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Tom HE Mason (tom.h.e.mason@gmail.com)
Marco Apollonio (marcoapo@uniss.it)
Roberta Chirichella (roberta.chirichella@gmail.com)
Stephen G Willis (s.g.willis@durham.ac.uk)
Philip A Stephens (philip.stephens@durham.ac.uk)

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Environmental change and long-term body mass declines in an alpine mammal

Tom HE Mason[1*]
[*] Corresponding author
Email: tom.h.e.mason@gmail.com

Marco Apollonio[2]
Email: marcoapo@uniss.it

Roberta Chirichella[2]
Email: roberta.chirichella@gmail.com

Stephen G Willis[1]
Email: s.g.willis@durham.ac.uk

Philip A Stephens[1]
Email: philip.stephens@durham.ac.uk

[1] School of Biological and Biomedical Sciences, University of Durham, South Road, Durham DH1 3LE, UK

[2] Department of Science for Nature and Environmental Resources, University of Sassari, via Muroni 25, I-07100 Sassari, Sardinia, Italy

Abstract

Introduction

Climate and environmental change have driven widespread changes in body size, particularly declines, across a range of taxonomic groups in recent decades. Size declines could substantially impact on the functioning of ecosystems. To date, most studies suggest that temporal trends in size have resulted indirectly from climate change modifying resource availability and quality, affecting the ability of individuals to acquire resources and grow.

Results

Here, we investigate striking long-term body mass declines in juvenile Alpine chamois (*Rupicapra rupicapra*), within three neighbouring populations in the Italian Alps. We find strong evidence that increasing population density and warming temperatures during spring and summer are linked to the mass declines. We find no evidence that the timing or productivity of resources have been altered during this period.

Conclusions

We conclude that it is unlikely that environmental change has driven body size change indirectly via effects on resource productivity or phenology. Instead, we propose that environmental change has limited the ability of individuals to acquire resources. This could be due to increases in the intensity of competition and decreases in time spent foraging, owing to high temperatures. Our findings add weight to a growing body of evidence for long-term body size reductions and provide considerable insight into the potential drivers of such trends. Furthermore, we highlight the potential for appropriate management, for instance increases in harvest size, to counteract the impacts of climate change on body mass.

Keywords

Body size, Body mass, Chamois, Climate change, Environmental change, Hunting, NDVI, Population density, Temperature, Ungulate

Introduction

Climatic and other environmental change has impacted species in a variety of ways, from altering their spatial distributions (e.g. [1]) to changing the timing of their annual events (e.g. [2]). Recently, focus has broadened to include the impacts of climate change on life-history traits, body condition and population processes (e.g. [3-6]). One emergent generality is that responses to climate change include widespread body size changes, particularly declines, which could have pronounced negative impacts on the functioning and productivity of ecosystems [7,8]. Body size declines driven by climate change have been recorded in the past, for instance in large ungulates during the Pleistocene, and are thought to have led to the extinction of some species [9].

A variety of climatic drivers of recent body size declines have been proposed. In ectotherms, higher metabolic rates are predicted in warmer environments [10], so climate change might lead to decreased body size, unless individuals can increase their rate of food intake [8]. In endotherms, in line with Bergmann’s rule [11], it could be beneficial to be smaller (and thus have a larger surface area to volume ratio) in warmer environments, due to a reduced need for heat conservation and a greater need for heat loss [12]. In mammals and birds, intra-specific trends between body size and both latitude [13,14] and temperature [15,16] have been observed, providing some support for this theory. However, the most frequently cited climatic driver of body mass declines is the indirect link via climatic impacts on resource availability, which has been implicated considerably more frequently than any other mechanism (reviewed in [7]). Climate and environmental change can alter the timing, quality and quantity of resources, affecting the rate at which individuals acquire resources to invest in growth and energy storage, and ultimately body size (e.g. [6,17]). Non-climatic processes can also drive body size change and could be playing a role alongside climate change. For example, in harvested animal populations, a preference for larger bodied individuals by hunters can drive selection for decreased body size [18,19].

