Why are chamois shrinking in the Alps: Investigating the effects of climate on the phenotype of chamois

Or

Climate warming has led to the shrinking by X kilos in juvenile Alpine chamois over the past X decades in southern Switzerland

**Shrinking Alpine chamois: climate warming has led to a 3kg decrease in juvenile body mass over 27 years in Southern Switzerland**

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Now the file is: …. But:

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**So we without those 2210 words we have … ca.2900 words… need to cut 400:**

* **As seen in other articles using climwin in BiolLett I can cut ca. 150 words from the Stat analysis and wrote most of it in the supplementary materials.**

**Abstract**

Over the past decades, climate change has driven changes in body size in numerous species, including the Alpine chamois (*Rupicapra rupicapra*). Here, we analyse 5635 1.5-year-old individuals from a population in the Ticino canton in the Swiss Alps from 1992 to 2018. Using the package *climwin* in R, we aim to find the exact time window when average ambient temperature primarily affects the body mass of juvenile Alpine chamois. The results show that the temperatures during the early lactation period (May 9th - July 2nd) are of particular importance for the growth of chamois. We also found a decline in average temperatures over this temporal window of 1.6°C over less than 30 years. These results suggest that the rising temperatures in the alpine regions could have significant consequences on the ecology and evolution of wild ungulates.

**Introduction**

As global changes induced by human activities accelerate, many species are undergoing phenotypic changes to adapt to their new environment (Hetem et al. 2014) with changes in their distribution and abundance, phenology, and morphology. One frequently reported response to climate warming is the change in animal body size and shape (Gardner et al. 2011; Sheridan and Bickford 2011; Ryding et al. 2021) since morphology has consequences on thermoregulation (Speakman and Król 2010). Indeed, a shrinking in body size leads to a larger surface-area-to-volume ratio, which allows animals to dissipate heat more efficiently in warmer environments (known as the Bergman rule; Bergmann 1847). In addition to heat dissipation, global warming is likely affecting body size through food availability and quality changes. Heat dissipation and nutrition is likely driving the phenotypic responses observed in free-living animals jointly (Gardner et al. 2011). This might be especially true in mammals where ambient temperature and the ability to dissipate heat have been demonstrated to constrain maternal milk production and offspring growth (Speakman and Król 2010; Simons et al. 2011).

In vertebrates with finite growth (like mammals and birds), the size that an individual reaches as an adult has critical consequences for reproductive success and overall fitness (Beauplet and Guinet 2007). As the adult size and mass are primarily determined by early growth conditions and juvenile size (e.g.,)(Festa-Bianchet et al. 2000), it becomes fundamental to investigate the effect of climatic conditions on the juvenile size (Garel et al. 2011). Juveniles usually have low energy reserves and have to allocate a substantial amount of those reserves to growth~~, making them particularly susceptible to adverse environmental conditions~~ (Hudson and White 1985; Gaillard et al. 2000). Therefore, a decline in adult size is to be most evident in the early growing stages because they lack reasonable energy reserves, which makes them sensitive to changing external biotic and abiotic factors (Forchhammer et al. 2001; Herfindal et al. 2006; Rughetti and Festa-Bianchet 2012). In mammals, early growth is divided into three phases: in utero, lactation, and post-weaning. The three phases are, however, not equally sensitive to climate warming. The in-utero phase is likely the less sensitive as offspring live in a stable thermal environment. In contrast, the lactation phase is likely the most sensitive, as offspring growth in size is the fastest during lactation and mother milk production is constrained by ambient temperature.

