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

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**Abstract**

Climate change has been hypothesised to be partly driving the change in size observed in numerous species. We investigated the body mass changes of 5635 yearling Alpine chamois (*Rupicapra rupicapra*) harvested in September at 1.5 years of age in the Swiss Alps (Ticino canton) in relation to temperature from 1992 to 2018. Yearling chamois shrank by 2.97kg while temperatures between May and July raised by 1.7°C. Warmer temperatures were associated with slower growth, with two periods having the strongest impact on the growth of chamois: birth and early lactation (May 9th - July 2nd) and, to a lesser extent, the summer (May 2nd until July 21st) previous to the harvest. Finally, analysing year-detrended mass and temperature data strongly supports the hypothesis that the increases in temperature during growth are responsible for the decrease in body mass of yearling chamois. Altogether, our results suggest that the rising temperatures in the Alpine regions could have significant consequences on the ecology and evolution of wild ungulates.

**Introduction**

As global changes induced by human activities accelerate, many species are undergoing phenotypic changes to adapt to their new environment [1], with changes in their distribution and abundance, phenology, and morphology. One frequently reported response to climate warming is the change in animal body size and shape [2–4] since morphology has consequences on thermoregulation [5]. Indeed, a shrinking in body size leads to a larger surface-area-to-volume ratio, which allows animals to dissipate heat more efficiently in warmer environments (Bergman rule; [6]). In addition, global warming is likely affecting body size through food availability and quality changes [7]. Heat dissipation and nutrition are likely driving the phenotypic responses observed in free-living animals jointly [2]. This might be especially true in mammals where ambient temperature and the ability to dissipate heat have been demonstrated to constrain maternal milk production and offspring growth [5,8].

In vertebrates with finite growth (like mammals and birds), the size that an individual reaches as an adult has critical consequences for reproductive success and overall fitness [9]. As the adult size and mass are primarily determined by early growth conditions and juvenile size (e.g., [10]), it becomes fundamental to investigate the effect of climatic conditions on the juvenile size [11]. Juveniles usually have low energy reserves and have to allocate a substantial amount of those reserves to growth [12,13]. Therefore, a decline in adult size is to be most evident in the early growing stages because they lack reasonable energy reserves, which makes them sensitive to changing external biotic and abiotic factors [14–16]. In mammals, early growth is divided into three phases: in utero, lactation, and post-weaning. The three phases are, however, not equally sensitive to climate warming. The in-utero phase is likely the less sensitive as offspring live in a stable thermal environment. In contrast, the lactation phase is likely the most sensitive, as offspring growth in size is the fastest during lactation and mother milk production is constrained by ambient temperature [5,8]

Here, we investigated the effect of climate change on changes in yearling size (i.e., 1.5 years of age) of Alpine chamois (*Rupicapra rupicapra*) using hunting data collected in the southern Swiss Alps from 1992 to 2018. The Alpine chamois is the most abundant ungulate of the European Alps [17], and its morphology and physiology are adapted to high-altitude (cold) environmental conditions [18]. Accordingly, most previous studies on the Alpine chamois have revealed a gradual shrinking in chamois body mass both in adults [16] and in juveniles [21,22] in the southern Alps. A recent study, however, did not find any change body mass or size in chamois and three other ungulate species in the eastern Alps [23], study region adjacent to ours. Although studies reporting a change in chamois body size have generally identified the critical period as the spring-summer temperatures over the first two years of life [16], no study has tried to precisely identify which time window during early life is most sensitive to climate warming and whether the shrinking in body size over time is associated with an elevation of temperature during this critical time window.

