<https://academic.oup.com/jmammal/article/93/5/1301/858721?login=true>

**Why are chamois shrinking in size 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

**Abstract**

1. 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. Previous research concentrated on the change of body size in different sexes of alpine chamois, however, little is known about the effect of climate change on chamois during the early growth stages. This study aims to find out whether rising temperatures during the gestation, lactation and juvenile period have contributed to the long-term declining size of alpine chamois. The data were analysed with the package *climwin* in R Studio, which finds the exact time window when a biological variable is most strongly affected by climate.

2. The results showed that the temperatures between the 1st and 29th of June during the lactation period are of particular importance for the growth of chamois. This time window correlates to the first few weeks of chamois’ lives when they are particularly vulnerable. The most likely explanation is that climate change can indirectly influence them by affecting the amount and content of milk produced by their mothers.

3. The period between June 8th and July 20th seems to be particularly important during the second year of chamois’ lives when they are independently foraging. Possibly this is because the climate during that time might indirectly affect juveniles (through competition and change in nutrients availability) or directly (by influencing their body ability to acquire resources).

4. Interestingly, there is no evidence that the temperatures during the gestation period can affect the foetus and lead to long-term body size decline. The reason for this might be because chamois are endotherms, therefore mothers have evolved protective mechanisms to buffer temperature stress on the foetus. 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.

5. *Synthesis and applications*. 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.

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)

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). By the end of the past century, the temperatures in the Alps have increased by more than twice the global average (Böhm et al. 2001) and they are expected to keep rising by 0.25℃ per decade until the middle of the 21st century (Gobiet et al. 2014). Changes are expected to encompass also other climate-defining variables such as precipitation patterns, global radiation, humidity, and extremes of temperature and precipitation, with impacts on the snow covers, and on altering events such as floods and droughts. 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. Numerous studies have shown that an alpine ungulate, the alpine chamois (*Rupicapra rupicapra*), has been gradually shrinking in size, while the temperatures in the Alps have been increasing (Garel et al. 2011; Mason et al. 2014; Chirichella et al. 2021).

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 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). Nonetheless, chamois generally inhabit the Alps from montane forests to alpine areas, and altitudinal variation in relation to temperature changes may occur (Reiner et al. 2021). The key growing periods during the early life of ungulates are the gestation period, lactation period, and juvenile period (Robbins and Robbins 1979).

THIS PARAGRAPH needs to be divided between here and the matmet

Chamois are capital breeders. Therefore, climate change may affect the body reserves of mothers, which in turn may influence their ability to reproduce and can affect the growth of the offspring during gestation (Hansen 2009). After birth, kids (the young of chamois) are being taken care of by their mothers until weaning which happens from three to six months after the kids are born (Gaillard et al. 2000). This period may be important when examining the effect of climate change, as the ambient temperature has been found to strongly influence the milk production and the quality of milk in large and small mammals (Liu et al. 2019) (Liu et al., 2019; Zhao et al., 2020). After the lactation period is over, juveniles start feeding on their own, which can make them more sensitive to climate change than adults (Chirichella et al. 2021). This is because they are still undergoing body growth and rising temperatures may influence that, for instance, through the quality of vegetation and/or their activity patterns.

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).

Previous research has shown a decrease in chamois body mass both in adults (Rughetti and Festa-Bianchet 2012) and in juveniles (Mason et al. 2014; Reiner et al. 2021), and identified the critical period as the spring-summer temperatures over the first 2 years of life (Rughetti and Festa-Bianchet 2012). We therefore aimed at assessing the effect of ambient temperature during three critical periods (before birth, lactation and juvenile) influences the growth of chamois while taking into account the altitudinal change in weight, as home range shift of individuals can be closely connected to climate change (Chen et al., 2011). We examined the effect of climate change on the 1.5-year-old alpine chamois using hunting data collected in the Swiss Alps from 1992 to 2018. Using an exploratory approach, this research aims at assessing the critical period for climatic conditions in determining the weight of juvenile chamois and by investigating the effects of climate change.

**WHY IS THIS WORK COOL? Climwin**

**Extra**

What is more, understanding the effect of environmental conditions on body size is of significant importance, as changes in individuals’ size can disrupt how a whole ecosystem functions (Jackson et al. 2021).

