Climate drives body mass changes in a mountain ungulate: shorter winters lead to heavier Alpine ibex

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Introduction

The European Alps have undergone rapid climate and environmental changes since the beginning of the 20th century, including a mean annual temperature increase of
more than 1.5°C (Rebetz and Reinhard 2008), nearly double the average increase in the Northern Hemisphere (Foster and Rahmstorf 2011). The increase in temperature has been accompanied by a substantial reduction in snow cover (Gottlieb and Mankin 2024), caused by fewer days with snowfall, thinner mean snow depth and faster snowmelt, increasing the snow-free period by about 10 days decade⁻¹ (Matiu et al. 2021, Vitasse et al. 2021). Warmer temperatures and reduced snow falls are expected to strongly affect mountain ecosystems (Rogora et al. 2018). For example, warm spring temperature and reduced snow cover affect plant growth (Wang et al. 2020), changing the quantity and timing of resources available for herbivores (Pettorelli et al. 2007). In the Alps, the phenology of herbaceous plants has advanced by an average of 5 days decade⁻¹ over the last 30 years (Vitasse et al. 2021). Research on how these changes affect animal communities has produced conflicting results, suggesting complex dynamics and likely interactions between multiple climate and ecological variables. It is also likely that effects differ according to which physical trait is considered. For example, while horn growth of Alpine ibex *Capra ibex* appears to be increasing under climate change (Büntgen et al. 2014), body size of another Alpine ungulate, the chamois *Rupicapra rupicapra*, is instead decreasing (Ruggetti and Festa-Bianchet 2012, Mason et al. 2017). Both results are linked to increased spring temperature and consequent earlier growth of vegetation, but the effects are opposite for the two traits. Climate models for the Alps predict warmer temperatures, lower summer precipitation and a higher frequency of extreme events (Rajczak and Schär 2017, Hodnebrog et al. 2019). The snow-free period will continue to increase, through a reduction of snow depth and snow cover, particularly during spring (Gobiet et al. 2014). A better understanding of the effects of these environmental changes on mountain species and ecosystems is therefore paramount for their conservation (Rogora et al. 2018).

Most mountain ungulates are capital breeders living in a strongly seasonal environment. During winter they rely on body reserves and low-quality forage, and incur high thermoregulatory costs (Signer et al. 2011), usually resulting in substantial loss of body mass (Apollonio et al. 2020). Consequently, they rely on resources available during the short summer to accumulate fat reserves for overwinter survival and for reproduction. Environmental variability can have both direct and indirect effects on body condition of mountain ungulates. Indirect effects are mostly caused by resource availability that can be influenced by temperature and precipitations (Pettorelli et al. 2005). Direct effects include thermoregulatory costs, imposed by both cold (Signer et al. 2011) and warm temperatures (Zhou et al. 2022) and changes in activity patterns, for example foraging (Mason et al. 2017) or space use (Büntgen et al. 2017, Herfindal et al. 2017).

Survival of adult herbivores is typically less affected by environmental conditions than survival of juvenile or senescent individuals (Toigo et al. 2007, Bergeron et al. 2022). Changes in body condition driven by environmental variability, however, can affect reproductive success of all sex-age classes. Resource availability during spring and summer is usually considered as the crucial factor affecting body mass (Parker et al. 2009). In temperate environments, however, stored body reserves and access to forage during winter can also affect body condition and reproductive success (Pettorelli et al. 2005, Albon et al. 2017). For female mammals, the most energetically demanding times are early spring to mid-summer, during late pregnancy and lactation (Parker et al. 2009). For males, the costliest time is the rut, that in temperate ungulates usually occurs in late autumn and early winter, well after the peak in availability of nutritious forage (Mysterud et al. 2004). Indeed, male ungulates usually lose more mass during winter compared to females (Apollonio et al. 2020) and suffer higher mortality when resources are limited (Barret 1982). Often, winter mortality is driven by body conditions (Denryter et al. 2022). Poor body condition in autumn and a large mass loss during winter could therefore compromise survival and reproductive success and consequently affect population dynamics.

Despite multiple studies, it remains unclear how seasonal variation in resource availability affects body mass of temperate ungulates under climate change. The effects of warmer temperatures on body condition and population dynamics of ungulates in temperate climates are often contrasting. The NAO (North Atlantic Oscillation), a large-scale climatic index linked to local temperature, precipitations and snow depth, positively affected summer body mass in red deer *Cervus elaphus* and domestic sheep *Ovis aries* in Norway but a strongly seasonal environment. During winter they rely on body mass of males would be important to quantify. In species
with strong sexual dimorphism and polygynous mating systems, such as most mountain ungulates, body conditions can strongly influence access to reproduction with cascading effects on population genetics, such as effective population size (Frankham 1995) and, ultimately, on population dynamics (Bozutto et al. 2019).