**Methods**

*Study system*

The Alpine chamois is an ungulate that shows early appearances of sexual dimorphism, with females reaching asymptotic body mass three years earlier (3.5 years) than males (6.2 years) [24–26]. In the Alps, chamois give birth in May [27] . Between May and July is the main period of lactation for kids (the young of chamois) and of increase in body mass for yearlings. Chamois are then weaned between 3 and 6 months of age [28]. Vegetation in the Alps usually begins growing right after snowmelt in April, peaking in July, thus providing an abundant and protein-rich food source for a relatively brief period of time [29]. Alpine chamois are distributed over a broad altitudinal range (500–3100 m; [30,31]) and can shift their range depending on the resource availability and climate conditions [22,32].

Data on the size of chamois were collected in the southern Alps of Switzerland (canton Ticino) and consist of records of the hunting bags from 1992 to 2018. The study area covers an area of 2700 km2 with an altitude varying from 250 to 2700 m asl. In Ticino, hunting starts at the beginning of September and the harvest plan is mainly completed within three weeks. All animals were sexed, aged and weighed (eviscerated). Hunters estimated age by counting the growth rings of their horns [33]. Overall, 34017 animals were harvested during the hunting period (age range: 0.5-22.5 years old). We analysed yearling data (1.5-year-old, 5635 individuals, 2491 females and 3144 males) to cover this species fastest period of growth [26]. By September, yearlings have been feeding on their own for nearly a year, but they are still vulnerable to external threats due to the decrease in maternal care and increased active grazing behaviour.

Daily mean ambient temperature (℃) from 1990 until 2018 (all the years needed for the analysis) was obtained from a Swiss meteorological station in the city of Lugano (273 m asl), in close proximity to the harvesting area. Other stations at higher altitudes inside the study area did not include all years needed, but have high correlation values with the station of Lugano (all Pearson r > 0.8).

*Statistical analysis*

As the use of arbitrary climate periods does not always explain the biological response in the best way possible [34], we investigated the variation in yearling body mass in relation to the variation in mean ambient temperature using the package *climwin* [36] in R v4.2.1 [35]. This package allows the detection of the exact time window when a biological variable is most strongly affected by an environmental variable. Further details on the analysis are provided in the electronic supplementary material 1.

The overall approach for the *climwin* analysis is to compare the support of the data for competing hypotheses and to formalise them into regression models [34]. Competing models are based upon a baseline model (not including weather effects) and ranked using the ΔAICc (difference in terms of the Akaike Information Criterion values calculated for a small sample size between the baseline model and the model of interest). Our baseline model was a linear model with the body mass of the yearling chamois in relation to sex and elevation. The function *slidingwin* creates a set of competing models testing windows of different lengths for the weather variable of interest (in this study the mean daily ambient temperature). Non-linear effects of temperature on body mass were investigated by testing for linear and quadratic trends. As parameters in *slidingwin*, we set an absolute time window with as reference day the September 24th (last date of harvest). We looked for windows between the reference dayand 661 days before (December 1st of 2 years before) to include the critical periods in a young chamois life: gestation, lactation, first winter and yearling. When the first window was found, we included it in the baseline model and re-run a *slidingwin* analysis to look for additional windows affecting body mass independently to our first window. Finally, we ran year-detrended analyses to demonstrate that year is not confounding the relationship between body mass and temperature [37]. We extracted the residuals of linear regressions between mass and year and between temperature and year. We then checked the linear regression between the residuals of the body mass and the residuals of the temperature.

**Results**

The final model included an effect of the sex of the individual, altitude and a quadratic effect of mean temperature between days 503 and 449 and between 145 and 65 from the reference day (24th September; Table 1 and Supplementary Materials 1). These climate windows are independent (Pearson’s test: cor = 0.24, t = 1.24, df = 25, p = 0.23) and equivalent to the period from May 9th until July 2nd of the year the individual is born and to May 2nd until July 21st of the year the animal was harvested. Most importantly, chamois body mass was lower with a higher average ambient temperature in the two best climatic windows (Table 1, Fig 1a,b). Yearling chamois were heavier when harvested at higher altitudes than at lower altitudes (Table 1, Fig 1c) and males are heavier than females (EMMs ± SE, males: 14.2 ± 0.05, females: 13.6 ± 0.06; Table 1).