**Methods**

**Study system**

Data were collected from the Alps in Ticino, the southernmost canton of Switzerland, over an area of 2700 km2 with an altitude varying from 250 to 2700 m asl. The climate in the mountain range is Alpine, with temperatures varying from mean temperatures of -12℃ in winter to mean temperatures of 15.5 ℃ in summer. The hottest and the sunniest month of the year is July with an average maximum temperature of 25℃, measured in the biggest city in the canton Lugano (World Weather & Climate Information, 2021).

In our study area, chamois give birth in April (Rughetti and Festa-Bianchet 2011). From May until July is therefore the main period of lactation for kids and of increase in body mass for yearlings. 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).

The data analysed in this study are the records of the Ticino hunting bags from 1992 to 2018. 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. For the estimation of the age of the shot chamois, measurement of the teeth and the growth rings of their horns were used (Schroder and Elsner-Schack). Due to the nature of the dataset, only information on individuals shot in September was available, so for the purpose of this study, only a 1.5-year-old animals were considered (7127 individuals, 3257 females and 3870 males). As chamois are usually weaned at 3 to 6 months of age (Scornavacca et al. 2018), a 1.5-year-old individual has been feeding on their own for nearly a year, is fully grown but still very vulnerable to external abiotic and biotic threats due to the decrease in maternal care and increase in active grazing behaviour.

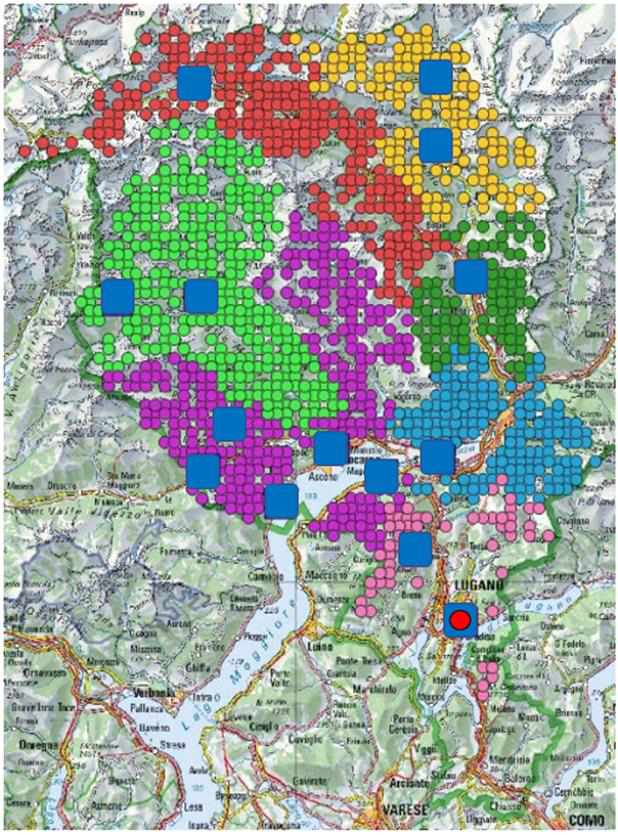


Figure 1. A map showing hunted chamois in the Ticino canton between 1992 and 2018. Different colours represent the seven districts where animals were hunted (red: Leventina,yellow: Blenio, light green: Vallemaggia, purple: Locarno, olive: Riviera, blue: Bellinzona, pink: Lugano). A dot represents the capture location of at least one chamois with a resolution of 1 km2. Blue squares indicate the location of meteorological stations in the canton and the blue square with a red dot represents the station where the weather data for this study was taken from. *Adapted from Ioset (2020).*

WHAT THE F…?

*Weather data*

Data for mean ambient temperature were obtained from a Swiss meteorological station in the city of Lugano. The station is in a close proximity to the area where the chamois were hunted. The data contains information about the daily mean ambient temperature (℃) for the years 1970 – 2020 but for the purpose of the study, only measurements of temperatures from 1992 to 2018 were used.

**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 change in weight of 1.5-year-old individuals in relation to 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). It is not always obvious exactly which environmental predictor or which life-history stage affects the expression of a trait the most. Therefore, for the aim of this study, three separate *climwin* analysis were carried out, in order to find out the relative contribution of mean ambient temperature during three different life stages.

Climwin analysis

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). The baseline model (without the addition of weather effects) was a linear model where the weight was analysed in relation to sex and elevation. A candidate model set was then created by including 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. An absolute time window was chosen for the analysis, As most of the chamois were 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 shooting period (September 24th).