Here, we investigated the effect of climate change on changes in juvenile size (i.e. at 1.5 years of age) of Alpine chamois (*Rupicapra rupicapra*) using hunting data collected in the southern Swiss Alps from 1992 to 2018. The Alpine chamois is the most abundant ungulate of the European Alps (Corlatti et al. 2011), and its morphology and physiology are adapted to high-altitude (cold) environmental conditions (Ascenzi et al. 1993). As the Alps have been identified as climate change hotspots (Ernakovich et al. 2014; Turco et al. 2015), Alpine animals are expected to show significant changes in their distribution (shift towards higher elevation), phenology, and morphology in response to climate warming (REF). Accordingly, most previous studies on the Alpine chamois have revealed a gradual shrinking in chamois body mass both in adults (Rughetti and Festa-Bianchet 2012) and in juveniles (Mason et al. 2014; Reiner et al. 2021). These studies have generally identified the critical period as the spring-summer temperatures over the first two years of life (Rughetti and Festa-Bianchet 2012). Nonetheless, a recent study did not find any body size or mass change in chamois or the other three ungulate species investigated during the study (Büntgen et al. 2020). No study has, however, tried to precisely identify which time window during early life is most sensitive to climate warming and whether the shrinking in size over time is associated with an elevation of temperature during this critical time window.

**Methods**

*Study system*

The Alpine chamois is an ungulate that shows early appearances of sexual dimorphism, with females reaching asymptotic body mass three years earlier (3.5 years) than males (6.2 years) (von Hardenberg et al. 2000; Bassano et al. 2003; Garel et al. 2009). In the Alps, alpine chamois give birth in April (Rughetti and Festa-Bianchet 2011). Between May and July is the main period of lactation for kids (the young of chamois) and of increase in body mass for juveniles. Chamois are then weaned between 3 and 6 months of age (Scornavacca et al. 2018). Vegetation in the Alps usually begins growing right after snowmelt in April, peaking in July, thus providing an abundant and protein-rich food source for a relatively brief period of time (Pettorelli et al. 2007). Alpine chamois are distributed over a broad altitudinal range (500–3100 m; (Shackleton 1997; Spitzenberger et al. 2001)) and can shift their range depending on the resource availability and climate conditions (Nesti et al. 2010; Reiner et al. 2021).

Data on the size of chamois were collected in the southern Alps of Switzerland (canton Ticino) and consist of records of the hunting bags from 1992 to 2018. The study area covers an area of 2700 km2 with an altitude varying from 250 to 2700 m asl. In Ticino, hunting starts at the beginning of September and the harvest plan is mainly completed within three weeks. All animals were sexed, aged and weighed (eviscerated). Hunters estimated age in the field by measuring the teeth and the growth rings of their horns (Schroder and Elsner-Schack 1985). Overall, 34 017 animals were legally harvested during the hunting period ranging from an age of 0.5 to 22.5 years old. For the purpose of this study, we considered juvenile individuals of 1.5 years old (5635 individuals, 2491 females and 3144 males). As of September, juveniles have been feeding on their own for nearly a year, but they are still very vulnerable to external abiotic and biotic threats due to the decrease in maternal care and increased active grazing behaviour.

Daily mean ambient temperature (℃) from 1990 until 2018 (to include all the years needed for the analysis) was obtained from a Swiss meteorological station in the city of Lugano (273 m asl), near the area where the chamois were hunted.

*Statistical analysis*

As the use of arbitrary climate periods does not always explain the biological response in the best way possible (van de Pol et al. 2016), we investigated the variation in weight of 1.5-year-old chamois in relation to the variation of mean ambient temperature using the software R version 4.2.1 (R Core Team 2022) and package *climwin* (Bailey and van de Pol 2016). This package allows the detection of the exact time window when a biological variable is most strongly affected by an environmental variable.

The overall approach for the *climwin* analysis is to compare the support of the data for competing hypotheses and to formalise them into regression models (van de Pol et al. 2016). Competing models are based upon a baseline model (without the addition of weather effects) and ranked using the ΔAICc, or the difference in terms of the Akaike Information Criterion values calculated for a small sample size between the baseline model and the model of interest. The model with the best support from the data has the lowest ΔAICc among competing models. The baseline model was a linear model with the body mass of the juvenile chamois in relation to sex and elevation. The function *slidingwin* creates a candidate set of competing models testing windows of different lengths for the weather variable of interest which, in this study, is the mean daily ambient temperature (℃). Non-linear effects of temperature on body weight were taken into account by checking for both linear and quadratic trends. As most of the chamois was harvested over two weeks at the end of September, we chose an absolute time window for the analyses instead of an individual-specific time window. As reference day, we decided on the last date of the harvesting period (September 24th), and we looked for windows between September 24th and 661 days before (December 1st of 2 years before) to include the critical periods in a young chamois life: gestation, lactation, first winter and juvenile. Further details on the analysis and its outputs are provided in the electronic supplementary material.