Over the course of the study, the mean temperature between May 2nd and July 21st (which encompasses our 2 climatic windows) increased by 0.06 °C per year (± 0.02 °C, T-value = 2.9, P = 0.007; Fig. 2a), leading to a 1.7°C increase in 27 years. On the other hand, the mean body mass of 1.5-year-old chamois decreased by 0.112 kg per year (± 0.006 kg, T-value = -17.81, P < 0.001; Fig. 2b), leading to an overall decrease in average mass of 2.92 kg during the years of the study. The analysis of year-detrended temperature and yearling body mass data show a significant positive association between mean temperatures between May 2nd and July 21st and yearling body mass (STATS; Fig. 2c).

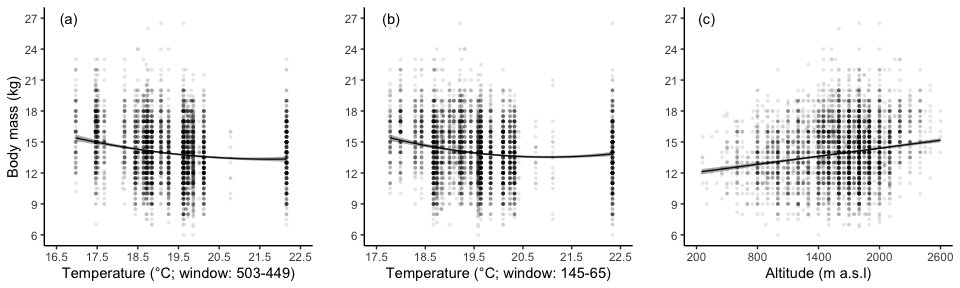
**Table 1**

Results of the linear model showing the quadratic effect of annual average temperature (°C) between May 9th and July 2nd of the birth year (window: 503-449) and between May 2nd and July 21st of the harvest year (window: 145-65), harvest elevation (m a.s.l.), and sex (Males vs Females) on body mass (kg) of harvested 1.5-year-old Alpine chamois. No. of observations: 5635 in 27 years.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| *Predictors* | *Estimate* | *SE* | *t* | *p* |
| Intercept | 11.867 | 0.153 | 77.775 | **<0.001** |
| T (window: 503-449) | -31.948 | 2.581 | -12.378 | **<0.001** |
| T (window: 503-449) ^2 | 14.294 | 3.262 | 4.382 | **<0.001** |
| T (window: 145-65) | -22.150 | 3.090 | -7.168 | **<0.001** |
| T (window: 145-65) ^2 | 21.821 | 2.787 | 7.829 | **<0.001** |
| Harvest elevation | 0.001 | 0.000 | 14.307 | **<0.001** |
| Sex [M] | 0.496 | 0.069 | 7.191 | **<0.001** |

**Figure 1**

Relationship between body mass (kg) of harvested 1.5-year-old Alpine chamois and the average temperature (°C) (a) between May 9th and July 2nd of the previous year and (b) between May 2nd and July 21st of the harvest year, and (c) altitude (m a.s.l.). Each dot is one observation (darker dots represent a higher number of observations); fitted lines in (a) and (b) are shown with 95 % confidence intervals (shaded areas).