Three different critical time windows were tested in the three *climwin* analysis (Fig. 2). The consideration of different time windows is important for the identification of the “best” time window. It also allows for the identification of co-occurring effects of short-lag and long-lag weather signals that could influence individuals in different stages of their lives (Bailey & van de Pol, 2016)

Figure 2. A graph that explains the choice of critical time windows to test in the *climwin* analysis and how they relate to time (days) according to the reference day (24th of September). [see pdf]

Window 1 (Juvenile period) (150-0 before reference day – 24th September)

The first tested window was the period before the 1.5-year-old chamois were shot. The last five months (day 150 / 24th of April) before the reference day (24th of September) were analysed, as this is the spring-summer period, when the juveniles are foraging and feeding on their own for the first time after the end of the cold months. In addition, they are not dependent on their mothers’ care anymore and therefore, they are expected to be vulnerable to changing biotic and abiotic factors. The autumn-winter period was not tested here because there is usually no significant growth happening during the cold months, as individuals are using resources and energy mainly trying to survive the harsh weather conditions, and not for growing (Monteith et al., 2013).

Window 2 (Lactation period) (480-365)

The second tested time window was the period from one year (day 365 / 24th of September) before the reference day (24th of September) until 1st of June (day 480), when the last births of chamois are expected since the young (kids) are born during late spring (May-June). This window has a length of 115 days, and it was chosen in order to examine whether the ambient temperature during the initial few months of the chamois’ lives, when they are nursed by their mothers, affects their body growth.

Window 3 (Gestation period) (661 – 481)

The last tested time window had a length of 180 days and covered the period of 661 days (1st of December) until 481 days (31st of May) before the reference day. This is the period when the mother was pregnant, up until the kids were born. The pregnancy of females lasts about 170 days, therefore the past six months before the end of the birth period were analysed to test whether climate has an indirect effect of individuals while they are growing during the gestation period.

Information criterion and validation of analyses

After the three analyses were performed in R, the timing of the best climatic windows (open and close) was determined using Akaike Information Criterion (ΔAICc). ΔAICc values provide means for model selection by estimating the quality of each model, relative to each of the other tested models. The best model has the lowest ΔAICc values. The next step was to test whether any of the signals might have occurred simply by chance by performing randomization with a small sample size. Finally, the best models were put together in a common model to test the relative contribution of each time period to the body mass of juvenile Alpine chamois.

**Presentation of results**

Most of the graphs for this project were produced by R but they were modified with the graphic design platform Canva.

For the last section of the results called “Relative contribution of climatic conditions during Lactation life stage and Juvenile life stage” the values for altitude, juvenile life stage and lactation life stage were scaled in R, so that the comparison of values is easier to interpret. However, in the same section, the graphs were presented with the original values because they make more biological sense.

**Results**

**Change of weight and ambient temperature (1992-2018)**

The results from a linear model concluded that time (years) had a significant role on the change of weight of 1.5-year-old chamois (P<0.001). Despite the big spread of the data, there was a pattern that pointed out the negative relationship between weight and time (Fig. 3A). The predictor explained about 4% of the variation in weight (R2 = 3.72%). The model indicated that the mean weight of 1.5-year-old chamois decreased by 0.082 kg per year (± 0.005 kg, T-value = -16.59, P < 0.001). What is more, they lost an average of 2.135 kg between 1992 and 2018 which is 15.08 % of their mean body weight (mean body weight = 14.16 kg).

The mean ambient temperature across all seasons increased significantly by 0.03 ℃ per year (±0.009℃, t-value = 3.10, P = 0.002), with a total increase of 0.77 ℃ over the period of the whole study (Fig. 3B).Those results pointed out an obvious change in the weight of chamois and maybe this was connected to the increase of ambient temperatures. Therefore, the analysis was proceeded by finding the exact time windows and life stages that might have affected the change in weight in juvenile alpine chamois.

**Identification of the best climate windows for Juvenile, Lactation and Gestation life stages**

All possible combinations for weather window models were tested with a *climwin* analysis in order to select the best model for each of the three chamois life stages (Juvenile, Lactation and Gestation). Fig. 4 shows the difference in model support (ΔAICc values) for the different time windows of an effect of mean ambient temperature on chamois’ weight, compared to a null model with no weather effect included. The results from the *climwin* analysis for the Juvenile life stage showed that the best supported model (ΔAICc = -279.71) assumes absolute time window with quadratic effect of mean temperature, going back from day 108 to day 66 from the reference day (24th September) (Fig. 4A; Table 1). This climate window has a length of 42 days and is the equivalent to the period from June 8th until July 20th the year when the alpine chamois were 1.5-year-old juveniles (Table 1).