**Results**

The results from the *climwin* analysis for the body mass of juvenile chamois indicated as the best-supported model (ΔAICc = -325.33; see Supplementary Materials 1) a model with an absolute time window with the quadratic effect of mean temperature in the window of time going back from day 503 to day 449 from the reference day (24th September) (Table 1). This climate window has a length of 54 days and is equivalent to the period from May 9th until July 2nd of the year when the individual is born (Table 1).

The final model included an effect of the sex of the individual and altitude and a quadratic effect of mean temperature between days 503 and 449. Most importantly, chamois weight was lower with a higher average ambient temperature in the best climatic window (Table 1, Fig 1a). Juvenile chamois harvested at higher altitudes were heavier than chamois harvested at lower altitudes (Table 1, Fig 1b). The results also showed that 1.5-year-old males are significantly heavier than females (EMMs ± SE, males: 14.2 ± 0.05, females: 13.6 ± 0.06; Table 1, Fig. 1c).

During the study, the mean temperature between May 9th and July 2nd increased by 0.06 °C per year (± 0.003 °C, T-value = 2.4, P = 0.024; Fig. 2a), leading to a 1.6°C increase in 27 years. On the other hand, the mean weight of 1.5-year-old chamois decreased by 0.112 kg per year (± 0.006 kg, T-value = -17.81, P < 0.001; Fig. 2b), leading to an overall decrease in average weight of 2.92 kg during the years of the study.

**Table 1**

Results of the linear model showing the quadratic effect of annual average temperature (° C) between May 9th and July 2nd (i.e. climatic window), harvest elevation (m a.s.l.), and sex (Males vs Females) on body mass (kg) of Alpine chamois harvested at 1.5 years of age. No. of observations 5635 in 27 years.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| *Predictors* | *Estimate* | *SE* | *t* | *p* |
| Intercept | 11.853 | 0.154 | 77.08 | **<0.001** |
| Temperature | -34.348 | 2.586 | -13.28 | **<0.001** |
| Temperature ^2 | 32.985 | 2.587 | 12.75 | **<0.001** |
| Harvest elevation | 0.001 | 0.000 | 14.19 | **<0.001** |
| Sex [M] | 0.521 | 0.069 | 7.50 | **<0.001** |

**Figure 1**

Relationship between body mass (kg) of harvested 1.5-year-old Alpine chamois and (a) the average temperature (°C) between May 9th and July 2nd, (b) altitude (m a.s.l.) and (c) sex (F = females in orange, M = males in blue). Each dot is one observation (darker dots represent a higher number of observations), and fitted lines in (a) and (b) are shown with 95 % confidence intervals (shaded areas).

Chart, scatter chart

Description automatically generated

**This would be how figure 1 changes using the model:**

**Sex + altitude + year + temperature (day93-78, linear) + (1|year)**

**There is still the effect of temperature but from the same season...**

**Chart, scatter chart

Description automatically generated**

**Figure 2**

Yearly trend of (a) the average temperature (° C) between May 9th and July 2nd from 1991 and 2017 and (b) body mass (kg) of harvested 1.5-year-old Alpine chamois between 1992 and 2018. Each dot is one observation (with darker dots representing a higher number of observations in (b)), and fitted lines are shown with 95 % confidence intervals (shaded areas).

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**Discussion**

Here we aimed to investigate the change in body weight of juvenile Alpine chamois in relation to warming temperatures. Our analyses identified a 2-month window during May and June of the preceding year as the most critical period determining the body weight at 1.5 years of age. This coincides, on average, with the last few weeks before the birth of a chamois kid and its first weeks of life. We also found that chamois harvested at higher elevations were heavier than the ones at lower elevations. In addition, the species showed sexual dimorphism in weight that is already apparent in juveniles. Lastly, our results also indicated a decrease in body mass and an increase in the mean ambient temperature during the identified window during the 27 years of this study (1992-2018).

