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

Giulia Masoero1\*, Kristina Georgieva Gencheva2, Pierre Bize3

1 Department of Biology, University of Ottawa, Canada

2 AFFILIATION?

3 Swiss Ornithological Institute, Seerose 1, 6204 Sempach, Switzerland

\* Corresponding author: [giulia.masoero@gmail.com](mailto:giulia.masoero@gmail.com) (?)

**ORCID**

GM: 0000-0003-4429-7726

PB: 0000-0002-6759-4371

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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 7217 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, this study aims to find the exact time window when average ambient mostly affects the body mass of juvenile alpine chamois and whether rising temperatures could have contributed to the long-term declining size of alpine chamois. The results show that the temperatures between the 1st and 29th of June during the lactation period are of particular importance for the growth of chamois, as the first few weeks of chamois’ lives when they are particularly vulnerable.

*What is more, the results also pointed out that the effects of altitude and temperature are of similar magnitude and alpine chamois might be trying to avoid heat stress by moving to higher altitudes. XXX???*

*Understanding the long-term effect of climate change on whole populations is particularly important, yet challenging, due to the need for huge and consistent data records. Therefore, the results from this study are crucial since they can provide information about chamois climate change sensitivity which can be of help for conservation practices.*

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

**Introduction**

As global environmental change accelerates, many species have undergone phenotypic changes as a result of adaptations to their new environment (Hetem et al. 2014). In particular, animals living in cold climate conditions have been facing serious challenges for survival due to the increase in their habitat’s temperature. A known adaptive response to cope with climate warming is the change in body size (Salewski et al. 2010; Sheridan and Bickford 2011), a response reported by an increasing number taxa (e.g.) (Yom-Tov 2001; Daufresne et al. 2009; Ozgul et al. 2009; Gardner et al. 2011; Weeks et al. 2020). However, it has been suggested that, as a result of anthropologic activity, recent climate change is happening much faster than in the past and therefore some species may not be able to adapt fast enough, which might lead to extinction (Sheridan and Bickford 2011). Specifically, it is known that shrinking body size has been suggested to be the third most common response of animals to rising temperatures (Gardner et al. 2011). Indeed as thermoregulation is directly affected by body size, having a smaller body size, and therefore a larger surface-area-to-volume ratio, would allow them to shed heat more efficiently (Bergman, 1847, as cited in Gardner et al. 2011).

In vertebrates with a finite growth, body size is an important indicator of fitness and reproductive success, and therefore pivotal to understanding factors that influence it (Beauplet and Guinet 2007; Garel et al. 2011). In most large mammals, reproduction is often at least partly fuelled by previously accumulated body reserves (Festa-Bianchet and Jorgenson 1998), and is affected by body mass (Gaillard et al. 2000). Structural body size depends mostly upon environmental conditions during the growth (Festa-Bianchet et al. 2000). Body mass is influenced by environmental conditions (e.g.) (Toïgo et al. 2006; Tveraa et al. 2013; Herfindal et al. 2020) and juvenile individuals are particularly susceptible to adverse environmental conditions as they have low energy reserves and as a large portion of their energies is allocated to growth (Hudson and White 1985; Gaillard et al. 2000). Furthermore, the mass of young individuals responds to both population density and vegetation abundance, and it therefore reflects overall resource availability (Garel et al. 2011). A decline in body mass in ungulated is therefore expected 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; Rughetti and Festa-Bianchet 2012). However, the long-term effect of abiotic factors, such as ambient temperature, on whole populations, adapted to cold climate environments, is still poorly understood.

The Alpine chamois (*Rupicapra rupicapra*) is the most abundant ungulate of the European Alps (Corlatti et al. 2011) and its morphology and physiology are adapted to high-altitude environmental conditions (Ascenzi et al. 1993). 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). As mountain areas, such 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), animals living in the Alps have been (and likely will have to keep on) facing several drastic environmental modifications, among which we can find changes in altitudinal ranges, phenology and morphology. In particular, previous research has shown 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), and generally identified the critical period as the spring-summer temperatures over the first 2 years of life (Rughetti and Festa-Bianchet 2012). Using hunting data collected in the Swiss Alps from 1992 to 2018, 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 on the body weight of juvenile chamois and the extent of climating changes in the study area.

**Methods**

*Study system*

In the Alps, our study species, the alpine chamois, gives birth in April (Rughetti and Festa-Bianchet 2011). Between May and July is therefore the main period of lactation for kids and of increase in body mass for yearlings. Chamois are weaned at 3 to 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).