The results from the *climwin* analysis for the lactation life stage showed that the best-supported model (ΔAICc = -305.69) assumes an absolute time window with a quadratic effect of mean temperature, going back from day 480 to day 452 from the reference day (Fig. 4B; Table 1). This climate window has a length of 28 days and is the equivalent to the period from June 1st until June 29th (Table 1) the year when the Alpine chamois were kids, still being taken care of by their mothers.

However, the results from the gestation life stage (Fig. 4C) did not detect a significant climate signal. Based on Fig. 4C and the “best” climatic window from the *climwin* analysis, which indicated a climatic window of 0 days and ΔAICc values of -279.29 (Table 1), it was indicated that the ambient temperature during that life stage does not seem to be biologically meaningful for the change of size of Alpine chamois. Therefore, the gestation life stage was no further examined in this study.

**Relative contribution of altitude, and climatic conditions during Lactation life stage and Juvenile life stage**

The *climwin* analysis was continued by further investigation of the relative contribution of each life stage, taking into account the sex of individuals as well as the altitude where they were shot.

The results showed that 1.5-year-old male individuals are significantly heavier than female ones (Table 2; Fig. 6A). From the scaled variables, the results show that the altitude has the strongest effect on the weight of chamois (0.486 ± 0.035) (Table 2; Fig, 6B). Furthermore, it looks like with increase of elevation, the weight of individuals also increases (Fig. 6B). Nonetheless, the linear effects of ambient temperature during the Lactation and Juvenile period are of similar magnitude as elevation (0.473 ± 0.051 and 0.403 ± 0.051) (Fig. 6C, D).

The results also show that the increase of ambient temperature during the best climatic windows over the course of the study had a similar effect for both the juvenile and lactation life stages – it led to a drastic decrease of the weight of individuals when the temperatures were increasing up to 21-22 ℃ before the reach of plato, followed by a slight increase of weight.

**Discussion**

The results from this study showed that the body weight of Alpine chamois in the Ticino canton in the Swiss Alps has been gradually decreasing from 1992 until 2018 while the mean ambient temperatures have been increasing. The long-term shrinking body size of chamois seems to be connected to increasing summer ambient temperatures during the crucial early growth stages. The first summer of independent foraging of juvenile chamois is the most important period, followed by the lactation period. What is more, it was found that the ambient temperatures during the gestation period do not seem to influence the growth of chamois. In addition, the species showed sexual dimorphism in weight that is already apparent at the kid-juvenile stages. Lastly, it was found that at higher elevation, thus colder environment, chamois are bigger.

*(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" \l "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" \l "ref-CR51" \o "Moen AN (1976) Energy conservation by white-tailed deer in the winter. Ecology 57:192–198)) and Gates and Hudson ([1979](https://link.springer.com/article/10.1007/s00265-016-2137-8" \l "ref-CR27" \o "Gates CC, Hudson RJ (1979) Effects of posture and activity on metabolic responses of Wapiti to cold. J Wildlife Manage 43:564–567)) 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" \l "ref-CR50" \o "Mason THE, Stephens PA, Apollonio M, Willis SG (2014) Predicting potential responses to future climate in an alpine ungulate: interspecific interactions exceed climate effects. Global Change Biol 20:3872–3882)). 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.

Chamois are endotherms, meaning that their bodies maintain constant body temperature, independent of the environment. It has been suggested that in mammals, mothers are able to buffer environmental changes by reducing the circadian variation of core body temperature (Wharfe et al., 2016). Another suggestion is that mothers may be able to suppress the febrile response (a controlled increase of body temperature, caused by elevation of the hypothalamic set (Zampronio et al., 2015)) to protect the embryo from thermal stress (Begg et al., 2007). One theory by (Nord & Giroud, 2020) proposed that if the thermal conditions during and after pregnancy are matching, this might result in the success of the offspring. However, the long-term effect of thermal challenges in mammals remains poorly understood and more research on the topic is needed.