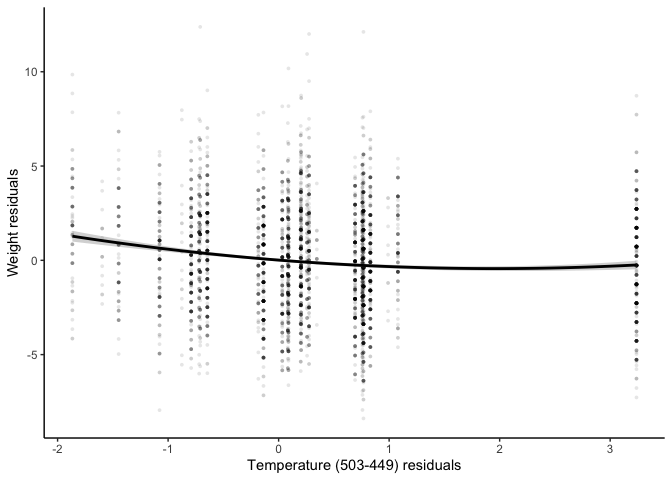


**Figure 2**

Yearly trend of (a) the average temperature (°C) between May 2nd and July 21st and (b) body mass (kg) of harvested 1.5-year-old Alpine chamois between 1992 and 2018, and detrended relationship between the residuals of the body mass and of the temperature (c). Each dot is one observation (darker dots representing a higher number of observations in (b)); fitted lines are shown with 95% confidence intervals (shaded areas).

Chart, scatter chart

Description automatically generated



**Discussion**

Here we showed a marked decrease in body mass of yearling chamois in relationship to an increase temperature during a critical time for their growth. Our results indicated a decrease in body mass of almost 3kg and an increase in the mean ambient temperature of ca. 1.7°C between late spring and early summer during this 27-year study (1992-2018), supporting what found in adults and yearlings [16,21,22]. We assessed that the temperatures during late spring and early summer around chamois birth and lactation and when they are 1 year of age, are crucial for chamois development. Our study supports the hypothesis that spring-summer temperatures are more critical than winter temperatures regarding phenotypic changes in seasonal environments [11,38], but make a further step by revealing that the critical period for chamois growth.

Climate change can affect chamois growth in several ways. First, by influencing the phenology of the plants they feed upon, births of chamois no longer coincide with the highest peak of vegetation growth as a result of the rising temperatures [39]. The lack of resources for the mother during the lactation period might influence the energy she invests into nursing, which may affect the kid’s growth. Furthermore, it has been suggested that fast phenological adaptation to this change is unlikely, as annual birth peaks of herbivores are mainly influenced by day length, not by the availability of resources [40]. Second, ambient temperature can strongly influence the nutrient intake of yearling chamois during growth both by altering the feeding activity [21] of young and adults. During heat days, chamois have been shown to reduce heat-generating activities (including foraging), likely in an attempt to avoid thermal overload [7]. Third, climatic conditions may affect the body reserves of mothers, which in turn can affect the offspring growth during gestation [41] and lactation. Ambient temperature can also directly affect the quantity and quality of milk production [42], with a temperature increase linked to a negative effect on milk yield in domesticated ungulates [43,44]. Furthermore, climate change can also affect milk composition, with a significant decline in milk protein and fat content [45,46].

Overall our results support previous studies stating the importance of climatic conditions for growing ungulates at high elevations and latitudes [14,16,22]. At high altitudes, in particular, animals can try to avoid heat stress by shifting their range to higher elevations [7] or eat during the night [47]. Several large ungulate species have already been gradually becoming more abundant at higher elevations in the past 30 years [48]. Indeed, our results are consistent with previous results, as they show that yearling chamois who were harvested at higher elevations, and thus, colder environments, have heavier body mass than the ones living in lower elevations. These findings, combined with our results, suggest that ungulates are expressing such changes in phenotype to cope with warming spring and summer temperatures. Still, it remains to be understood if this body size change will be revealed as detrimental to surviving the harsh wintering conditions at high elevations.

Our results show a phenotypic change in a wild ungulate population that could lead to changes in life-history traits with significant consequences for the species population dynamics. Body size is a fundamental determinant of individual survival and reproduction (e.g., [50–53]) and the warming climate could therefore act as a selective pressure with long-term effects [54]. Further studies should monitor populations using long-term projects with marked individuals [55] to better investigate the ecological and evolutionary consequences of body size change in ungulates.

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**Data accessibility**

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

**Authors' contributions**

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

**Competing interests**

We declare we have no competing interests.

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