark-recapture methods. In: Williams BK, et al., editors. *Analysis and management of animal populations.*: Academic Press.

Yoccoz NG. 2020. Seasonal climate change and marmot demography. *Proc Natl Acad Sci USA.* 117(32):18921–18923. [doi:10.1073/pnas.2012792117](https://doi.org/10.1073/pnas.2012792117)