*Effect of ambient temperature during Lactation period*

Chamois kids are usually born during the period end of May/beginning of June, and the results from this study showed that the temperatures immediately after birth (from 1st of June until 29th of June) are crucial for the development of individuals. During the first few weeks of kids’ growth, mothers are at the peak of lactation which is largely associated with peak vegetative abundance (Robbins & Robbins, 1979). According to a study by Chirichella et al. (2021), due to climate change, births of chamois no longer coincide with the highest pick of vegetation growth. The lack of resources for the mother during lactation period might influence the energy she invests into nursing which may affect kid body growth. Furthermore, it has been suggested that fast 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 & Forchhammer, 2008).

The change in ambient temperature might also affect the amount of milk produced by mothers. 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).

The temperatures in Ticino in June are high, therefore, there might have been heat waves that caused chamois mothers to reduce their DMI, which could have resulted in decline in milk amount and milk nutrients available for their kids. That, combined with the vulnerable state of the new-born chamois, might be the reason for the gradual decline in the weight of chamois kids during the lactation period over time. However, those are only suggestions, based on previous studies on different ungulates. More studies, examining the milk production of female chamois, close to giving birth and after giving birth, will help scientist understand the effect of climate change on milk production and therefore on the development of offspring. However, this can be complicated, as the data for this study was collected from hunting bag record from the hunting period in September when no pregnant animals could be found. We suggest a capture-mark-recapture method during the period May/June, when calves are being born, for future data collection in the Ticino canton. This suggestion is based on a study, examining pregnant reindeers in Svalbard, since the approach for it was effective while avoiding culling of animals (Veiberg et al., 2017). They marked female calves in their first winter and recaptured them each year to check whether they were pregnant by examining the progesterone levels in their blood plasma. The capture-mark-recapture method might be a good approach for examining the change of nutrients in the milk of lactating female chamois.

*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.

*Effect of altitude*

Animals in mountain habitats can try to avoid heat stress by shifting their range to higher elevations where the temperature change is less drastic (Brivio et al., 2019). Indeed, the results from this study were 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. Interestingly, the scaled results from the analysis, showing the contribution of each factor to chamois body weight, pointed out that altitude has a similar effect on body mass, as temperature. A study by Büntgen et al. (2017) showed that chamois, ibex, red deer, and roe deer have been gradually becoming more abundant in higher elevations since 1991 which gives us more thorough insight into large ungulate population dynamics (Fig. 7, Büntgen et al., 2017).

Those findings, combined with our results, suggest that ungulates are expressing such change in behaviour as an attempt to cope with climate change. However, the increased number of ungulates with similar diets who shift their range towards higher elevations may cause problems as the carrying capacity of mountain tops will be reduced. This is a serious issue that might lead to interspecific competition for resources, which might affect the way the whole ecosystem functions.

**Conclusions**

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.

**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. 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.

Böhm R, Auer I, Brunetti M, Maugeri M, Nanni T, Schöner W. 2001. Regional temperature variability in the European Alps: 1760–1998 from homogenized instrumental time series. International Journal of Climatology. 21(14):1779–1801. doi:10.1002/joc.689.

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.

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.

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.

Daufresne M, Lengfellner K, Sommer U. 2009. Global warming benefits the small in aquatic ecosystems. Proceedings of the National Academy of Sciences. 106(31):12788–12793. doi:10.1073/pnas.0902080106.

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. 1998. Selfish mothers: reproductive expenditure and resource availability in bighorn ewes. Behavioral Ecology. 9(2):144–150. doi:10.1093/beheco/9.2.144.

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.

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.

Gobiet A, Kotlarski S, Beniston M, Heinrich G, Rajczak J, Stoffel M. 2014. 21st century climate change in the European Alps—A review. Science of The Total Environment. 493:1138–1151. doi:10.1016/j.scitotenv.2013.07.050.

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, Tveraa T, Stien A, Solberg EJ, Grøtan V. 2020. When does weather synchronize life-history traits? Spatiotemporal patterns in juvenile body mass of two ungulates. Journal of Animal Ecology. 89(6):1419–1432. doi:10.1111/1365-2656.13192.

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.

Jackson MC, Pawar S, Woodward G. 2021. The Temporal Dynamics of Multiple Stressor Effects: From Individuals to Ecosystems. Trends in Ecology & Evolution. 36(5):402–410. doi:10.1016/j.tree.2021.01.005.

