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

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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 warming accelerates, many species shift their range or must undergo 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 face climate warming is the change in body size (Salewski et al., 2010; Sheridan & Bickford, 2011). 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 extinctions (Sheridan & 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). The reason behind this response lies in the fact that thermoregulation is directly affected by body size since smaller bodies have a larger surface-area-to-volume ratio, allowing them to shed heat more efficiently (Bergman, 1847, as cited in Gardner et al. 2011).

In large mammals, body mass is an indication of fitness and reproductive success and that is why it is important to understand factors that influence it (Beauplet & Guinet, 2007; Garel et al., 2011). Primarily, in ungulates, a decline in body mass is expected to be most obvious in the early growing stages because they lack proper energy reserves while growing, which makes them sensitive to changing external biotic and abiotic factors (Forchhammer et al., 2001; Rughetti & Festa-Bianchet, 2012). 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).

Alpine chamois (*Rupicapra rupicapra*) are highly polygynous mountain-dwelling ungulates, showing early appearances of sexual dimorphism, with females reaching asymptotic body mass three years earlier (3.5 years) than males (6.2 years) (Bassano et al., 2003; Garel et al., 2009; Hardenberg et al., 2000). Alpine chamois are highly mobile and can shift their range altitudinally, depending on the resource availability and climate conditions (Nesti et al., 2010). Numerous studies have shown that the alpine chamois (*Rupicapra rupicapra)* have been gradually shrinking in size, while the temperatures in the Alps have been increasing (Chirichella et al., 2021; Garel et al., 2011; Mason, Apollonio, et al., 2014). Mountains, such as the Alps, have been identified as climate change hotspots (Turco et al., 2015). 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°C per decade until the middle of the 21st century (Gobiet et al., 2014). 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 key growing periods during the early life of ungulates are the gestation period, lactation period, and juvenile period (Robbins & Robbins, 1979). 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; 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 (Garel et al., 2011; Klein, 1965).

When it comes to research, most papers focus on changes in body size between different sexes in adults (Rughetti et al, 2012; Ioset, 2020), however, there is not a lot of research on the effect of climate change on body size during crucial early life-history stages of alpine chamois. It is still to be discovered whether the ambient temperature during the pregnancy of the mother, the lactation period and the juvenile period influence the growth of chamois. Therefore, this project has an exploratory approach and it will try to fill in those research gaps by finding out exactly which time of the year and during which critical life stage the weight of chamois is most strongly affected by climate change. What is more, we account for altitudinal change of weight, as home range shift of individuals can be closely connected to climate change (Chen et al., 2011). Here, we examine the effect of climate change on the 1.5-year-old alpine chamois in the Swiss Alps from 1992 to 2018.

Methods

Study area

Data were collected from a part of the Alps in the southernmost canton of Switzerland, called Ticino. The study hunting area covers 2700 km^2. The climate in the mountain range is Alpine, with temperatures varying from mean temperatures of -12°C in winter to mean temperatures of 15.5 °C in summer. The hottest and the sunniest month of the year is July with an average maximum temperature of 25°C, measured in the biggest city in the canton Lugano (World Weather & Climate Information, 2021). The area where the chamois were hunted had an altitude varying from 250 to 2700 m asl. Hunting was practiced in seven different districts: Leventina, Blenio, Vallemaggia, Locarno, Riviera, Bellinzona and Lugano (Fig. 1., Ioset, 2020).