In ungulates, body mass is an important indicator of fitness [20,21] and can respond rapidly to environmental change [6]. High body mass is commonly related to high reproductive success (e.g. [22]) and survival (e.g. [23]). As such, changes in body mass can have important effects on population dynamics [6,21]. The indirect link between climate, resources and ungulate body mass is well studied and could be strongly influenced by climate change [24,25]. However, environmental change could also directly affect the ability of ungulates to acquire resources, particularly in seasonal environments, which could lead to temporal body mass change. For instance, changes in population density can alter the intensity of competition for resources, affecting the ability of individuals to forage and grow [26,27]. There is some evidence from other taxa of links between density and temporal body size change [28]. In recent decades, warming climates have led to changing snow cover and depth in some areas [29], altering the costs of locomotion and foraging for some species [30]. In alpine species, high temperatures in spring and summer can cause heat-stress, reducing the time individuals can spend foraging [31]. As a result, we propose that, in alpine areas, which have been strongly affected by climate warming [32], reductions in time spent foraging due to higher thermoregulatory costs could lead to reduced body size. Climate change is predicted to drive similar changes in temperature-dependent activity budgets in other taxa [33,34]. Furthermore, temperature induced changes in foraging behaviour have been detected in experimental studies [35].

Here, we explore long-term variation in the body mass of juveniles in three neighbouring populations of Alpine chamois (*Rupicapra rupicapra*) in the Italian Alps. The body condition of juvenile ungulates is particularly responsive to environmental variation [25,26,36]. This is largely because juveniles invest highly in growth, and not in reproduction, meaning that their body condition is very sensitive to the availability of resources. Experiencing poor environmental conditions in youth can suppress growth rates and result in smaller body size at maturity [6], which could have important implications for population dynamics. We begin by investigating whether there have been consistent, long-term changes in chamois body mass across sexes and populations. Having identified the existence of temporal trends in body mass, we seek to tease apart the different drivers of these trends. For reasons discussed below (see Methods), we dismiss the role of artificial selection driven by hunting. Consequently, motivated by the findings reviewed above, we seek to evaluate the evidence for three plausible drivers of body size change:

1. Climate-mediated changes in vegetation productivity or phenology, altering resource quality and availability
2. Climate-mediated changes in behaviour, altering access to resources
3. Changes in population density, altering per-capita resource availability

Methods

Study area

The study area is located in Trento Province in the Central-Eastern Italian Alps (46°02’N, 10°38’E), across three chamois hunting districts: Adamello (area = 373 km^2), Presanella (146 km^2) and Brenta (263 km^2). The area is forested up to the tree-line at about 2,000 m, above which it consists of Alpine meadows, rocky outcrops, scree fields and open rock faces. The average altitude varies among the districts, though with considerable overlap (mean altitude ± SD: Adamello, 1,901 ± 616 m; Presanella, 2,098 ± 540 m; Brenta, 1,594 ± 603 m). Adamello and Presanella are characterised by nutrient-poor siliceous vegetation whilst Brenta is characterised by nutrient-rich calcareous vegetation [37]. Typically, meadows in Adamello and Presanella are dominated by *Festuca scabriculmis* and *Carex curvula*, whilst those in Brenta are composed of *Sesleria albicans* and *Carex firma*. Throughout the study area, meadows are grazed by small herds of livestock (sheep, goats and cows) during summer, a practice that has been maintained at consistent levels throughout the study period. Several potential predators of chamois were present during the study, including a small, stable population of brown bear (*Ursus arctos*) in Brenta, a very small number of Eurasian lynx

(*Lynx lynx*) and the golden eagle (*Aquila chrysaetos*). However, predation on chamois is very rare here (personal communication, Adamello Brenta Nature Park, Trento Province, Italy).

Body mass data

Chamois are hunted every year between mid-September and late-December. Data were collected on the eviscerated body mass and day of shooting of 10,455 yearling (≈1.5 year olds; hereafter juveniles) Alpine chamois (5,762 males and 4,693 females), hunted between 1979 and 2010 (see Additional file 1 for annual breakdowns of sample size). Hunting is heavily regulated and there is little potential for artificial selection by hunters, as chamois can easily detect hunters in the predominantly open habitat and will flee from hunters at particularly large distances [38,39]. Moreover, there is no evidence of hunters preferentially harvesting larger bodied age-classes in these populations [38]. Hunting pressure on yearlings varies among sites (mean proportion of yearlings hunted in census years: Adamello males, 0.40 ± 0.01; Adamello females, 0.32 ± 0.01; Presanella males, 0.32 ± 0.01; Presanella females, 0.24 ± 0.02; Brenta males, 0.37 ± 0.01; Brenta females, 0.31 ± 0.02). In order to account for intra-seasonal variation in body mass, which is not the focus of this study, a published model of seasonal body mass change [38], which considers inter-annual mass variation, was used to estimate juvenile mass standardised to a specific day of the year. Annual estimates (n = 32) of mean juvenile body mass were produced for each sex, within each site, standardised to day 300 of the year (27th October) (see Figure 1). Body mass was estimated after the vegetation growing season (hereafter 'growing season') because body condition at that time will have been influenced by the spring and summer environment, which is thought to have a strong influence on ungulate body mass [40].