Chamois kids are usually born towards the end of May, and the results from this study showed that the temperatures around their birth (from the 9th of May until the 2nd of July) are crucial for the development of individuals. As chamois are capital breeders, climatic conditions may affect the body reserves of mothers, which in turn can affect the growth of the offspring during gestation (Hansen 2009) and lactation. After birth, kids are taken care of by their mothers until weaning which happens from three to six months after the kids are born (Gaillard et al. 2000). Mothers are lactating during the first few weeks of kids’ growth, which is also primarily associated with peak vegetative abundance (Robbins and Robbins 1979).

Here we showed a marked increase in temperature (1.6°C in 27 years) during a critical time for young chamois growth and a clear relationship between the shrinking size of alpine chamois and the increasing ambient temperatures in the Alps. Previous studies have reported a negative temporal trend in the body weight of alpine chamois in relation to the rising temperatures in adults and juveniles (Rughetti and Festa-Bianchet 2012; Mason et al. 2014; Reiner et al. 2021), suggesting the decreasing quality of foraging conditions as the main factor. Plants are affected by rising temperatures, particularly at high elevations, and their primary productivity is lower in springs and summers with unusually high temperatures and water limitation (Ciais et al. 2005; Reichstein et al. 2007). With this study, we support previous findings, but we also make a further step by revealing that the critical period for chamois growth is during lactation and by suggesting that climatic conditions, and therefore forage availability and quality, when mother chamois give birth are fundamental in driving the development of young ungulates.

Climate change can affect chamois growth in several ways, firstly by influencing the phenology of the plants they feed upon. Indeed, it was recently found that, as a result of the rising temperatures, births of chamois no longer coincide with the highest peak of vegetation growth (Chirichella et al. 2021). The lack of resources for the mother during the lactation period might influence the energy she invests into nursing, which may affect the kid’s growth. Furthermore, it has been suggested that fast phenological adaptation to this change is unlikely, as annual birth peaks of herbivores are mainly influenced by the length of days, not by the availability of resources (Post and Forchhammer 2008).

Secondly, on top of the phenological mismatch, ambient temperature can strongly influence the nutrient intake of juvenile chamois during growth both by altering the feeding activity (Mason et al. 2014) of young and adults and by affecting the quantity and quality of milk production (Liu et al. 2019). During heat days, chamois have been shown to reduce heat-generating activities (including foraging), likely in an attempt to avoid thermal overload (Brivio et al. 2016). Previous studies on domesticated ungulate species have found that an increase in temperature and humidity has a negative effect on milk yield (Upadhyay et al. 2007; Gorniak et al. 2014). Furthermore, climate change can also affect milk composition, with a significant decline in milk protein and fat content (Knapp and Grummer 1991; Gantner et al. 2011). Climate change likely strongly impacts the growth of chamois kids by affecting the foraging activity of lactating mothers and their milk production.

It has been suggested before that spring-summer temperatures are more critical than winter temperatures regarding phenotypic changes in seasonal environments (Klein 1965; Garel et al. 2011), and our study supports this hypothesis. On the other hand, the survival chances of large individuals are better than that of smaller ones in harsh wintering conditions such as those found at high latitudes and elevations when food is scarce or unavailable (Loison et al. 1999; Herfindal et al. 2006), and a large body mass is positively correlated with snow depth (Reiner et al. 2021). While we here show that late spring temperatures are changing in our study, previous studies have not yet established a decrease in average snow depth in the Alps (Reiner et al. 2021). These findings, combined with our results, suggest that ungulates are expressing such change in phenotype to cope with warming spring and summer temperatures. Still, it remains to be understood if this body size change will be revealed as detrimental to surviving the harsh wintering conditions at high elevations.