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

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.

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.

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.

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.

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.

Reiner R, Zedrosser A, Zeiler H, Hackländer K, Corlatti L. 2022. Habitat and climate shape growth patterns in a mountain ungulate. Ecology and Evolution. 12(3):e8650. doi:10.1002/ece3.8650.

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.

Salewski V, Hochachka WM, Fiedler W. 2010. Global warming and Bergmann’s rule: do central European passerines adjust their body size to rising temperatures? Oecologia. 162(1):247–260. doi:10.1007/s00442-009-1446-2.

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

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.

Spitzenberger F, Bauer K. 2001. Die Säugetierfauna Österreichs. Bundesministerium für Land-und Forstwirtschaft, Umwelt und Wasserwirtschaft. [accessed 2022 Jul 2]. https://scholar.google.com/scholarlookup?title=Die%20S%C3%A4ugetierfauna%20%C3%96sterreichs%2C%20Gr%C3%BCne%20Reihe%20des%20Bundesministeriums%20f%C3%BCr%20Land-und%20Forstwirtschaft%2C%20Umwelt%20und%20Wasserwirtschaft&publicationyear=2001&author=Spitzenberger%2CF&author=Bauer%2CK&author=Mayer%2CA&author=Wei%C3%9F%2CE&author=Preleuthner%2CM&author=Sackl%2CP&author=Sieber%2CJ.

Toïgo C, Gaillard J-M, Van Laere G, Hewison M, Morellet N. 2006. How does environmental variation influence body mass, body size, and body condition? Roe deer as a case study. Ecography. 29(3):301–308. doi:10.1111/j.2006.0906-7590.04394.x.

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.

Tveraa T, Stien A, Bårdsen B-J, Fauchald P. 2013. Population Densities, Vegetation Green-Up, and Plant Productivity: Impacts on Reproductive Success and Juvenile Body Mass in Reindeer. PLOS ONE. 8(2):e56450. doi:10.1371/journal.pone.0056450.

Weeks BC, Willard DE, Zimova M, Ellis AA, Witynski ML, Hennen M, Winger BM. 2020. Shared morphological consequences of global warming in North American migratory birds. Norris R, editor. Ecol Lett. 23(2):316–325. doi:10.1111/ele.13434.

Yom-Tov Y. 2001. Global warming and body mass decline in Israeli passerine birds. Proceedings of the Royal Society B: Biological Sciences. 268(1470):947–952. doi:10.1098/rspb.2001.1592.

**OLD**

Bailey, L. D., & van de Pol, M. (2016). climwin: An R Toolbox for Climate Window Analysis. *PLOS ONE*, *11*(12), e0167980. https://doi.org/10.1371/journal.pone.0167980

Bassano, B., Perrone, A., & von Hardenberg, A. (2003). Body weight and horn development in Alpine chamois, Rupicapra rupicapra (Bovidae, Caprinae). *Mammalia*, *67*(1). https://doi.org/10.1515/mamm.2003.67.1.65

Baumgard, L. H., & Rhoads, R. P. (2012). Ruminant Nutrition Symposium: Ruminant Production and Metabolic Responses to Heat Stress1,2. *Journal of Animal Science*, *90*(6), 1855–1865. https://doi.org/10.2527/jas.2011-4675

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. https://doi.org/10.1098/rspb.2007.0454

Begg, D. P., Kent, S., Mckinley, M. J., & Mathai, M. L. (2007). Suppression of endotoxin-induced fever in near-term pregnant rats is mediated by brain nitric oxide. *Am J Physiol Regul Integr Comp Physiol*, *292*, 2174–2178. https://doi.org/10.1152/ajpregu.00032.2007.-Over

Bergmann, C. (1847). Über die Verhaltnisse der Warmeokonomie der Thierezuihrer Grosse. Gottinger Studien, 3, 595-708.