Data on alpine chamois body size were collected from the Alps in canton Ticino, Switzerland, and are constituted by the 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. Overall, 34 017 animals were legally shot during the hunting period ranging from an age of 0.5 to 22.5 years old. All animals were sexed, aged and weighted (eviscerated). Both males and females have horns all year round, even though female ones tend to be shorter. 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). For the purpose of this study, we were interested in juveniles, and we, therefore, considered only individuals 1.5 years old, as only information on individuals shot in September was available (5635 individuals, 2491 females and 3144 males). As of September, juveniles have been feeding on their own for nearly a year, and are fully grown but are still very vulnerable to external abiotic and biotic threats due to the decrease in maternal care and increase in active grazing behaviour.

Data for daily mean ambient temperature (℃) during the years of the study (1992-2018) were obtained from a Swiss meteorological station in the city of Lugano. The station is 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 weight of 1.5-year-old individuals in relation to the variation of mean ambient temperature using the R package *climwin*, and the function *slidingwin* which detects the exact time window when a biological variable is most strongly affected by climate (Bailey and van de Pol 2016).

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 shot 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 shooting period (September 24th) and we looked for windows between September 24th and 661 days before (December 1st of 2 years before) to include the three critical periods of a young chamois life: gestation, lactation and juvenile. Details on the analysis and outputs of the analysis 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 shot at higher altitudes were heavier than chamois shot 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**

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| *Predictors* | *Estimate* | *SE* | *t* | *p* |
| Intercept | 99.4056 | 6.3050 | 15.7662 | **<0.001** |
| Sex [M] | 0.5212 | 0.0695 | 7.5045 | **<0.001** |
| Altitude | 0.0013 | 0.0001 | 14.1934 | **<0.001** |
| Temperature | -8.5261 | 0.6389 | -13.3458 | **<0.001** |
| Temperature ^2 | 0.2060 | 0.0162 | 12.7502 | **<0.001** |

Figure 1

Chart, scatter chart

Description automatically generated

Figure 2

Chart, scatter chart

Description automatically generated

**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 and their first weeks of life. We found that chamois shot 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 of the identified window during the years of the 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, climate change may affect the body reserves of mothers, which in turn can affect the growth of the offspring during gestation (Hansen 2009). *After birth, kids (the young of chamois) 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). Unfortunately, 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).

* Result clim – lactation – why is this phase important. Which period were other studies identifying (correlation with lactation?).

On top of the phenological mismatch, ambient temperature has been found to strongly influence the quantity and quality of milk production in large and small mammals (Liu et al. 2019). 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).

*There are not many studies examining the effect of heat stress on the milk production of Alpine chamois, but numerous studies, conducted with other ungulates, have suggested that an increase in temperature and humidity have a negative effect on milk yield. A study on Murrah buffaloes in India, found that milk production can be reduced to up to 30% during the days after a significant increase in ambient temperature (Upadhyay et al., 2007). That study was conducted in an environment with extreme heat changes, but another study found that even mild changes in climate can impact the milk production in Holstein dairy cows in temperate climate conditions (Gorniak et al., 2014). The researchers suggested that one reason for this might be that heat stress causes animals to reduce dry matter intake (DMI) which results in reduced milk production. Another reason might be result of changes in nutrient partitioning by the animals due to increased ambient temperatures. Heat stress might lead to a decrease of the amount of adipose tissue in lactating animals, which leaves glucose as their main energy resource for milk production (Baumgard & Rhoads, 2012; Rhoads et al., 2009). Milk composition can also be affected by climate change. According to Brügemann et al., (2012) the main reason for change in nutrient content might be heat stress and reduced DMI. As a result, a significant decline in milk protein and fat content has been noticed (Gantner et al., 2011; Knapp & Grummer, 1991).*

Animals in mountain habitats can try to avoid heat stress by shifting their range to higher elevations (Brivio et al., 2019) and a study by Büntgen et al. (2017) showed that several large ungulate species (chamois, ibex, red deer, and roe deer) have been gradually becoming more abundant in higher elevations in the past 30 years (Fig. 7, Büntgen et al., 2017). Indeed, our results are consistent with this theory and showed that the effect of elevation goes the same way as the effect of temperature - juvenile chamois who live in higher elevations, and thus, colder environments, have higher body mass than the ones living in lower elevations

Those findings, combined with our results, suggest that ungulates are expressing such change in behaviour as an attempt to cope with climate change.