Overall our results support previous studies stating the importance of climatic conditions for growing ungulates at high elevations and latitudes (Forchhammer et al. 2001; Rughetti and Festa-Bianchet 2012; Reiner et al. 2021). At high altitudes, in particular, animals can try to avoid heat stress by shifting their range to higher elevations (Brivio et al. 2016). Several large ungulate species (e.g. Alpine chamois, ibex *Capra ibex*, red deer *Cervus elaphus*, and roe deer *Capreolus capreolus*) have already been gradually becoming more abundant in higher elevations in the past 30 years (Büntgen et al. 2017). Indeed, our results are consistent with previous results, as they show that juvenile chamois who were harvested in higher elevations, and thus, colder environments, have higher body mass than the ones living in lower elevations.

Our results show a phenotypic change in a wild, ungulate population that could lead to changes in life history traits with significant consequences for the population dynamics of the species. Body size is a fundamental determinant of individual survival and reproduction (e.g.) (McElligott et al. 2001; Coltman et al. 2002; Kruuk et al. 2002; Newbolt et al. 2017) and the warming climate could therefore act as a selective pressure with long-term effects (Ozgul et al. 2009). Further studies should monitor populations using long-term projects with marked individuals (Clutton-Brock and Sheldon 2010) to better investigate the ecological and evolutionary consequences of body size change in ungulates.

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**Data accessibility**

All data and code used for statistical analysis and plots are provided via the Open Science Framework at “link for OSF project”

**Authors' contributions**

G.M., K.G.G and P.B. conceived the study. P.B. collected the data. G.M. and K.G.G performed the statistical analyses. G.M. and K.G.G drafted the manuscript and all authors provided inputs at all stages. All authors approved the final version of this manuscript, and all authors agree to be held accountable for the work performed therein.

**Competing interests**

We declare we have no competing interests.

**References**

Ascenzi P, Clementi ME, Condò SG, Coletta M, Petruzzelli R, Polizio F, Rizzi M, Giunta C, Peracino V, Giardina B. 1993. Functional, spectroscopic and structural properties of haemoglobin from chamois (Rupicapra rupicapra) and steinbock (Capra hircus ibex). Biochemical Journal. 296(2):361–365. doi:10.1042/bj2960361.

Bailey LD, van de Pol M. 2016. climwin: An R Toolbox for Climate Window Analysis. Joseph S, editor. PLoS ONE. 11(12):e0167980. doi:10.1371/journal.pone.0167980.

Bassano B, Perrone A, Hardenberg AV. 2003. Body weight and horn development im Alpine chamois, Rupicapra rupicapra (Bovidae, Caprinae). 67(1):65–74. doi:10.1515/mamm.2003.67.1.65.

Beauplet G, Guinet C. 2007. Phenotypic determinants of individual fitness in female fur seals: larger is better. Proceedings of the Royal Society B: Biological Sciences. 274(1620):1877–1883. doi:10.1098/rspb.2007.0454.

Bergmann C. 1847. Über die Verhältnisse der Wärmeökonomie der Thiere zu ihrer Grösse. Abgedruckt aus den Göttinger Studien. 3:595–708.

Brivio F, Bertolucci C, Tettamanti F, Filli F, Apollonio M, Grignolio S. 2016. The weather dictates the rhythms: Alpine chamois activity is well adapted to ecological conditions. Behav Ecol Sociobiol. 70(8):1291–1304. doi:10.1007/s00265-016-2137-8.

Büntgen U, Greuter L, Bollmann K, Jenny H, Liebhold A, Galván JD, Stenseth NC, Andrew C, Mysterud A. 2017. Elevational range shifts in four mountain ungulate species from the Swiss Alps. Ecosphere. 8(4):e01761. doi:10.1002/ecs2.1761.

Büntgen U, Jenny H, Galván JD, Piermattei A, Krusic PJ, Bollmann K. 2020. Stable body size of Alpine ungulates. Royal Society Open Science. 7:200196. doi:10.1098/rsos.200196.