Böhm, R., Auer, I., Brunetti, M., Maugeri, M., Nanni, T., & Schöner, W. (2001). Regional temperature variability in the European Alps: 1760-1998 from homogenized instrumental time series. *International Journal of Climatology*, *21*(14), 1779–1801. https://doi.org/10.1002/joc.689 25

Brivio, F., Zurmühl, M., Grignolio, S., von Hardenberg, J., Apollonio, M., & Ciuti, S. (2019). Forecasting the response to global warming in a heat-sensitive species. *Scientific Reports*, *9*(1). https://doi.org/10.1038/s41598-019-39450-5

Brügemann, K., Gernand, E., König Von Borstel, U., & König, S. (2012). Defining and evaluating heat stress thresholds in different dairy cow production systems. *Archives Animal Breeding*, *55*(1), 13–24. https://doi.org/10.5194/aab-55-13-2012

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

Chen, I.-C., Hill, J. K., Ohlemüller, R., Roy, D. B., & Thomas, C. D. (2011). Rapid Range Shifts of Species Associated with High Levels of Climate Warming. *Science*, *333*(6045), 1024–1026. https://doi.org/10.1126/science.1206432

Chirichella, R., Stephens, P. A., Mason, T. H. E., & Apollonio, M. (2021). Contrasting Effects of Climate Change on Alpine Chamois. *Journal of Wildlife Management*, *85*(1), 109–120. https://doi.org/10.1002/jwmg.21962

Forchhammer, M. C., Clutton-Brock, T. H., Lindström, J., & Albon, S. D. (2001). Climate and population density induce long-term cohort variation in a northern ungulate. *Journal of Animal Ecology*, *70*(5), 721–729. https://doi.org/10.1046/j.0021-8790.2001.00532.x

Gaillard, J.-M., Festa-Bianchet, M., Yoccoz, N. G., Loison, A., & To¨ıgo, C. T. (2000). *Temporal Variation in Fitness Components and Population Dynamics of Large Herbivores Introduction: Widespread Large Herbivores in Variable Environments*. www.annualreviews.org

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, 61, 56–63.* 26

Gardner, J. L., Peters, A., Kearney, M. R., Joseph, L., & Heinsohn, R. (2011). Declining body size: A third universal response to warming? In *Trends in Ecology and Evolution* (Vol. 26, Issue 6, pp. 285–291). https://doi.org/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. https://doi.org/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. https://doi.org/10.1644/08-MAMM-A-287.1

Gobiet, A., Kotlarski, S., Beniston, M., Heinrich, G., Rajczak, J., & Stoffel, M. (2014). 21st century climate change in the European Alps-A review. *Science of the Total Environment*, *493*, 1138–1151. https://doi.org/10.1016/j.scitotenv.2013.07.050

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. https://doi.org/10.1080/1745039X.2014.950451

Hansen, P. J. (2009). Effects of heat stress on mammalian reproduction. In *Philosophical Transactions of the Royal Society B: Biological Sciences* (Vol. 364, Issue 1534, pp. 3341–3350). Royal Society. https://doi.org/10.1098/rstb.2009.0131

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. https://doi.org/10.1046/j.1439-0310.2000.00579.x

Hetem, R. S., Fuller, A., Maloney, S. K., & Mitchell, D. (2014). Responses of large mammals to climate change. *Temperature*, *1*(2), 115–127. https://doi.org/10.4161/temp.29651 27

Ioset, N. (2020). Recent evolution of chamois weight: Exploring Ticino’s hunting data (Master Thesis). Department of Biology, University of Freiburg, Freiburg

Ioset, N. (2020). *Recent evolution of chamois weight: Exploring Ticino’s hunting data*.

Jackson, M. C., Pawar, S., & Woodward, G. (2021). The Temporal Dynamics of Multiple Stressor Effects: From Individuals to Ecosystems. *Trends in Ecology & Evolution*, *36*(5), 402–410. https://doi.org/10.1016/j.tree.2021.01.005

Klein, D. R. (1965). Ecology of Deer Range in Alaska. *Ecological Monographs*, *35*(3), 259–284. https://doi.org/10.2307/1942139

Knapp, D. M., & Grummer, R. R. (1991). Response of Lactating Dairy Cows to Fat Supplementation During Heat Stress. *Journal of Dairy Science*, *74*(8), 2573–2579. https://doi.org/10.3168/jds.S0022-0302(91)78435-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-Australasian Journal of Animal Sciences*, *32*(9), 1332–1339. https://doi.org/10.5713/ajas.18.0743

Mason, T. H. E., Apollonio, M., Chirichella, R., Willis, S. G., & Stephens, P. A. (2014). Environmental change and long-term body mass declines in an alpine mammal. *Frontiers in Zoology*, *11*(1). https://doi.org/10.1186/s12983-014-0069-6

Mason, T. H. E., Stephens, P. A., Apollonio, M., & Willis, S. G. (2014). Predicting potential responses to future climate in an alpine ungulate: interspecific interactions exceed climate effects. *Global Change Biology*, *20 12*, 3872–3882.