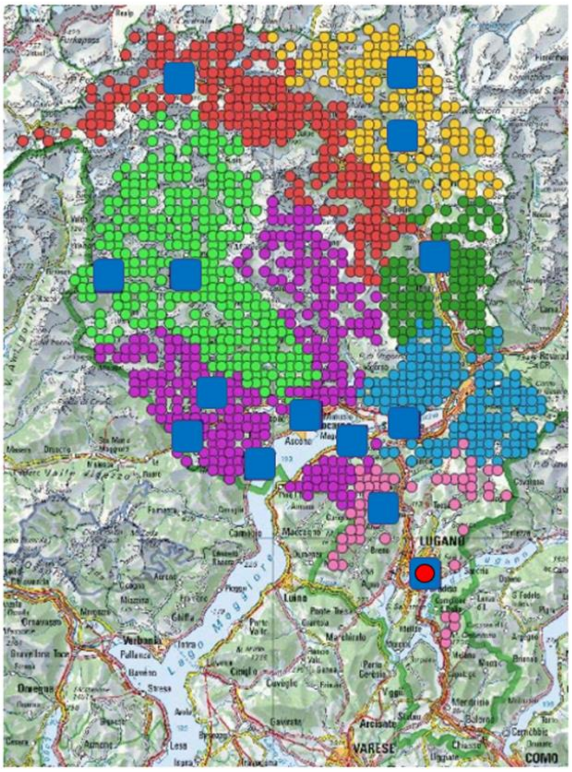

Figure 1. A map showing hunted chamois in the Ticino canton between 1992 and 2018. Different colours represent the seven districts where animals were hunted (red: Leventina,

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 km^2. 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).*

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 (°C) for the years 1970 – 2020 but for the purpose of the study, only measurements of temperatures from 1992 to 2018 were used.

Choice of age group

The target group that was analysed in this study was 1.5-year-old alpine chamois (*Rupicapra rupicapra*). The choice of age group was influenced by the life cycle of chamois and seasonal changes in climate and vegetation. The 1.5-year-old chamois are juveniles who have been feeding on their own for nearly a year. Chamois are usually weaned at 3 to 6 months of age (Scornavacca et al., 2018), therefore by 1 year of age, the chamois are fully grown but still very vulnerable to external abiotic and biotic threats. The original set of data did not contain information about 1-year old individuals and therefore, the next best target group was decided to be the 1.5-year-old individuals. With the decreasing maternal care and increasing grazing behaviour, the change of ambient temperature is expected to affect the survival and the body mass of juveniles a lot more, compared to other age groups.

Hunting records data

The data, analysed in this study were from Ticino hunting bag records from 1992 to 2018. Overall, 34 017 animals were legally shot during the hunting period, which lasted for two weeks in September. The data included animals from the age of 0.5 to 22.5 years old but for the purpose of this study, only a subset of the data was used. The data subset with the target age group (1.5-year-old animals) included information about 7127 individuals. All animals were sexed and weighted (eviscerated). Juvenile chamois have low sexual size dimorphism, compared to adults (Garel et al., 2009, 2011), which might have led to some inaccuracies in the young animals data. Out of the 7127 individuals, 3257 were female and 3870 were male. 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.

Statistical analysis

The statistical programme Minitab was used to create linear models to examine the change of weight of 1.5-year-old individuals and the change of mean ambient temperature throughout the study. The aim was to examine the nature of the relationships. Afterward, it had to be decided which analysis would be the most appropriate one in order to examine whether the mean ambient temperature of the area, where the chamois were shot, is connected to the change in body size.

When it comes to analysing the impact of climate change, the most common method is the use of arbitrary climate periods, which do not always explain the biological response in the best way possible (van de Pol et al., 2016). Sometimes if a trait shows no response to a weather variable, the reason might be a wrong choice of selected period to test when the trait is most sensitive to the predictor. For that reason, the data for this project was analysed via the R package *climwin*, and the function *slidingwin* which detects the exact time window when a biological variable is most strongly affected by climate (van de Pol et al., 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 this *climwin* analysis was to compare the support by the data for competing hypotheses and to formalize them into regression models (van de Pol et al., 2016). To begin with, a baseline model was determined, without the addition of weather effects. The most appropriate approach seemed to be a simple linear model since the weight of the 1.5-year-old chamois was equally distributed. The weight was analysed in relation to sex and elevation, so the resulted baseline model was baseline = lm(weight ~ sex + altitude, data = data).

Following this, a candidate model set was created by including the weather variable of interest. The choice of variable for this study was mean ambient temperature (°C). 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, and therefore, it was assumed that all individuals share the same weather window. The reference day was chosen, by picking the last day in September, during which any individuals were shot (September 24th). In addition, it was tested whether the relationship between weight and temperature can be nonlinear so both linear and quadratic response curves were included.