Chirichella R, Stephens PA, Mason THE, Apollonio M. 2021. Contrasting Effects of Climate Change on Alpine Chamois. The Journal of Wildlife Management. 85(1):109–120. doi:10.1002/jwmg.21962.

Ciais P, Reichstein M, Viovy N, Granier A, Ogée J, Allard V, Aubinet M, Buchmann N, Bernhofer C, Carrara A, et al. 2005. Europe-wide reduction in primary productivity caused by the heat and drought in 2003. Nature. 437(7058):529–533. doi:10.1038/nature03972.

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 in Ecology & Evolution. 25(10):562–573. doi:10.1016/j.tree.2010.08.002.

Coltman DW, Festa-Bianchet M, Jorgenson JT, Strobeck C. 2002. Age-dependent sexual selection in bighorn rams. Proceedings of the Royal Society of London Series B: Biological Sciences. 269(1487):165–172. doi:10.1098/rspb.2001.1851.

Corlatti L, Lorenzini R, Lovari S. 2011. The conservation of the chamois Rupicapra spp. Mammal Review. 41(2):163–174. doi:10.1111/j.1365-2907.2011.00187.x.

Ernakovich JG, Hopping KA, Berdanier AB, Simpson RT, Kachergis EJ, Steltzer H, Wallenstein MD. 2014. Predicted responses of arctic and alpine ecosystems to altered seasonality under climate change. Global Change Biology. 20(10):3256–3269. doi:10.1111/gcb.12568.

Festa-Bianchet M, Jorgenson JT, Réale D. 2000. Early development, adult mass, and reproductive success in bighorn sheep. Behavioral Ecology. 11(6):633–639. doi:10.1093/beheco/11.6.633.

Forchhammer MC, Clutton-Brock TH, Lindström J, Albon SD. 2001. Climate and population density induce long-term cohort variation in a northern ungulate. Journal of Animal Ecology. 70(5):721–729. doi:10.1046/j.0021-8790.2001.00532.x.

Gaillard J-M, Festa-Bianchet M, Yoccoz NG, Loison A, Toigo C. 2000. Temporal Variation in Fitness Components and Population Dynamics of Large Herbivores. Annual Review of Ecology and Systematics. 31:367–393.

Gantner V, Mijić P, Kuterovac K, Solić D, Gantner R. 2011. Temperature-humidity index values and their significance on the daily production of dairy cattle. Mljekarstvo : časopis za unaprjeđenje proizvodnje i prerade mlijeka. 61(1):56–63.

Gardner JL, Peters A, Kearney MR, Joseph L, Heinsohn R. 2011. Declining body size: A third universal response to warming? Trends in Ecology and Evolution. 26(6):285–291. doi:10.1016/j.tree.2011.03.005.

Garel M, Gaillard J-M, Jullien J-M, Dubray D, Maillard D, Loison A. 2011. Population abundance and early spring conditions determine variation in body mass of juvenile chamois. Journal of Mammalogy. 92(5):1112–1117. doi:10.1644/10-MAMM-A-056.1.

Garel M, Loison A, Jullien J-M, Dubray D, Maillard D, Gaillard J-M. 2009. Sex-Specific Growth in Alpine Chamois. Journal of Mammalogy. 90(4):954–960. doi:10.1644/08-MAMM-A-287.1.

Gorniak T, Meyer U, Südekum K-H, Dänicke S. 2014. Impact of mild heat stress on dry matter intake, milk yield and milk composition in mid-lactation Holstein dairy cows in a temperate climate. Archives of Animal Nutrition. 68(5):358–369. doi:10.1080/1745039X.2014.950451.

Hansen PJ. 2009. Effects of heat stress on mammalian reproduction. Philosophical Transactions of the Royal Society B: Biological Sciences. 364(1534):3341–3350. doi:10.1098/rstb.2009.0131.

von Hardenberg A, Bassano B, Peracino A, Lovari S. 2000. Male Alpine Chamois Occupy Territories at Hotspots Before the Mating Season. Ethology. 106(7):617–630. doi:10.1046/j.1439-0310.2000.00579.x.

