**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 an almost 3kg decrease in juvenile body mass over 27 years in Southern Switzerland

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**Key words**: climate change, *climwin*, gestation, juveniles, lactation, large ungulates, life stages, Switzerland, Ticino canton

**Journal**: Biology letters

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**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 mostly 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 important consequesnces 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). For example, one frequently reported responses to climate warming is the shrinking in animal body size (Gardner et al. 2011) since a change in size has a direct consequence on thermoregulation (REF). 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, climate warming is also likely to affect body size through changes in food availability and quality, with heat dissipation and nutrition likely to conjointly drive the phenotypic responses observed in free living animals (REF).

In response to global environmental changes induced by human activities, many species show changes in their distribution and abundance, phenology, and morphology (Hetem et al. 2014). One of the most frequently reported morphological changes in response to global warming is the decrease in body size of animals (Gardner et al. 2011). This is because a decrease in body size leads to an increase in the surface-to-volume ratio, which allows animals to dissipate heat more efficiently in warmer environments (the so-called Bergman rule; Bergmann 1847). In addition to heat dissipation, global warming is also likely to affect body size through changes in food availability and quality, with heat dissipation and nutrition likely to jointly drive the phenotypic responses observed in free-ranging animals (Gardner et al. 2011). This might be especially true in mammals where ambient temperature and the ability to dissipate heat has been demonstrated to constraint maternal milk production and offspring growth (REF).

Mammals have finite growth, and the size that an individual reaches as an adult has critical consequences for reproductive success and overall fitness (Beauplet and Guinet 2007). As adult size and mass is largely determined by early growth conditions and juvenile size (REF), it becomes fundamental to investigate the effect of climatic conditions on juvenile size (Garel et al. 2011). Juveniles have usually 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 obvious in the early growing stages because they lack proper 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). XXX

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 (Turco et al. 2015) and are also among the most vulnerable ones (Ernakovich et al. 2014), 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, 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) (but see Büngten et al. 2020), and generally identified the critical period as the spring-summer temperatures over the first 2 years of life (Rughetti and Festa-Bianchet 2012). 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.

, we examined the effect of climate change on the 1.5-year-old alpine chamois over a period of time encompassing the three critical periods for chamois growth (before birth, lactation and juvenile). This research aims at using, for the first time on chamois, the exploratory tool *climwin* for detecting periods of climate sensitivity for the body weight of juveniles while taking into account the altitudinal variation. Furthermore, we aimed at investigating the over-time change in the body weight of juvenile chamois and the extent of

Alpine chamois show 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). Alpine chamois are distributed over a broad altitudinal range over a broad altitudinal range (500–3100 m; (Shackleton 1997; Spitzenberger and Bauer 2001)) and can shift their range altitudinally, depending on the resource availability and climate conditions (Nesti et al. 2010; Reiner et al. 2021).

**Methods**

*Study system*

The Alpine chamois is an ungulate that show 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 therefore 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 source of food for a relatively brief period of time (Pettorelli et al. 2007). Alpine chamois are distributed over a broad altitudinal range over a broad altitudinal range (500–3100 m; (Shackleton 1997; Spitzenberger and Bauer 2001)) and can shift their range altitudinally, 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 mostly completed within three weeks. All animals were sexed, aged and weighted (eviscerated). Age was estimated in the field by hunters using the measurement of 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 are still very vulnerable to external abiotic and biotic threats due to the decrease in maternal care and increase in active grazing behaviour.

Daily mean ambient temperature (℃) from 1990 until 2018 (to include all the years needed for the analysis) were obtained from a Swiss meteorological station in the city of Lugano (XXX asml), in close proximity to the area where the chamois were hunted.

*Statistical analysis*

As the use of arbitrary climate periods do 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 by the data for competing hypotheses and to formalize 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, in this study 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 during a two-week period 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 chose 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) (Fig. 4A; 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 sex of 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 XXXA). Juvenile chamois harvested at higher altitudes were heavier than chamois harvested at lower altitudes (Table 1, Fig XXXB). The results also showed that 1.5-year-old male individuals are significantly heavier than female ones (EMM ± SE, males: 14.2 ± 0.05, females: 13.6 ± 0.06, Table 1; Fig. XXXC).

During the study, 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), leading to an overall decrease in average weight of 2.92 kg during the years of the study. On the other hand, 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), leading to a 1.6°C increase in 27 years.

**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.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| *Predictors* | *Estimate* | *SE* | *t* | *p* |
| Intercept | 99.4056 | 6.3050 | 15.76 | **<0.001** |
| Temperature | -8.5261 | 0.6389 | -13.35 | **<0.001** |
| Temperature ^2 | 0.2060 | 0.0162 | 12.75 | **<0.001** |
| Harvest elevation | 0.0013 | 0.0001 | 14.19 | **<0.001** |
| Sex [M] | 0.5212 | 0.0695 | 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 (M = males, F = females). 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

**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).

Chart, scatter chart

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**Discussion**

Here we aimed at investigating 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 important period determining the body weight at 1.5 years of age. This coincides with the last few weeks before the birth of a chamois kid and its first weeks of life. We found that chamois harvested at higher elevations were larger 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 9th of May until 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 largely 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 period for young chamois growth and it can be seen that there is a clear relationship between the shrinking size of alpine chamois and the increasing ambient temperatures in the Alps. Previous studies have already reported a negative temporal trend in body weight of alpine chamois in relation to the rising temperatures both in adults and juveniles (Rughetti and Festa-Bianchet 2012; Mason et al. 2014; Reiner et al. 2021), suggesting decreasing in foraging conditions as the main factor. Plants are expected to be strongly affected by rising temperatures, particularly at high elevations, and plant 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, and 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 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 youngs 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). It is therefore likely that climate change has a strong impact on the growth 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 important than winter temperatures in regard to 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 in fact 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 shown that there has not yet been 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 as an attempt to cope with warming spring and summer temperatures, but it remains to be understood if this body size change will be revealed as detrimental to surviving the harsh wintering conditions found 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) and 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 major 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 mark individuals (Clutton-Brock and Sheldon 2010) to better investigate the ecological and evolutionary consequences of body size change in ungulates.

**Acknowledgements**

We thank the managers of the hunting and fishing federal office of Ticino, Switzerland, and the Swiss federal office of meteorology and climatology (MeteoSchweiz) for collecting the data and making them available to us.

**Funding**

GM is supported by a Marie Skłodowska-Curie postdoctoral fellowship from the European Union’s Horizon 2020 research and innovation programme.

**Data accessibility**

Data and code used for these analyses are available on XXX:

**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.

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