Figure 1 Temporal juvenile body mass trends. Long-term temporal trends in body masses of juvenile chamois **a)** males and **b)** females in the three study sites between 1979 and 2010. Points are annual mass estimates standardised to day 300 and straight lines are fitted trends.

There were clear negative temporal body mass trends in all sexes and sites (Figure 1). In order to examine drivers of deviations from the long-term trends (i.e. years in which mean body mass was particularly high or low, even given the trend), the body mass time series were detrended by fitting linear models and calculating residuals. However, detrending can remove long-term fluctuations related to environmental change trends [41,42], which are of primary interest to us. As a result, we modelled body mass data, to examine drivers of long-term trends, and also modelled body mass residuals, to examine drivers of deviations from the trends.

Environmental and demographic data

A range of climatic and non-climatic factors might be expected to influence chamois body mass. Negative effects of population density on mass are common in ungulates [26,27]. In the absence of natural predation, these effects generally operate through increased intra-specific competition at higher population densities, resulting in lower per-capita food intake, particularly during periods when food is scarce [43-45]. To investigate density-dependence in these chamois populations, site-specific population density estimates were used from total population censuses performed in September every year between 1981 and 2009 (with the exception of 1990 and 1991; data from these years were excluded from the analysis). Each year, a set of simultaneous censuses was performed from vantage points across different blocks of each hunting district. It was assumed that density estimates from this time of year would reflect the population density over the previous growing season.

To investigate a possible direct thermoregulatory link between climate and body mass, we calculated yearly site-specific estimates of mean daily growing season temperature between 1982 and 2007 from high-altitude meteorological stations located in each of the three study sites (Data provided by The Forecasts and Organization Office, Civil Protection and Infrastructures Department, Trento Province, Italy). Differences in the elevation of weather stations among sites contributed to inter-site temperature differences (see Figure 2a). However, this did not affect our analysis since the drivers of body mass trends were examined separately in each site and, additionally, temperatures were standardised within sites, along with all other environmental predictors (see 'Modelling variation in mass and mass residuals'). The bounds of the growing season were estimated using snow cover data, also from meteorological stations located within each site. The growing season was defined as the period between the snow-melt in spring, when snow cover was reduced to 0% (which generally occurs between late March and early May), and the first significant snowfall in winter that results in new snow settling on the ground (which generally occurs between early November and late December).

Figure 2 Temporal trends in population density and mean growing season temperature. Long-term variation in **a)** mean growing season daily maximum temperature, between 1982 and 2007, and **b)** population density, between 1981 and 2009, in Adamello (black), Presanella (red) and Brenta (green). Gaps show years with missing data. It should be noted that whilst the three study areas do differ in their climate, some of the observed inter-site differences in temperature in a) are due to variation in the elevation of weather stations among areas.

To investigate the effect of vegetation productivity and phenology on mass, NDVI (normalised difference vegetation index) data were used as a measure of vegetation productivity, processed by the Global Inventory Modelling and Mapping Studies group (GIMMS; [46,47]). These data are global at a 0.07 degree resolution (approximately 8 km by 8 km) and are available at fortnightly intervals between 1982 and 2006 (thus slightly restricting the yearly data range for analyses). In order to focus on vegetation types utilised by chamois for foraging, such as alpine meadows and sparsely vegetated areas, only NDVI pixels dominated by such vegetation types were considered. To do this the Corine land-cover 2006 data-set at a 100 m resolution [48] was used to select only NDVI pixels within each site containing less than 25% coniferous woodland. As each of the three sites encompassed a number of these NDVI pixels, mean NDVI from these pixels was calculated for each fortnightly time period, within each site. Previous studies have implicated a number of metrics relating to annual NDVI variation as being important to ungulate body condition (e.g. [24,25]). Here, we seek to derive NDVI metrics in a standardised fashion, despite inherent noise in NDVI estimates caused by factors such as cloud cover, water, snow or shadow [47]. As in previous studies [49], we used a smoothed function to characterise variation in NDVI with time in a given year. The following function was used (see Additional file 2, for an illustration of the functional form):

$$\overline{p}(s,y,t)=\alpha_{s,y}+\left(\beta_{s,y}-\alpha_{s,y}\right)*\exp\left(-\left|\frac{t-t*}{\sigma_{s,y}}\right|^{z_{s,y}}\right).$$