Herfindal I, Solberg EJ, Sæther B-E, Høgda KA, Andersen R. 2006. Environmental phenology and geographical gradients in moose body mass. Oecologia. 150(2):213–224. doi:10.1007/s00442-006-0519-8.

Hetem RS, Fuller A, Maloney SK, Mitchell D. 2014. Responses of large mammals to climate change. Temperature. 1(2):115–127. doi:10.4161/temp.29651.

Hudson RJ, White RG, editors. 1985. Bioenergetics of wild herbivores. Boca Raton, Fla: CRC Press.

Klein DR. 1965. Ecology of Deer Range in Alaska. Ecological Monographs. 35(3):259–284. doi:10.2307/1942139.

Knapp DM, Grummer RR. 1991. Response of Lactating Dairy Cows to Fat Supplementation During Heat Stress. Journal of Dairy Science. 74(8):2573–2579. doi:10.3168/jds.S0022-0302(91)78435-X.

Kruuk LEB, Slate J, Pemberton JM, Brotherstone S, Guinness F, Clutton-Brock T. 2002. Antler Size in Red Deer: Heritability and Selection but No Evolution. Evolution. 56(8):1683–1695. doi:10.1111/j.0014-3820.2002.tb01480.x.

Liu J, Li L, Chen X, Lu Y, Wang D. 2019. Effects of heat stress on body temperature, milk production, and reproduction in dairy cows: a novel idea for monitoring and evaluation of heat stress — A review. Asian-Australas J Anim Sci. 32(9):1332–1339. doi:10.5713/ajas.18.0743.

Loison A, Langvatn R, Solberg EJ. 1999. Body mass and winter mortality in red deer calves: disentangling sex and climate effects. Ecography. 22(1):20–30. doi:10.1111/j.1600-0587.1999.tb00451.x.

Mason TH, Apollonio M, Chirichella R, Willis SG, Stephens PA. 2014. Environmental change and long-term body mass declines in an alpine mammal. Frontiers in Zoology. 11(1):69. doi:10.1186/s12983-014-0069-6.

McElligott AG, Gammell MP, Harty HC, Paini DR, Murphy DT, Walsh JT, Hayden TJ. 2001. Sexual size dimorphism in fallow deer (Dama dama): do larger, heavier males gain greater mating success? Behav Ecol Sociobiol. 49(4):266–272. doi:10.1007/s002650000293.

Nesti I, Posillico M, Lovari S. 2010. Ranging behaviour and habitat selection of Alpine chamois. Ethology Ecology & Evolution. 22(3):215–231. doi:10.1080/03949370.2010.502316.

Newbolt CH, Acker PK, Neuman TJ, Hoffman SI, Ditchkoff SS, Steury TD. 2017. Factors influencing reproductive success in male white-tailed deer. The Journal of Wildlife Management. 81(2):206–217. doi:10.1002/jwmg.21191.

Ozgul A, Tuljapurkar S, Benton TG, Pemberton JM, Clutton-Brock TH, Coulson T. 2009. The Dynamics of Phenotypic Change and the Shrinking Sheep of St. Kilda. Science. 325(5939):464–467. doi:10.1126/science.1173668.

Pettorelli N, Pelletier F, Hardenberg A von, Festa-Bianchet M, Côté SD. 2007. Early Onset of Vegetation Growth Vs. Rapid Green-up: Impacts on Juvenile Mountain Ungulates. Ecology. 88(2):381–390. doi:10.1890/06-0875.

van de Pol M, Bailey LD, McLean N, Rijsdijk L, Lawson CR, Brouwer L. 2016. Identifying the best climatic predictors in ecology and evolution. Methods in Ecology and Evolution. 7(10):1246–1257. doi:10.1111/2041-210X.12590.

Post E, Forchhammer MC. 2008. Climate change reduces reproductive success of an Arctic herbivore through trophic mismatch. Philosophical Transactions of the Royal Society B: Biological Sciences. 363(1501):2369–2375. doi:10.1098/rstb.2007.2207.