The Alpine ibex is a good model to study the effect of environmental variations on body condition and growth. The species shows strong sexual segregation and high sexual dimorphism. Males can weigh up to 120 kg, more than twice the mass of females (Brambilla et al. 2022a). Similarly to other mountain ungulates in temperate climates, Alpine ibex rut during winter (December–January) and show strong seasonal mass changes. In addition, Alpine ibex have a long period of growth. Maximum body size in females is reached at around five years (Toigo et al. 2002), but males keep gaining mass until 10–12 years (Brambilla et al. 2022a). Male Alpine ibex also have an unusual age-specific survival pattern compared to most other ungulates: after the first winter, yearly survival rate remains very high until 10–11 years, then rapidly declines (Toigo et al. 2007). The effects of climate change on this species are not clear: adult survival of both sexes seems to decrease during winters with deep snow (Jacobson et al. 2004). On the other hand, Pettorelli et al. (2007) found that reduced snow cover and rapid spring vegetation growth reduced juvenile survival. In addition, warming temperatures are expected to reduce time spent foraging as a behavioural thermoregulatory response (Mason et al. 2017, Brivio et al. 2019).

Here we analyze a unique long-term data series of repeated body mass measurement of individual wild Alpine ibex in Gran Paradiso National Park (GPNP, in the north-western Italian Alps) to investigate whether climate change affected male body mass over the last two decades and which factors influenced seasonal body mass changes. We first tested whether autumn body mass and seasonal mass changes of male Alpine ibex had changed over 23 years, between 2000 and 2022. Second, we used structural equation modelling (SEM) (Shipley 2009) to investigate direct and indirect relationships between environmental and phenological variables and body mass. We predicted that winter mass change directly affects body mass at the end of the following summer and hence that winter and early spring environmental conditions influence autumn body mass.

Data collection

Male Alpine ibex were weighed on a platform scale baited with salt (Bassano et al. 2003). Marked males were repeatedly weighed each summer from 2000 to 2022 from late May/early June to mid-August or September (Toigo et al. 2007). Mean ± SD longevity of males in the study area was 10.9 ± 2.7 years and did not change over the study (11.5 ± 2.5 for animals born in 1987–2000, and 10.2 ± 2.7 for animals born in 2000–2015).

Data analysis

All data handling and analyses were performed in the R environment (www.r-project.org).

Body mass

To obtain comparable measures for each animal each year, repeated individual body mass measurements were analysed with a linear mixed effects model (R library ‘lme4’, Bates et al. 2015) with a quadratic effect of age, a linear effect of the square root of days since 1 May as predictor variables (Martin and Pelletier 2011) and individual identity as a random effect, with each individual having random intercept and slope. The square root of measurement date linearized
the relationship between body mass and date, accounting for asymptotical summer mass gain (Douhard et al. 2018). A separate model was built for each year of data collection. From each model, we extracted spring and autumn body mass for each individual and calculated seasonal mass changes. Spring body mass was that predicted by the model on 1 June and autumn body mass was that predicted on 1 September. Absolute summer mass change was calculated as the difference between autumn and spring mass of the same year and absolute winter mass change as the difference between spring mass of a given year and autumn mass of the previous year (Fig. 1). To better quantify changes in body conditions independently of size we also calculated relative (%) mass changes in winter and summer as the percentage change in mass relative to the starting mass of each season. Unless otherwise stated, absolute mass changes (referred to in the text as mass changes) were used in analyses.

Density

Censuses were conducted every year during the first week of September by the personnel of Gran Paradiso National Park using block-counts over the entire park (Jacobson et al. 2004, Mignatti et al. 2012). To measure ibex density in the study area we used the total number of individuals counted in the surveillance area of Levionaz.

Weather variables

Snow depth, temperature and precipitations from 1962 to 2022 were gathered from a meteorological station (Iren S.p.A.) near Lake Serrù at 2240 m a.s.l., approximately 10 km from the study area. The same dataset was previously used for studies of population dynamics of Alpine ibex in Gran Paradiso (Jacobson et al. 2004, Mignatti et al. 2012). Daily values were