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)

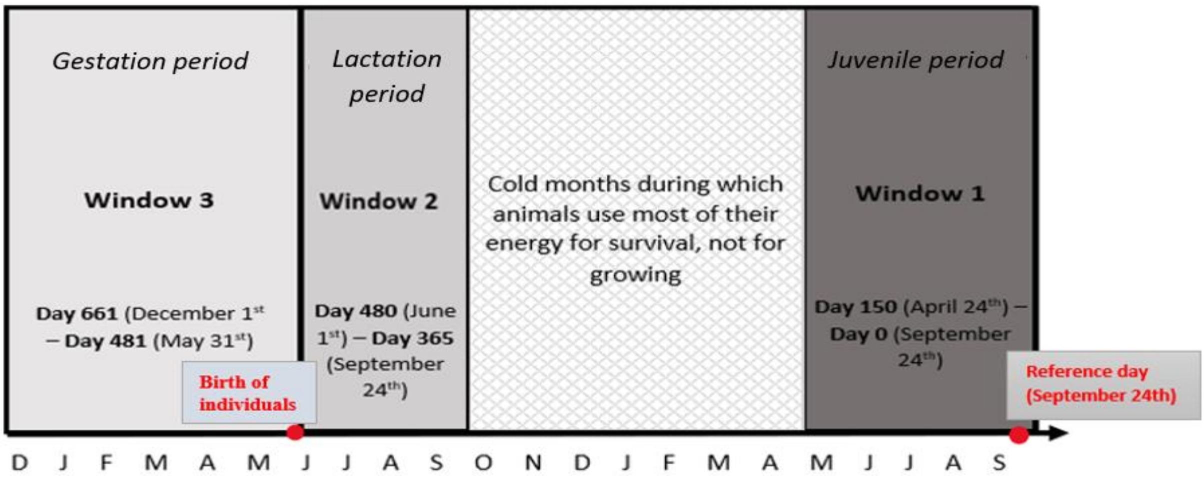

Figure 2. A graph that explains the choice of critical time windows to test in the *climwin* analysis and how they relate to time (days) according to the reference day (24th of September).

Window 1 (Juvenile period)

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)

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)

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 ($R^2 = 3.72\%$). 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 °C per year (±0.009°C, t-value = 3.10, $P = 0.002$), with a total increase of 0.77 °C 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.