R Core Team. 2022. R: A language and environment for statistical computing. R Foundation for Statistical Computing. https://www.R-project.org/.

Reichstein M, Ciais P, Papale D, Valentini R, Running S, Viovy N, Cramer W, Granier A, Ogée J, Allard V, et al. 2007. Reduction of ecosystem productivity and respiration during the European summer 2003 climate anomaly: a joint flux tower, remote sensing and modelling analysis. Global Change Biology. 13(3):634–651. doi:10.1111/j.1365-2486.2006.01224.x.

Reiner R, Zedrosser A, Zeiler H, Hackländer K, Corlatti L. 2021. Forests buffer the climate-induced decline of body mass in a mountain herbivore. Global Change Biology. 27(16):3741–3752. doi:10.1111/gcb.15711.

Robbins CT, Robbins BL. 1979. Fetal and Neonatal Growth Patterns and Maternal Reproductive Effort in Ungulates and Subungulates. The American Naturalist. 114(1):101–116. doi:10.1086/283456.

Rughetti M, Festa-Bianchet M. 2011. Effects of early horn growth on reproduction and hunting mortality in female chamois. Journal of Animal Ecology. 80(2):438–447. doi:10.1111/j.1365-2656.2010.01773.x.

Rughetti M, Festa-Bianchet M. 2012. Effects of spring-summer temperature on body mass of chamois. Journal of Mammalogy. 93(5):1301–1307. doi:10.1644/11-MAMM-A-402.1.

Ryding S, Klaassen M, Tattersall GJ, Gardner JL, Symonds MRE. 2021. Shape-shifting: changing animal morphologies as a response to climatic warming. Trends in Ecology & Evolution. 36(11):1036–1048. doi:10.1016/j.tree.2021.07.006.

Schroder W, Elsner-Schack IV. 1985. Correct age determination in chamois. In: The biology and management of mountain ungulates. (Lovari S., ed.). London, United Kingdom: Croom Helm. p. 65–70.

Scornavacca D, Cotza A, Lovari S, Ferretti F. 2018. Suckling behaviour and allonursing in the Apennine chamois. Ethology Ecology & Evolution. 30(5):385–398. doi:10.1080/03949370.2017.1423115.

Shackleton DM. 1997. Wild sheep and goats and their relatives : status survey and conservation action plan for Caprinae. [accessed 2022 Jul 2]. https://policycommons.net/artifacts/1373021/wild-sheep-and-goats-and-their-relatives/1987236/.

Sheridan JA, Bickford D. 2011. Shrinking body size as an ecological response to climate change. Nature Climate Change. 1(8):401–406. doi:10.1038/nclimate1259.

Simons MJP, Reimert I, van der Vinne V, Hambly C, Vaanholt LM, Speakman JR, Gerkema MP. 2011. Ambient temperature shapes reproductive output during pregnancy and lactation in the common vole (Microtus arvalis): a test of the heat dissipation limit theory. Journal of Experimental Biology. 214(1):38–49. doi:10.1242/jeb.044230.

Speakman JR, Król E. 2010. Maximal heat dissipation capacity and hyperthermia risk: neglected key factors in the ecology of endotherms: Heat dissipation limit theory. Journal of Animal Ecology. 79:726–746. doi:10.1111/j.1365-2656.2010.01689.x.

Spitzenberger F, Bauer K, Mayer A, Weis E, Preleuthner M, Sackl P, Sieber J. 2001. Die Säugetierfauna Österreichs. Bundesministerium für Land-und Forstwirtschaft, Umwelt und Wasserwirtschaft.

Turco M, Palazzi E, von Hardenberg J, Provenzale A. 2015. Observed climate change hotspots. Geophysical Research Letters. 42(9):3521–3528. doi:10.1002/2015GL063891.

Upadhyay RC, Singh SV, Kumar A, Gupta SK, Ashutosh. 2007. Impact of Climate change on Milk production of Murrah buffaloes. Italian Journal of Animal Science. 6(sup2):1329–1332. doi:10.4081/ijas.2007.s2.1329.