Figure 1. Seasonal changes in body mass of Alpine ibex, vegetation phenology and weather. Top: measures used to estimate spring (1 June) and autumn (1 September) body mass and seasonal mass changes. Points are raw mass measurements of ibex V1SL, aged 7–9 years in 2015–2017. Male ibex gain and lose mass seasonally but also increase in size and gain mass until 10–12 years of age. The second box shows seasonal changes in NDVI from 1 June 2015 to 31 December 2017, and the measures used to calculate the vegetation phenology variables (OS = onset of spring). For representation purposes, all grassland pixels (both at low and high altitude) were used to describe NDVI changes over time. The third box shows the weather variables calculated for different seasons and the date of the census used to measure density (1 September). The seasonal subdivision to calculate weather variables, body mass and mass changes is provided in the bottom box.
aggregated into seasonal measures with seasons based on the movements of ibex in the study area (Brambilla et al. 2022) (Fig. 1). Seasons were thus defined as November–March (winter), April–May (spring), June–August (summer) and September–October (autumn). For each year, we calculated spring and summer average precipitation, minimum and maximum temperature and winter snow (average daily snow depth, day of first snow during winter, day of snow melt and length (days) of snow cover). After checking for correlations among independent variables and based on our hypothesis, spring and summer average precipitation, spring and summer maximum temperature and winter average daily snow depth were used for further analysis. Correlations between meteorological variables as well as visualization of long-term temporal trends of variables not included in the analysis are provided as Supporting information. Linear regressions as a function of year were performed to visualize temporal trends in weather variables over the same time frame of the study (2000–2022) and over the longer term (1962–2022, only presented in the Supporting information).

Vegetation phenology

To describe vegetation phenology, we used optical satellite images extracted from MODIS data (sensor TERRA, NASA LP DAAC 2014) available since 2000. MODIS data are particularly useful for seasonal time series analysis because of their daily temporal resolution. Their coarse spatial resolution (250 m) is in our case sufficient to capture a clean signal of the surface of interest, since several pure pixels covering homogeneous grasslands are available. NDVI images were downloaded as raster files including the entire Gran Paradiso National Park over the study period (2000–2022) using the ‘MODISstp’ package (Busetto and Ranghetti 2016) and choosing the collection MOD09Q1, which provides composite NDVI images for 8-day periods where each pixel contains the best possible observation during the 8-day period, selected based on high observation coverage, low view angle, absence of clouds or cloud shadow and aerosol loading. Each raster file was assigned to the fourth day of its 8-day period. The images were further processed as suggested by Ranghetti et al. (2016): we first selected only grassland pixels from Corine Land Cover (© European Union, Copernicus Land Monitoring Service 2018, European Environment Agency EEA). To increase the resolution of the raster files and improve the selection of grassland pixels, we divided each pixel in 4, assigning to each sub-pixel the same value as the original larger pixel (using the ‘disaggregate’ function with factor n = 2 in ‘raster’ R package). To obtain homogeneous time series and daily values, for each selected pixel we then smoothed the time series for each year of the study with a spline interpolation (using ‘npreg’ R package (Helwig 2022) and selecting the smoothing parameters with generalized cross validation method and n = 10 knots).

From each pixel time series for each year, we finally extracted the four metrics described below and in Fig. 1.

- NDVI maximum value (NDVI max): maximum value of NDVI reached for each year. NDVI max was calculated for the area at high altitude as, at the time of the peak in NDVI, ibex had moved to high altitude pastures.
- Day of NDVI maximum value (day NDVI max): the date of maximum NDVI value at high altitude, considered as a proxy for seasonal peak in vegetation fresh biomass and quality. NDVI max and day NDVI max were not added as covariates in the analysis but were used to calculate the length of the green-up period experienced by Alpine ibex considering their altitudinal migrations.
- Onset of spring (OS): the day when NDVI reached 51% of its maximum that year. The threshold value was computed for the study area by Ranghetti et al. (2016). OS is a proxy for the day when spring forage starts to be readily available. OS was calculated separately for the two areas used by ibex in spring at low altitude (OS low) and summer at higher altitude (OS high). OS low considered only grassland pixels below 2000 m and is representative of the conditions experienced by ibex during early spring. OS high considered only alpine grassland and pixels above 2000 m and represents the phenology of the vegetation used by ibex during summer.
- Length of the green-up period (length green-up): the number of days between the onset of spring at low altitude (OS low) and when the maximum NDVI (day NDVI max: peak in vegetation fresh biomass and quality available to ibex) at high altitude is reached. The length of the green-up was calculated for each year as: length green up = day NDVI max – OS low. The length of the green-up period is a proxy of the speed of the green-up. Longer green-up seasons indicate a slower and more spatially heterogeneous maturation of the vegetation.

Aggregated yearly values were obtained by calculating the median value for all pixels of a given year. Linear regressions of the different values as a function of year were performed to visualize temporal trends (2000–2022) in phenological variables during the study.