Monteith, K. L., Stephenson, T. R., Bleich, V. C., Conner, M. M., Pierce, B. M., & Bowyer, R. T. (2013). Risk-sensitive allocation in seasonal dynamics of fat and protein reserves in a long-lived mammal. *Journal of Animal Ecology*, *82*(2), 377–388. https://doi.org/10.1111/1365-2656.12016 28

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

Nord, A., & Giroud, S. (2020). Lifelong Effects of Thermal Challenges During Development in Birds and Mammals. *Frontiers in Physiology*, *11*. https://doi.org/10.3389/fphys.2020.00419

Post, E., & Forchhammer, M. C. (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. https://doi.org/10.1098/rstb.2007.2207

Rhoads, M. L., Rhoads, R. P., VanBaale, M. J., Collier, R. J., Sanders, S. R., Weber, W. J., Crooker, B. A., & Baumgard, L. H. (2009). Effects of heat stress and plane of nutrition on lactating Holstein cows: I. Production, metabolism, and aspects of circulating somatotropin. *Journal of Dairy Science*, *92*(5), 1986–1997. https://doi.org/10.3168/jds.2008-1641

Robbins, C. T., & Robbins, B. L. (1979). *Fetal and Neonatal Growth Patterns and Maternal Reproductive Effort In Ungulates and Subungulates* (Vol. 114, Issue 1).

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

Salewski, V., Hochachka, W. M., & Fiedler, W. (2010). Global warming and Bergmann’s rule: do central European passerines adjust their body size to rising temperatures? *Oecologia*, *162*(1), 247–260. https://doi.org/10.1007/s00442-009-1446-2

Scornavacca, D., Cotza, A., Lovari, S., & Ferretti, F. (2018). Suckling behaviour and allonursing in the Apennine chamois. *Ethology Ecology & Evolution*, *30*(5), 385–398. https://doi.org/10.1080/03949370.2017.1423115 29

Sheridan, J. A., & Bickford, D. (2011). Shrinking body size as an ecological response to climate change. In *Nature Climate Change* (Vol. 1, Issue 8, pp. 401–406). https://doi.org/10.1038/nclimate1259

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

Upadhyay, R. C., Singh, S. v., Kumar, A., Gupta, S. K., & Ashutosh, A. (2007). Impact of Climate change on Milk production of Murrah buffaloes. *Italian Journal of Animal Science*, *6*(SUPPL. 2), 1329–1332. https://doi.org/10.4081/ijas.2007.s2.1329

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

Veiberg, V., Loe, L. E., Albon, S. D., Irvine, R. J., Tveraa, T., Ropstad, E., & Stien, A. (2017). Maternal winter body mass and not spring phenology determine annual calf production in an Arctic herbivore. *Oikos*, *126*(7), 980–987. https://doi.org/10.1111/oik.03815

Wharfe, M. D., Wyrwoll, C. S., Waddell, B. J., & Mark, P. J. (2016). Pregnancy Suppresses the Daily Rhythmicity of Core Body Temperature and Adipose Metabolic Gene Expression in the Mouse. *Endocrinology*, *157*(9), 3320–3331. https://doi.org/10.1210/en.2016-1177

World Weather & Climate Information. (n.d.). Climate and average monthly weather in Canton of Ticino, Switzerland. World Weather & Climate Information. Retrieved December 11, 2021, from https://weather-and-climate.com/average-monthly-Rainfall-Temperature-Sunshine-region-canton-of-ticino-ch,Switzerland

Zampronio, A. R., Soares, D. M., & Souza, G. E. P. (2015). Central mediators involved in the febrile response: effects of antipyretic drugs. *Temperature*, *2*(4), 506–521. https://doi.org/10.1080/23328940.2015.1102802 30

Zhao, Z. J., Hambly, C., Shi, L. L., Bi, Z. Q., Cao, J., & Speakman, J. R. (2020). Late lactation in small mammals is a critically sensitive window of vulnerability to elevated ambient temperature. *Proceedings of the National Academy of Sciences of the United States of America*, *117*(39), 24352–24358. https://doi.org/10.1073/pnas.2008974117