* Sex?
* Changes in climate, are the chamois also changing in altitude?

**Findings in accordance with what is known, then what we added**

It has been suggested that in seasonal environments, spring-summer temperatures are a lot more important when phenotypic change, such as weight, is considered, compared to winter temperatures (Klein 1965; Garel et al. 2011) and our study supports this hypothesis.

There is a clear relationship between the shrinking size of alpine chamois and the increasing ambient temperatures in the Alps. We concluded that the ambient temperature has the biggest effect on the development of chamois’ body size during the first few weeks after birth and the hottest parts of the summer during the second year of their lives. Interestingly, the effect of temperature during gestation does not seem to be significant for the change in body size of chamois. Those findings are of significant importance for understanding how a whole population in the Alps changes as a result of climate change. This could be of help for wildlife management programmes, since shrinking in size of large herbivores could also be correlated to higher mortality rate and this could influence the way a whole ecosystem functions, for instance, by affecting prey abundance. This study adds up to a growing body of evidence that climate change is a serious threat for numerous species and future research can help scientists track changes and act accordingly.

“Most studies suggest heavier individuals with increasing altitude and latitude (Ericsson et al., 2002; Herfindal et al., 2014), where typically short but intense summers are followed by long and harsh winters” (Reiner et al. 2022)

Changes in size over the years.

Is body mass as young similar to adults, if yes

*It seems plausible that the decreasing trend of body mass in Alpine chamois will have far- reaching impacts on populations living in open alpine habitats, since higher body mass is expected to improve winter survival for both sexes, and reproduction in females (Festa-Bianchet et al., 2019; Stearns, 1992). Though spring temperatures are generally increasing in our study area (Figure 3a), previous research has not yet shown a decrease in average snow depth (Reiner et al., 2021), suggesting that climateinduced declines in body mass may potentially lead to increased winter mortality due to lower energy reserves of chamois, especially at high elevations (Reiner, 2015; Rughetti et al., 2011).* *Whether chamois respond to increasing temperatures by moving to lower altitudes will also depend on other factors such as the presence of large predators, the availability of suitable food resources, resource competition with other ungulates (Corlatti et al., 2019), as well as on human-wildlife conflicts in relation to forestry and recreation (cf. Ciach & Pęksa, 2019; Schnidrig- Petrig & Ingold, 2001). [Reiner 2022]*

*(Rughetti and Festa-Bianchet 2012)* [*Ciais et al. (2005)*](javascript:;)*reported a strong decrease in plant primary productivity across Europe in 2003 relative to previous years. The unusually warm July was proposed as the main cause of this reduction, although there is some debate as to whether water limitation or high temperatures had the strongest effect on plant productivity (*[*Reichstein et al. 2007*](javascript:;)*). In our study sites, unusually warm temperatures also were recorded in 2005, 2006, 2007, and 2009 (*[*Fig. 1*](javascript:;)*). Examination of our data suggests that high spring-summer temperatures in 2003–2009 were the main cause of reduction in yearling mass. Although reduced plant productivity in 2003 could explain low yearling body mass that year, the persistence of low mass in subsequent years was likely because of continuing similar environmental conditions. Our analysis suggests an additive effect of high temperatures experienced over the first 2 summers of life on the mass of yearlings in autumn (*[*Table 2*](javascript:;)*). That result confirms the importance of environmental conditions during early growth for large herbivores ([Forchhammer et al. 2001](javascript:;); [Nussey et al. 2007](javascript:;)). A decline in mass also was evident in adults. In large herbivores, female body condition often affects offspring mass, mostly at high population density when females reduce maternal care (*[*Festa-Bianchet and Jorgenson 1998*](javascript:;)*). Therefore, the reduction in adult female mass could reinforce the negative effect of high temperatures on yearling mass.*