Temporal trends in body mass

To detect possible temporal trends in body mass, we built autoregressive linear mixed models of autumn mass, summer and winter mass change and relative (%) summer and winter mass change as a function of year from 2000 to 2022. Age, as a quadratic term, was added as explanatory variable to account for the known growth trajectory of male Alpine ibex (Bergeron et al. 2010). Individual identity was included as a random effect. Only animals aged 3–13 years were included, as younger males were usually in female groups and very rarely came to the platform scale, while males aged 14 years and older were few (≈ 6% of the total) and suffered high mortality (Toïgo et al. 2007).

Factors affecting body mass and body mass changes

To investigate whether seasonal body mass changes were dependent on mass at the start of the season, we used mixed
effects models similar to those described in the previous paragraph. Seasonal mass changes were modelled as a function of starting mass: winter mass change as a function of body mass in the previous autumn and summer mass change as a function of mass in the previous spring (Supporting information).

Because we considered variables with different nested structures, we could not use classical covariance-based structural equation modelling (SEM). Instead, we used piecewise SEM without latent variables (path models) to infer direct and indirect causal relationships between body mass changes, autumn body mass and environmental and phenological variables and tested the fit of the model using d-separation (Shipley 2000, 2009, 2016). We produced a directed acyclic graph (DAG) to describe the expected relationships between the variables. Details on the expected relationships are presented below. Then, free covariances were added to the DAG to deal with correlated errors between pairs of variables due to unknown latent variables to produce a mixed acyclic graph (MAG). To obtain the d-separation basis set of our model including free covariances, this MAG was then converted to a d-separation equivalent MAG following Shipley and Douma (2021). The DAG to MAG conversion and the identification of d-separation claims were obtained with the R package 'CauseAndCorrelation' (Shipley 2016). If all of the conditional independence predictions of our causal model, as encoded in the MAG, exist in the data then the resulting Fisher’s C statistic will follow a χ² distribution. A significant value of the C-statistic (p < 0.05) is evidence that the data do not agree with the hypothesized model while a non-significant value provides provisional evidence in favour of it.

The MAG with all tested paths as well as the added free covariances is provided in the Supporting information and included: autumn body mass, winter mass change and summer mass change. These measures were expected to influence each other and to be affected by ibex density and seasonal meteorological and phenological variables. In particular, winter mass change was expected to be influenced by winter snow, by spring temperature and precipitations and by the starting date of the growing season at low altitude (OS low), as male ibex usually remain at low altitude until early June. In addition, winter mass change was expected to be influenced by ibex density through intraspecific competition. Summer mass change was expected to be affected by spring and summer weather and by resource availability at high altitude, including OS high and length of the green-up season and ibex density. Autumn mass was expected to be dependent upon mass changes in the previous seasons, summer weather and ibex density. Finally, phenological variables (OS low, OS high and length of the green-up season) were expected to be affected by the seasonal weather variables that were added to the MAG as independent variables. To account for the known strong age effects on mass (Bergeron et al. 2010), age was added as a quadratic term, for both mass and mass changes. Path coefficients were extracted from piecewise regressions as specified in the d-separation equivalent graph. An analysis of the effects of environmental effects on density was not within the scope of this work. Therefore, density was added as an external variable: no causal paths were drawn from the environmental variables to density and free-covariances were added to control for possible correlations. In the SEM, phenological variables were modelled with linear regressions while autumn mass and mass changes were modelled with linear mixed effects models adding individual identity as a random effect and a temporal autocorrelation structure (corAR1). Models were graphically checked for residuals homogeneity and standard diagnostics were performed for all models included in the SEM. Following the same procedure described above, we finally tested an alternative MAG excluding the non-significant paths of the first hypothesised model. Both models were supported (global goodness-of-fit of both models was p > 0.05) and the coefficients of the two models did not show major changes. Therefore, to present and discuss of all the paths initially hypothesised, we reported in the results the coefficients of the first hypothesised model that also includes non-significant paths.

Results

The initial dataset included 3548 body mass measurements, collected over 23 years on 181 Alpine ibex males (mean ± SD of measurement per individual = 19.60 ± 19.01, min = 1, max = 102). We included in the final analysis 724 seasonal estimates on 179 individuals of autumn body mass and summer mass change (mean ± SD of measures per individual = 4.04 ± 2.48, min = 1, max = 11) and 499 estimates on 142 individuals of winter mass change (mean ± SD of measures per individual = 3.51 ± 2.27, min = 1, max = 10).

Temporal trends in body mass

The average autumn body mass of male Alpine ibex increased substantially over 23 years (Fig. 2, Table 1). Averaged over all ages, the increase was 4.7 kg (± 2.1), or about 5.4% of the average mass at the beginning of the study. For males aged 7 and 8 years, the increase was up to 15%. The increase was significant for nearly all age classes (Fig. 2a). The oldest individuals (13 years), however, showed a significant decline in autumn mass.