Here, $\overline{p}\left(s,y,t\right)$ is predicted NDVI at time-period t in site s and year y, $\alpha_{s,y}$ and $\beta_{s,y}$ are minimum and maximum NDVI respectively in site s and year y, $\sigma_{s,y}$ is a parameter related to the width of the function and $z_{s,y}$ is a parameter describing the shape of the function. Variation in NDVI data, $p(s,y,t)$, about the predicted mean was beta distributed. Thus, the likelihood of the model parameters, $\theta_{s,y}$, given the data, parameterised by $\overline{p}\left(s,y,t\right)$ and the dispersion coefficient $\square_{s,y}$, is

$$L\left(\theta_{s,y}\right)=\prod_{t}\frac{\Gamma\left(a_{s,y,t}+b_{s,y,t}\right)}{\Gamma\left(a_{s,y,t}\right)\Gamma\left(b_{s,y,t}\right)}p_{s,y,t}^{a_{s,y,t}-1}\left(1-p_{s,y,t}\right)^{b_{s,y,t}-1},$$

where Γ(x) is the gamma function, $a_{s,y,t}=\overline{p}_{s,y,t}/\phi_{s,y}$ and $b_{s,y,t}=\left(1-\overline{p}_{s,y,t}/\phi_{s,y}\right)$. The most parsimonious fit was identified using Akaike's Information Criterion (AIC) [50,51].

The most parsimonious fitted relationships between mean NDVI and time in each year and site were calculated. Using these relationships, four NDVI metrics, described below, were calculated relating to vegetation productivity and phenology. All four of the metrics selected have been highlighted as important either to juvenile chamois specifically or to other ungulate species [47,52]. Previously, climate-induced changes in spring growing conditions [53] have been linked to higher juvenile body mass in ungulates, including chamois [52], due to longer growing-seasons and higher vegetation quality [24]. However, warmer springs have also been linked to negative impacts on body mass as higher temperatures lead to faster rates of vegetation 'green-up' and, thus, a shorter period of access to nutrient-rich emergent vegetation associated with early spring [25,54]. Here, the following four metrics were used: maximum rate of spring green-up, growing season duration, maximum NDVI and total growing season NDVI. Maximum rate of spring green-up ($\mathrm{NDVI}_{\mathrm{rate}}$) was calculated as the maximum first derivative of $\overline{p}_{s,y}\left(t\right)$ (i.e. the maximum rate of NDVI increase). The duration of the growing season ($\mathrm{NDVI}_{\mathrm{dur}}$) was calculated as the length of time between the maximum second derivative of $\overline{p}_{s,y}\left(t\right)$ (the start date of the growing season; when the rate of NDVI increase is increasing at its maximum rate) and the minimum second derivative of $\overline{p}_{s,y}\left(t\right)$ (the end date of the growing season; when NDVI is decreasing most rapidly). Maximum NDVI ($\mathrm{NDVI}_{\mathrm{max}}$) was calculated as the maximum value of $\overline{p}_{s,y}\left(t\right)$ and total growing-season NDVI (INDVI) as the integral of $\overline{p}_{s,y}\left(t\right)$ within the bounds of the growing-season. An illustration of the calculation of these metrics can be seen in Additional file 2.