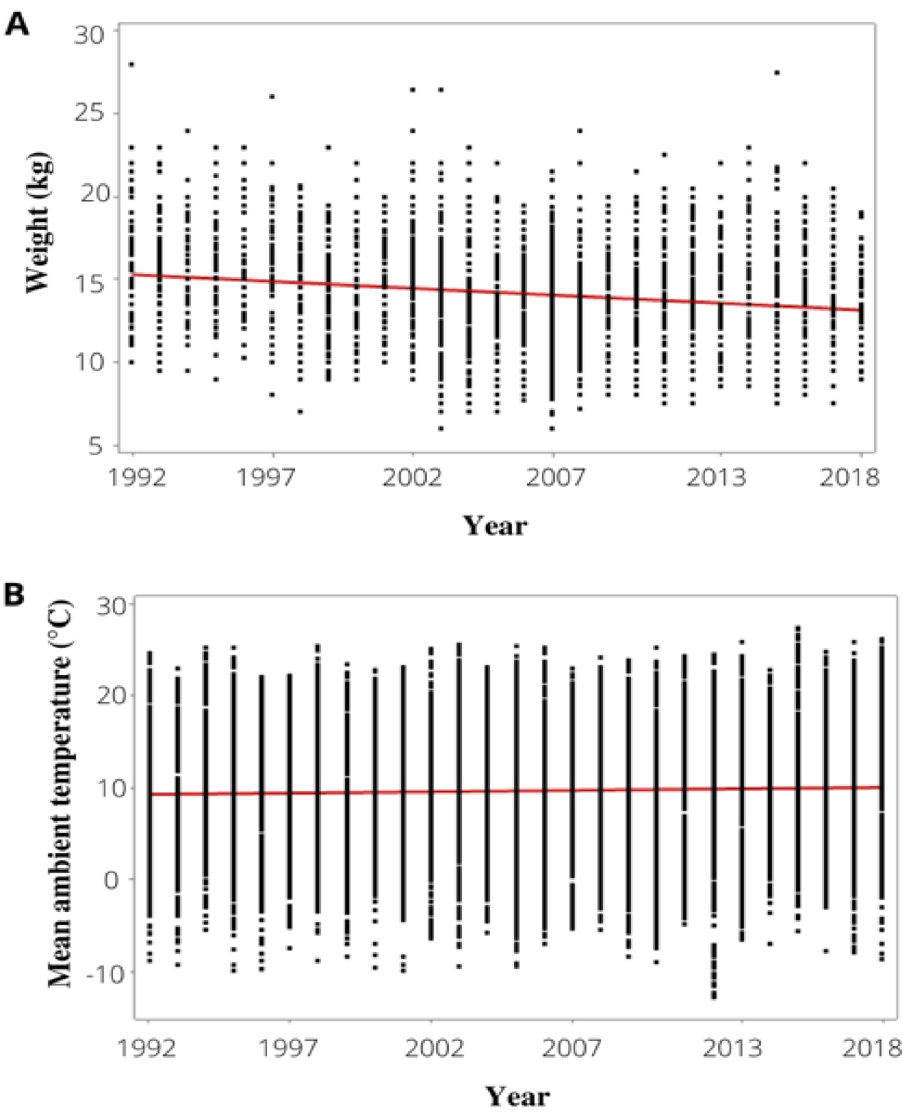

Figure 3. **(A)** The graph represents the change of weight (kg) of 1.5-year-old chamois Rupicapra rupicapra (N=7127) over the years 1992-2018. Each point represents data from a different individual, equation: Y = 178.88-0.08213X. **(B)** Change of mean ambient temperature °C over the whole period of the study, equation: Y = -49.8 + 0.02965X

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 absolute time window with 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.

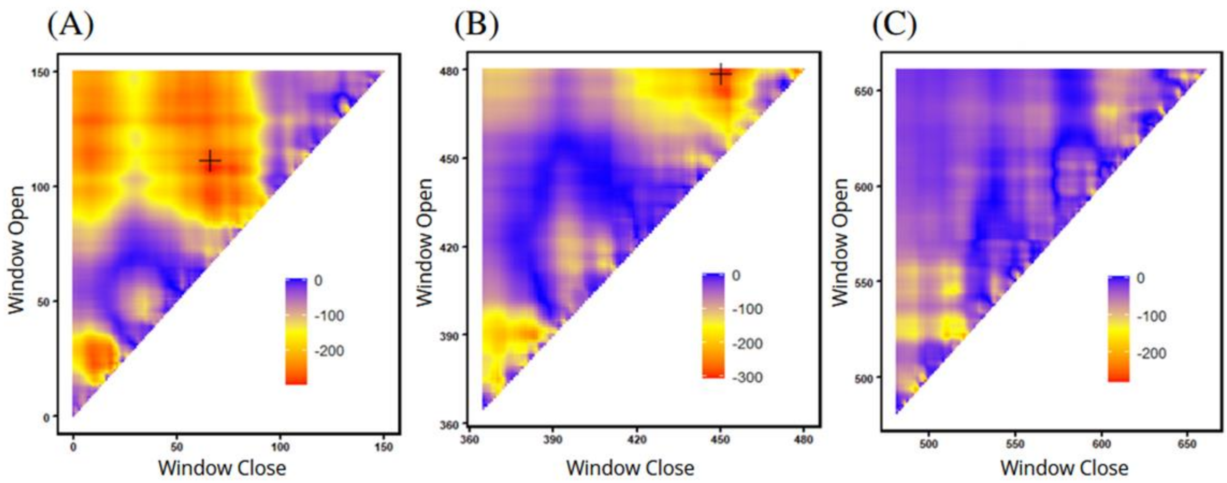

Figure 4: Illustration of the visual output of the *climwin* analyses. Those panels show the model (ΔAICc) for all fitted time windows tried, shown for each combination of Window open (y-axis) and Window close (x-axis) for juvenile period **(A)**, lactation period **(B)** and gestation period **(C).** Models with the lowest ΔAICc (red) are the best supported (colours show the ΔAICc levels compared to the null model. Strongly supported windows will often be grouped together.