Over the study period, the trend for summer mass changes was negative, while that of winter mass changes was positive. Over all ages, both trends were significant (Table 1) but not for all age classes (Fig. 2b–c). The overall relationship was significant for both absolute and relative changes: in recent years, male ibex gained less mass during summer and lost less mass during winter, compared to 20 years ago (Table 1).

Temporal trends in meteorological and phenological variables

Several meteorological and phenological variables changed over the years of the study (Fig. 3). Specifically, the estimated OS at low altitude was about 14 days earlier in 2022 than in 2000 while the day of maximum NDVI remained stable.
Accordingly, the length of the green-up period increased by about 18 days. Over the longer term (1962–2022), both spring and summer temperature increased (Supporting information), with summer temperature showing a significant increase also over the last 23 years (Fig. 3). Winter snow depth showed a strong decrease over the long term (Supporting information), although the decrease was not significant when the analysis was restricted to the last 23 years (Fig. 3). The day of snow melt and the length of snow cover were correlated to winter show depth and showed a similar trend with snow melt occurring earlier and the length of snow cover being shorter in the recent years (Supporting information).

Figure 2. (a) Autumn body mass adjusted to 1 September, (b) summer mass change and (c) winter mass change from 2000 to 2022 of male Alpine ibex aged 3–13 years in Valsavarenche, Gran Paradiso National Park, Italy. Summer mass change was the difference between autumn body mass (adjusted to 1 September) and spring body mass (adjusted to 1 June), winter mass change was the difference between spring body mass and autumn body mass of the previous year. Each box represents a different age class, as indicated in the grey box over each plot. For each age we also report estimates and p-values of separate linear regressions for mass or seasonal mass change as a function of year (significance codes: *** p < 0.001, ** 0.001 < p < 0.01, * 0.01 < p < 0.05, . 0.05 < p < 0.08, ns p > 0.08). Plots for relative mass changes are provided in the Supporting information. The outputs of the global models including all age classes and accounting for individual growth trajectories are presented in Table 1.
Factors affecting body mass and mass changes

Our tested SEM is presented in Fig. 4. The coefficients of the models, including non-significant relationships, are provided in Table 2. A DAG including all tested paths, free-covariance relationships between variables and the exact specification of the DAG, MAG and d-separation claims tested in the SEM are provided in the Supporting information. Global goodness-of-fit of the tested model was $C^2 = 15.03$ with 14 df, $p = 0.24$. That of the model where non-significant paths were removed was $C^2 = 27.90$ with 22 df, $p = 0.18$.

The SEM confirmed that all body mass measures were strongly dependent on age (Table 2, Fig. 4): male ibex gain about 10 kg per year until about 10–11 years of age (Fig. 2). In addition, autumn mass was positively influenced by both winter and summer mass changes: animals that lost less mass the previous winter and gained more mass during summer were heavier in September. Summer mass change was negatively correlated with winter mass change: animals that lost less mass in winter gained less mass the following summer. In addition, ibex that were heavier in spring gained relatively less mass in summer and those that were heavier in autumn lost more mass the following winter (Supporting information).

Focusing on the effects of environmental variables on body mass and mass changes (Table 2, Fig. 4), we found that early springs reduced winter mass loss. The main factor affecting winter mass change was the timing of OS low, indicating that delayed green-up at low altitude caused greater mass loss. At high density, ibex lost more mass during winter. When accounting for the other variables, snow depth did not have an effect on winter mass change. Spring precipitations and temperature did not appear to affect winter mass changes. Age and previous winter mass change had the strongest effect on mass change the following summer while neither ibex density nor any environmental variables had a significant effect. Finally, autumn body mass was most strongly affected, in addition to age, by summer and winter mass changes, and weakly by summer temperature. Density did not affect autumn body mass.

Considering weather and phenology (Fig. 3), we found that the onset of spring both at low and at high altitude was delayed by winter snow depth (positive relationship). The OS at both altitudes was also delayed by spring precipitations (positive relationship), with a stronger effect at high altitude where much spring precipitation fell as snow. Higher spring temperatures advanced OS (negative relationship). Longer green-up seasons, measured as the number of days between the OS at low altitude and the maximum NDVI value, occurred in years with early OS but cool springs, and dry and cool summers. The length of the green-up season also increased with previous winter snow.