Modelling variation in mass and mass residuals

Environmental predictors were standardised by z-transformation within each site, as follows: $z_{s,y}=\left(x_{s,y}-\overline{x}_{s}\right)/\sigma$, where $z_{s,y}$ is a z-transformed predictor in year y and site s, $x_{s,y}$ is the untransformed predictor, $\overline{x}_{s}$ is the site-specific mean of that predictor and σ_s the site-specific standard deviation. General linear models were fitted to examine variation in body mass and body mass residuals using *R* version 2.12.0 [55]. Juvenile phenotypic quality is thought to be strongly influenced by lagged environmental effects [40]. As such, lagged environmental factors [56,57], affecting the availability and accessibility of resources to mothers, as well as population density [36,58], affecting the intensity of competition for resources, can be strong predictors of juvenile body mass. To account for lagged environmental effects on juvenile mass, density, temperature and NDVI data were used not only from year *y* (the year a cohort was shot), but also from year *y*-1 (the year of a cohort's birth). Models were fitted with all possible biologically meaningful combinations of population density, $NDVI_{rate}$, $NDVI_{dur}$, $NDVI_{max}$, INDVI and temperature, from years *y* and *y*-1. Models were considered with either the same intercept or different intercepts for males and females. In each site, several of the predictors were highly correlated (Pearson correlation coefficients ≥ 0.6), for instance $NDVI_{dur}$ with INDVI, and $density_y$ with $density_{y-1}$. To avoid problems of multicollinearity, highly correlated predictors were not permitted in the same model (but were permitted separately). Given the temporal range of the predictors, and to use the same temporal range of data in each model, data were used for the 19 years between 1983 and 2006, excluding 1990, 1991 and 1992, years for which estimates of $density_y$ and/or $density_{y-1}$ are not available (population censuses were not performed in 1990 and 1991). In order to identify the most parsimonious models, we used the two-step model selection process suggested by Richards [51]. First, all models having an AIC within six units of the smallest AIC calculated were selected (i.e. $\Delta AIC \leq 6$). Second, in order to remove overly complex models, we disregarded those that had a higher AIC value than any simpler nested model. To investigate the potential for sex-specific environmental effects, we tested for sex interaction terms with all predictors within models in each site's top model set. To assess the relative importance of different predictors, Akaike model averaged coefficients were calculated from all models in each site's top model set [50]. Since we wanted to compare how the relative importance of predictors varied among sites, model averaged coefficients were z-transformed within each site. This standardised coefficients from different sites to the same scale, allowing the most important effects to be readily compared among sites.

Results

Juvenile chamois body masses decreased strongly between 1979 and 2010 in all three populations (Figure 1). The extent of this decrease varied considerably among sexes and sites but decreases in male mass have been more pronounced than decreases in female mass in all sites (slopes of temporal mass trends ± SE: Adamello males, −0.11 ± 0.01; Adamello females, −0.03 ± 0.02; Presanella males, −0.17 ± 0.02; Presanella females, −0.13 ± 0.01; Brenta males, −0.05 ± 0.01; Brenta females, −0.04 ± 0.01). Decreases have been less pronounced in Brenta than in the other two sites. There have been striking increases in growing season temperatures in all sites between 1982 and 2007 (Figure 2a). During the same period, all three populations increased in density substantially, peaking in the mid-1990s before declining slightly in recent years (Figure 2b). This growth coincides with the implementation of stricter controls on hunting in the area (including increases in the number of rangers and a more strictly enforced quota system). In contrast, there have been no pronounced long-term trends in the four NDVI metrics between 1982 and 2006, although growing seasons have tended to be longer (Figure 3b) and more productive (Figure 3d) between 2004 and 2006.

Figure 3 Temporal variation in standardised NDVI metrics. Long-term variation in standardised **a)** maximum rate of NDVI increase ($NDVI_{rate}$), **b)** growing season duration ($NDVI_{dur}$), **c)** maximum NDVI ($NDVI_{max}$) and **d)** total growing season NDVI (INDVI) between 1982 and 2006 in Adamello (black), Presanella (red) and Brenta (green).

The most parsimonious body mass models fitted the observed data well (Table 1, Figure 4) (R^2: Adamello, 0.78; Presanella, 0.83; Brenta, 0.69). In comparison, the fits of body mass residual models were poor (R^2: Adamello, 0.44; Presanella, 0.13; Brenta, 0.36; see Additional file 3); thus, our inferences focus on models that describe longer-term changes in body mass, rather than those focused on explaining variation around the long-term trend. Temperature, density and NDVI all appear to play a role in describing long-term variation in juvenile body mass (Table 1, Figure 5). Within each site, the top set of body mass models contains a number of closely competing models (Table 1) but clear and consistent patterns across sites are illustrated by model averaging (Figure 5). Temperature and/or density have the strongest negative effects on mass in all sites (Figures 5 and 6). Furthermore, strong negative effects of temperature and density in the current year are present in all of the top models within Adamello and Presanella (Table 1), providing good evidence for these effects. A slightly weaker negative effect of lagged temperature appears in most of the top models for these sites. In Brenta, there is some evidence for a negative effect of temperature, which appears in the top three models in this site but there is no evidence of a density effect. Despite mass declines in males being consistently stronger than in females (Figure 1), we found no support for any interaction terms between sex and environmental predictors, suggesting that there are not strong differences in the magnitude of environmental effects on body mass between males and females. The lack of evidence for sex-specific effects could stem from the slightly restricted temporal range of data used in the analysis.