	Function	DeltaAICc	Window Open	Window Close	Window Length (days)
Juvenile	linear	-259.06	Day 94 (**June 22**)	Day 79 (**July** 7)	15
	quadratic	-297.71	Day 108 (**June 8**)	Day 66 (**July 20**)	42
Lactation	linear	-193.38	Day 466 (**June 15**)	Day 449 (**July 2**)	17
	quadratic	-305.69	Day 480 (**June** 1)	Day 452 (**June 29**)	28
Gestation	linear	-192.02	Day 493 (**May 19**)	Day 492 (**May 20**)	1
	quadratic	-279.29	Day 498 (**May 14**)	Day 498 (**May 14**)	0

Table 1**.** The table shows the ΔAICc values, Window Open and Window Close for the best fitted climatic periods for the three life stages (Juvenile, Kid and Gestation) of alpine chamois *Rupicapra rupicapra*, as well as the length of the windows.

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

The *climwin* analysis was continued by furter 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). Furhermore, it looks like with increase of elevation, the weight of individuals also increases (Fig. 6B). Nontheless, 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 °C before the reach of plato, followed by a slight increase of weight.

Coefficients	Estimate	Standard Error	P-value
Intercept	13.529	0.063	<0.005
Sex (male)	0.532	0.071	<0.005
Altitude	0.486	0.035	<0.005
Juvenile stage	-0.403	0.051	<0.005
Juvenile stage^2	0.207	0.028	<0.005
Kid stage	-0.473	0.051	<0.005
Kid stage^2	0.185	0.027	<0.005

Table 2**.** The table shows the relative contribution of each factor (sex, elevation, juvenile stage and lactation stage) to the change of weight of chamois, as well as SE and p-values. The values for altitude, juvenile and lactation stage were scaled to ease the comparison of values.