*(Brivio et al. 2016) Climate is another time cue for chamois activity: they adjusted their activity responding to variations of the wind-chill factor, as well as to changes in precipitation levels and, during winter, snow abundance and solar radiation. The interaction between air temperature and wind speed (wind-chill factor) appeared to influence chamois activity rhythms, either by reducing or by stirring daily activity levels. The response of chamois activity to temperature was parabolic for both sexes: in July for instance, the highest activity levels occurred during days with mean temperatures around 3–7 °C characterised by weak wind speed, while a decline in activity levels was observed at higher and lower temperatures (Fig.*[*4*](https://link.springer.com/article/10.1007/s00265-016-2137-8#Fig4)*). Such effect of temperature was exacerbated by wind speed and DMA reached minimum levels during windier and colder days. Therefore, activity appeared to be strictly dependent upon animal thermal balance. On the one hand, when air temperatures are below the animals’ thermoneutral zone and wind intensifies, the decrease in activity can be seen as a strategy to lower the costs of thermoregulation by seeking shelter (in time budget terms, by resting) in order to prevent heat loss, which may be exacerbated by the higher evapotranspiration caused by the wind. Likewise, Moen (*[*1976*](https://link.springer.com/article/10.1007/s00265-016-2137-8#ref-CR51)*) and Gates and Hudson (*[*1979*](https://link.springer.com/article/10.1007/s00265-016-2137-8#ref-CR27)*) showed that lying position and inactivity significantly reduce the metabolic costs of thermoregulation in cold weather. On the other hand, when air temperatures rise above the species’ thermoneutral zone, the reduction of activity may be an attempt to avoid thermal overload by reducing such heat-generating activities as feeding, moving and possibly even social interaction. This result is consistent with a previous observational study on Alpine chamois, which were reported to allocate less time to foraging with increasing temperatures during summer (Mason et al.*[*2014*](https://link.springer.com/article/10.1007/s00265-016-2137-8#ref-CR50)*). In this respect, chamois appeared not to take advantage of wind as an agent reducing thermal overload and, according to our results, wind speed was likely perceived just as a disturbance during both cold and warm days.*

*Lack of evidence of effect of ambient temperature during Gestation period*

Our results showed that the mean ambient temperatures during the gestation period do not have a significant effect on the development and growth of young chamois. In line with our findings, Chirichella et al., (2021) suggested that the main problem of rising temperatures is the effect they have on the survival of the young, once they are born, rather than during pregnancy. Their study on chamois found that change in temperature does not affect the condition of mothers significantly and reproduction in females remains stable with rising temperatures.

*Effect of ambient temperature during Juvenile period*

The results from this study showed that the temperatures during the first summer after the chamois have been weaned are the most important for the change in their weight. This is the time when juveniles are foraging on their own for the first time after weaning and after the cold season. They invest all the acquired energy from food into growth, instead of reproduction and therefore, that period is crucial for their development. However, according to our results, the effect of temperatures during this period is not much stronger than the effect of temperatures during the lactation period. This might be because during lactation, they get a lot of care from their mothers, compared to the period after weaning. A study by (Rughetti & Festa-Bianchet, 2012) found that the increase in spring-summer ambient temperatures during the first two years of chamois lives have a negative effect on their weight which is consistent with the findings from our study. The researchers suggested that this is an ecological response to high temperatures and if the temperatures keep rising in subsequent years, it could lead to evolutionary pressure with long-term effects on the life history of chamois.

The temperatures from the 8th of June until the 20th of July seem to be particularly important for the development of chamois during the juvenile period. The sunniest and the hottest days of the year in the Ticino canton are registered during June and July. During those months, the resource availability is supposed to be at its peak. The most common suggestion for the shift in size in herbivorous animals is the reduced quality and amount of vegetation due to climate change (Gardner et al., 2011; Sheridan & Bickford, 2011). According to Sheridan and Bickford (2011) the increase in temperatures can lead to water limitations which can affect respiration and plant growth and nutrients. Reduced food nutrients and foraging area can potentially limit body growth in large ungulates; however, this has not been found to be the case when it comes to Alpine chamois. Instead, it has been proposed that changes in climate in the Alps can directly limit the ability of chamois to acquire resources since rising temperatures may cause heat stress and can result in animals spending less time foraging and more time resting during the day (Mason, Apollonio, et al., 2014). Therefore, the heat stress may force juveniles to change their activity pattern. However, chamois have been found to reduce their overall foraging time when the temperatures are high, not only during the day (Tom H.E. Mason et al., 2014).

Population density and competition for forage after weaning has also been suggested to influence yearlings’ body mass (Mason, Apollonio, et al., 2014). According to Mason, Apollonio, et al., (2014), as a result of the stricter hunting control, the intraspecific competition for resources might have led to reduced food intake by individuals which could have resulted in decrease in weight. The effect might be particularly strong on yearlings since they acquire resources directly for the first time after weaning and this makes them vulnerable. However, the analyses in this study did not account for changes in population density due to the lack of data. A deeper insight on the matter would require future studies to account for intraspecific competition, related to climate change.

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**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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