### Discussion

Male Alpine ibex in the study population are now substantially heavier than two decades ago, some age classes by as much as 10 kg, or about 15%. Although changes in body size directly
or indirectly tied to climate change have been reported for other ungulates (Ozgul et al. 2009), to the best of our knowledge none have been as large over only two decades. What explains this substantial increase in body mass? Ibex appeared to lose less mass over the winter but also to gain less mass over summer. Therefore, the increase in autumn body mass despite a decrease in summer mass appears to be mostly due to a decreased mass loss during winter. The decreased winter mass loss seems mostly related to spring resource availability, affected by winter and spring meteorological variables, and to density. In recent years, male Alpine ibex reach the beginning of the new vegetation growing season without depleting the body reserves that they had accumulated over the previous summer. This interpretation was reinforced by the SEM that showed that autumn body mass was directly influenced by mass change during the previous winter: animals that lost less mass during winter were heavier the following autumn. As expected, the SEM confirmed that summer mass changes also strongly influenced autumn body mass and summer mass changes were greater when animals were lighter in spring. At the same time, abundant snow during winter increased the length of the green-up period, possibly because it slowed vegetation maturation at high altitude, as shown in Arctic ecosystems (Cooper et al. 2011), thus postponing the peak in NDVI. Longer green-up seasons, likely indicating a slower and more spatially heterogeneous maturation of the vegetation, provide herbivores with high-quality resources for a longer time (Pettorelli et al. 2007). A study of seasonal biomass dynamics in a Tibetan alpine grassland showed that climate change promoted both earlier phenology and faster growth (Wang et al. 2020). The same study, however, found no overall changes in total annual biomass production. Changes in the timing of trophic resources, but not in the total amount of resources available, could partly explain the observed decrease in summer mass gain. A direct measure of vegetation quality and availability during the snow-free season will enhance the understanding of the underlying mechanisms.

The only two environmental factors affecting winter mass change were the starting date of the vegetative season (OS) and ibex density while snow did not have an effect. At low
altitude, where male Alpine ibex spend late winter and early spring and have access to the first fresh forage after snow melt, the growing season started almost two weeks earlier over the time frame of our study. Mean snow depth showed a decreasing trend in the last 60 years but no clear trend in the last two decades. SEM suggested that, during a shorter winter, ibex lost less mass. This is not surprising: if snow melts and vegetation starts to grow earlier, the period when animals need to rely on stored fat is shorter. In addition, ibex had greater winter mass loss in years of high density, while no effect of density was observed on summer mass change or autumn body mass. Intraspecific competition for resources seems therefore to occur only during winter, further strengthening the hypothesis that winter resource availability and conditions were the strongest drivers of seasonal body mass dynamics. The effect of density on winter mass change may also be related to increased competition and hence increased energy expenditure during rutting seasons with high density.

Increased summer precipitation has also been shown to reduce the growth rate of Alpine ibex populations in Switzerland and to amplify the negative effects of inbreeding (Bozzuto et al. 2019). Despite lower summer mass gain, however, ibex at our

Finally, we underline that the individual $R^2$ for the body mass measures ranged from 0.36 to 0.60. Therefore, additional variables not included in the SEM likely influence body mass changes.

The unexpected decrease in summer mass gain highlights how responses to climate change can be difficult to predict a priori. Maximum daily food intake and maximum amount of stored fat may be constrained by physical and physiological limits (Owen-Smith 2002), potentially explaining why summer mass gain did not increase. However, the apparent decrease in summer mass gain is unlikely to be explained by physiological limitations. Lower summer mass gain can also be expected if body condition in spring approaches the optimal amount of autumn body reserves: animals that are heavier in spring will have to gain less mass to reach the same, or even higher, autumn body mass than lighter animals. Relative summer mass gain was indeed smaller for animals that were heavier the previous autumn (Supporting information). Finally, reduced summer mass gain could also result from a reduction in resource quality during summer or from increased summer temperatures, which may reduce ibex foraging activity and force them to forage in sub-optimal areas (Mason et al. 2017).

Figure 4. Direct acyclic graph (DAG) of the confirmed relationships between variables affecting mass and mass change of male Alpine ibex. When the measure is relative to the previous year, $y^{-1}$ is added next to the variable. The same applies when the measure was relative to the final months of year $y^{-1}$ and first months of year $y$ (for measures collected during winter). Black arrows represent negative relationships and brown arrows positive relationships. Path width is proportional to the value of the path coefficients, provided on each arrow. Path coefficients are also presented in Table 2. Non-significant paths were not included in the DAG to improve figure readability but are provided in Table 2. A DAG with all tested relationships, including non-significant ones, as well as free-covariance relationships between variables, is provided in the Supporting information.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Path Coefficient</th>
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<tr>
<td>Winter $(y-1)$ snow depth</td>
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<tr>
<td>Spring precipitation</td>
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<td>Spring temperature</td>
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<td>Summer precipitation</td>
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<td>Summer temperature</td>
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<tr>
<td>Autumn body mass</td>
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<td>IBEX density $(y-1)$</td>
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<tr>
<td>Age $-1.31$ Age$^2$ 0.92</td>
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<tr>
<td>Age $1.31$ Age$^2$ -1.36</td>
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<td>Age $3.07$ Age$^2$ -2.40</td>
<td></td>
</tr>
</tbody>
</table>

Table 2.
study site are now much heavier than two decades ago and our findings suggest that the main proximal driver of body mass dynamics in male Alpine ibex is winter mass change.