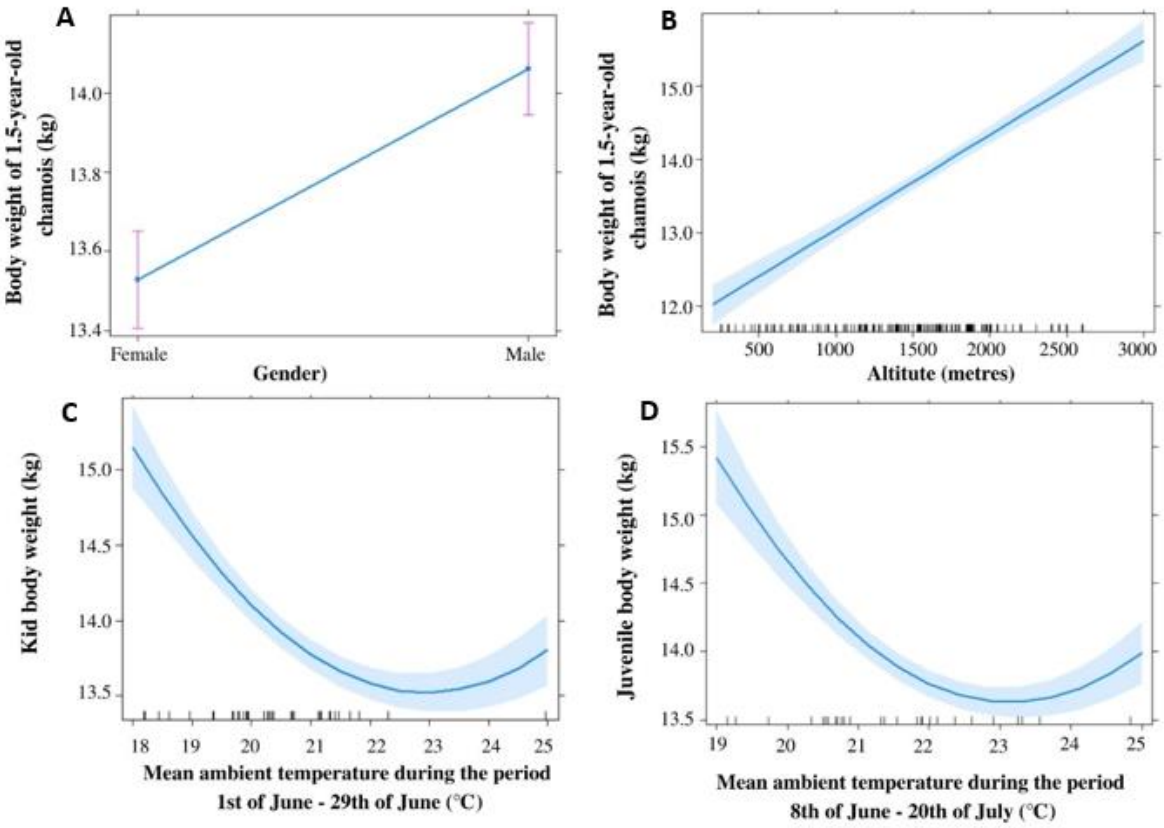

Figure 6. **(A)** A graph representing the difference between the mean body weight (kg) of 1.5-year-old female and male chamois. **(B)** The effect of altitude on the body weight (kg) of 1.5-year-old chamois. **(C)** The effect of mean ambient temperature (°C) for the best climatic window for Lactation life stage of chamois, during which weight of kids was most strongly affected by climate, over the course of the study (1992 – 2018). **(D)** The effect of mean ambient temperature (°C) for the best climatic window for Juvenile life stage of chamois, during which weight of individuals was most strongly affected by climate, over the course of the study (1992 – 2018).

Discussion

The results from this study showed that the body weight of Alpine chamois (*Rupicapra rupicapra)* 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.

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. Furhermore, 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.

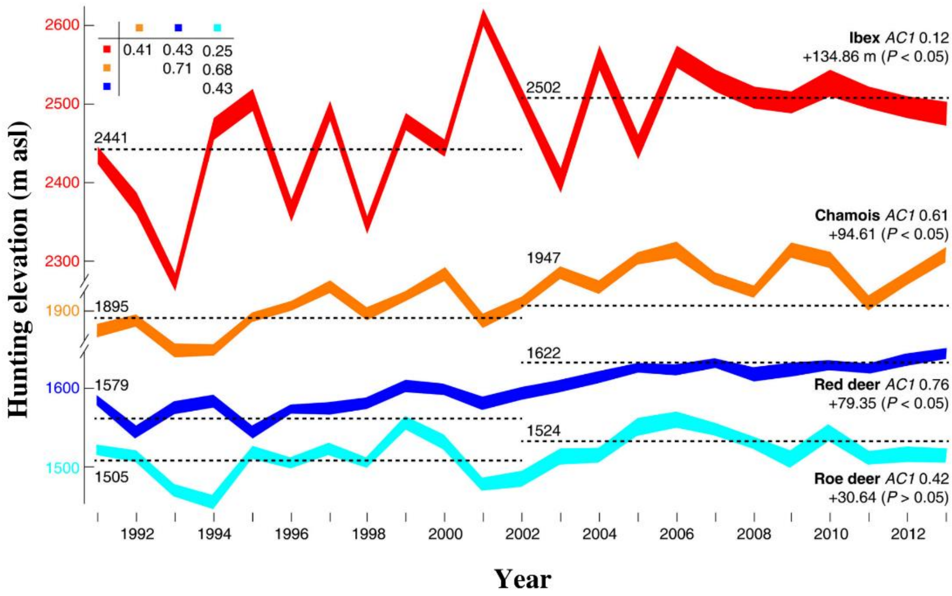

Figure 7. Annual variation in mean harvest elevation (±1 standard error as independently calculated each year from 1991 to 2013) of 17,637 ibex, 85,306 chamois, 68,588 red deer, and 59,034 roe deer, with the horizontal dashed lines referring to early/late split period means (≤/≥ 2002 to ensure equal window length). *Adapted from (Büntgen et al., 2017)*

Conclusion

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.

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