Alpine plants and animals likely evolved with snowy winters and cool summers. The climate is changing, with consequences that are difficult to predict and sometimes contrasting (Pettorelli et al. 2005, Ozgul et al. 2009, Ruggetti and Festa-Bianchet 2012, Büntgen et al. 2020, Chirichella et al. 2021). In the Alps, temperatures are increasing, snow is decreasing (Gottlieb and Mankin 2024) and spring phenology has advanced at a rate of 5 days per decade (Vitasse et al. 2021). A similar trend was observed in our study area, with an increase in summer temperature of 0.08°C year⁻¹ and OS occurring earlier by 0.63 days year⁻¹. Mysterud et al. (2001) suggested that winter climatic variability influenced herbivore body mass indirectly through summer foraging conditions. Our results showed that winter and early spring conditions, coupled with density, may also directly affect herbivore body mass and must therefore be considered when investigating the effect of climate changes on body mass of Alpine species.

Alpine ibex may have less control over mass loss in winter than over mass gain in summer, as reported for bighorn sheep (Festa-Bianchet et al. 1996). The rut is in early winter; therefore, males must calibrate their reproductive efforts

Table 2. Coefficients, standard errors and p-values of paths included in the SEM. The tested variables not included in the final model and the corresponding non-significant p-values are in italics. Path coefficients are reported to allow comparison of effect sizes. Global goodness-of-fit of the model was C=21.40 with 16 df, p=0.16. Marginal (R²m) and conditional (R²c) individual R² for the body mass variables of interests were: Autumn body mass: R²m=0.56, R²c=0.56; Summer mass change: R²m=0.26, R²c=0.36; Winter mass change: R²m=0.38, R²c=0.62. Marginal R² for the phenological variables were: OS low altitude: R²m=0.43; OS high altitude: R²m=0.51; Length of the green-up season: R²m=0.75.

<table>
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<th>Path coefficients</th>
<th>SE</th>
<th>p</th>
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<td>Ibex density</td>
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without knowing how conditions may change during the following three months of winter. Although rutting activities appear to decline in years with deep snow (Apollonio et al. 2013), male Alpine ibex likely calibrate their reproductive effort also based on their body condition, as shown in other ungulates (Ortega et al. 2022). This interpretation is supported by the results provided in the Supporting information that show that animals lost more mass during winter if they were heavier in autumn. Shorter winters caused an increase in the peak body mass reached by male Alpine ibex, with potential effects on their reproductive efforts. Male Alpine ibex grow slowly: their mass increases by about 10 kg each year from 2 to about 10–12 years of age, when it reaches a plateau and then starts a senescent decrease (Brambilla et al. 2022a). Our results show that male Alpine ibex now reach an age-specific body mass that two decades ago was typical of animals 2–3 years older (Fig. 2), with potentially important implications for life history, mating success and population dynamics. Body mass affects male reproductive success in ungulates (Newbolt et al. 2017, Markussen et al. 2019) and an increase in autumn mass could lead to an increase in male reproductive effort. Much winter mass loss in highly polygynous ungulates usually occurs during the rut (Apollonio et al. 2020), indicating reliance on stored resources for male–male competition and access to mates. In addition, there seems to be a threshold in rut mass loss that males do not cross, probably to avoid compromising their survival (Apollonio et al. 2020). That threshold suggests differential allocation to rutting activities by males of different body mass. Heavier males may have more stored reserves that can be used during the rut, likely increasing reproductive effort. In addition, the substantial increase in mass among young adults, aged 7–8 years (Fig. 2), may make some young individuals competitive during the rut, possibly increasing male–male competition and reducing mating skew. An increase in the number of reproductive males may be beneficial, given the low genetic variability and high inbreeding rate of the species (Biebach and Keller 2009, Brambilla et al. 2018, Bozzuto et al. 2019).

Winter conditions are important drivers of Alpine ibex population dynamics. Until the mid-1980s, the dynamics of the Gran Paradiso population were mainly driven by winter snow depth (Jacobson et al. 2004), with high winter mortality occurring in years of deep snow and density. In recent decades, however, the local ibex population has declined despite decreased winter precipitations (Jacobson et al. 2004, Mignatti et al. 2012). The recent decline was caused by low overwinter survival of kids, which appeared to be negatively affected by the more rapid vegetation maturation in spring (Pettorelli et al. 2007). The effect of snow on Alpine ibex seems therefore to be non-linear, with negative effects on population dynamics of both very high and very low snow precipitations (Mignatti et al. 2012) and to vary according to sex and age class, because of different mechanisms: reduced over-winter survival of all age classes in years with high snow cover and high density, and reduced over-winter survival of kids in years with early and fast springs caused by reduced snow cover. Our results further suggest that earlier springs have a positive effect on male body conditions. This apparent contradiction might be due to the strong sexual segregation typical of most mountain ungulates. In Alpine ibex, males and females with young use different habitats, except for the rut (December–January) (Villaret and Bon 1998, Ruckstuhl and Neuhaus 2002). Females in the study area are usually found at higher altitude during spring and summer and may therefore not benefit from earlier onset of spring at low altitude, hence of a longer green-up. In addition, the timing of female energetic expenditure to ensure kid survival is usually more constrained than that of males (Douhard et al. 2018) potentially explaining the opposite site effect of the same changes. Plasticity in spatial behaviour, resource acquisition and consumption likely allows ibex males to take advantage of the shorter winters and longer green-ups. At the same time, species (or sex/age classes) that are more constrained in space and time by their life cycle, may be more strongly affected by the change in timing of resource availability compared to their reproductive phenology, as observed in other studies (Pettorelli et al. 2007, Ozgul et al. 2009, Ruggetti and Festa-Bianchet 2012, Chirichella et al. 2021). Changes in seasonal availability and quality of resources can affect differently different life-history traits and sex/age classes and hence can have complex consequences for population dynamics.

Over the last two decades, male Alpine ibex showed a proportional increase in mass higher than reported by any other study on vertebrates. Reduced mass loss during winter led to an increase in autumn body mass of up to 10%. Our study reveals that winter conditions can directly shape body mass of vertebrates in seasonal environments, providing a novel perspective for the understanding of the effect of climate changes on the ecology of Alpine species. Our findings also suggest that the relationship between environmental variables and life history traits is complex, non-linear and likely varies among sex/age classes. This complexity has important implications for population dynamics and conservation, and merits attention in future studies. Finally, we underline that this work was possible only through long-term monitoring of individually recognizable animals, showing once again the importance of long-term individual-based data for conservation, especially in times of environmental changes (Clutton-Brock and Sheldon 2010, Festa-Bianchet et al. 2017).

Speculations

While our data show changes in mass dynamics, it remains unclear to what extent, if any, ibex also changed in skeletal size. Given the apparent slight decrease in summer mass gain, we speculate that there may be selective pressure against ibex being ‘too big’ or ‘too fat’. Perhaps very fat ibex are more subject to thermal stress during warm summers, or are more prone to accidents or less able to escape predators, such as wolves that have recently recolonized the study area. Finally, a more rapid attainment of asymptotic mass may change the distribution of male mating success and possibly decrease mating skew, as younger and more abundant age classes may have become more competitive for dominance status.
Acknowledgements – This work would have not been possible without the passionate contribution of several students and research assistants who collected body mass data for decades and to whom we are extremely grateful. Gran Paradiso National Park ensured logistics in the study area. We are also deeply thankful to the warden of Gran Paradiso National Park for capturing and marking animals, to Stefanie Muff and Benjamin Larue for helpful discussion on data analysis, and to Bill Shipley for support with handling latent variables in SEM. We thank Iren S.p.A. for providing meteorological data. Open access funding provided by Universitat Zurich.

Permits – Capture protocols were developed to minimize adverse effects on animal welfare and were authorised by the Italian Ministry of the Environment (authorisation no. 25114 of 21/09/2004).

Author contributions

Alice Brambilla: Conceptualization (lead); Data curation (lead); Formal analysis (lead); Writing – original draft (lead); Writing – review and editing (equal). Achaz von Hardenberg: Data curation (supporting); Formal analysis (supporting); Methodology (equal); Writing – review and editing (equal). Bruno Bassano: Methodology (supporting); Writing – review and editing (supporting). Luigi Ranghetti: Formal analysis (supporting); Methodology (supporting); Writing – review and editing (supporting). Lukas Keller: Methodology (supporting); Writing – review and editing (supporting). Marco Festa-Bianchet: Formal analysis (supporting); Methodology (supporting); Supervision (equal); Writing – original draft (supporting); Writing – review and editing (equal).

Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.w9ghx3fz6 (Brambilla et al. 2024).

Supporting information

The Supporting information associated with this article is available with the online version.

References


2017. Elevational range shifts in four mountain ungulate species from the Swiss Alps. – Ecosphere 8: e01761.