Table 1 Set of most parsimonious body mass models

Site	Temp$_{y}$	Temp$_{y-1}$	Dens$_{y}$	Dens$_{y-1}$	NDVI$_{dur,y}$	NDVI$_{dur,y-1}$	INDVI$_{y}$	INDVI$_{y-1}$	NDVI$_{max,y}$	NDVI$_{max,y-1}$	NDVI$_{rate,y}$	NDVI$_{rate,y-1}$	Sex	K	R^2	ΔAIC	weight
Adamello	**−0.42**	**−0.21**	**−0.61**				**−0.18**					**0.22**	**0.32**	**8**	**0.78**	**0.0**	**0.24**
	−0.35	−0.19	−0.60			−0.21	−0.13						0.32	8	0.77	0.7	0.17
	−0.39	−0.18	−0.57			−0.21							0.32	7	0.76	1.8	0.10
	−0.42	−0.21	−0.61				−0.18					0.22		7	0.75	2.4	0.07
	−0.35	−0.19	−0.60			−0.21	−0.13							7	0.75	3.0	0.05
	−0.39		−0.68			−0.22	−0.12						0.32	7	0.75	3.3	0.05
	−0.47		−0.69				−0.17					0.21	0.32	7	0.75	3.6	0.04
	−0.39	−0.16	−0.56					−0.18					0.32	7	0.75	3.6	0.04
	−0.46	−0.20	−0.55									0.18	0.32	7	0.75	3.7	0.04
	−0.38		−0.67				−0.13	−0.20					0.32	7	0.74	3.7	0.04
	−0.39	−0.18	−0.57			−0.21								6	0.73	3.9	0.03
	−0.42		−0.65			−0.22							0.32	6	0.73	3.9	0.03
	−0.42		−0.64					−0.20					0.32	6	0.73	4.7	0.02
	−0.39		−0.68			−0.22	−0.12							6	0.72	5.3	0.02
	−0.47		−0.69				−0.17					0.21		6	0.72	5.5	0.02
	−0.39	−0.16	−0.56					−0.18						6	0.72	5.5	0.02
	−0.46	−0.20	−0.55									0.18		6	0.72	5.6	0.01
	−0.42		−0.65			−0.22								5	0.71	5.6	0.01
Presanella	**−0.58**	**−0.27**	**−0.53**		**0.28**					**−0.17**	**0.19**		**−0.41**	**9**	**0.83**	**0.0**	**0.36**
	−0.59	−0.25	−0.58		0.19					−0.14			−0.41	8	0.81	1.7	0.15
	−0.57	−0.27	−0.51		0.26						0.16		−0.41	8	0.81	1.9	0.14
	−0.58	−0.26	−0.55		0.18								−0.41	7	0.80	2.3	0.11
	−0.52	−0.26	−0.63							−0.14			−0.41	7	0.80	3.4	0.07
	−0.51	−0.26	−0.60										−0.41	6	0.78	3.7	0.06
	−0.67		−0.63		0.19								−0.41	6	0.78	4.8	0.03
	−0.58	−0.26	−0.55		0.18									6	0.78	5.1	0.03
	−0.63		−0.66				0.16						−0.41	6	0.77	5.6	0.02
	−0.62		−0.70							−0.14			−0.41	6	0.77	5.8	0.02
	−0.61		−0.68										−0.41	5	0.76	5.9	0.02
Brenta	**−0.40**							**0.43**		**0.21**		**0.13**	**1.06**	**7**	**0.69**	**0.0**	**0.24**
	−0.32							0.38		0.27	−0.11		1.06	7	0.69	0.1	0.23
	−0.34							0.38		0.25			1.06	6	0.67	0.1	0.23
			−0.34					0.34		0.22			1.06	6	0.66	1.1	0.14
				−0.32				0.36		0.21			1.06	6	0.65	2.8	0.06
	−0.44							0.41				0.20	1.06	6	0.65	3.3	0.05
			−0.37					0.29					1.06	5	0.62	4.6	0.02
	−0.37							0.34					1.06	5	0.61	5.4	0.02
				−0.36				0.32					1.06	5	0.60	5.9	0.01

Top model set containing models with a ΔAIC that is ≤6 and lower than all simpler nested versions [51]. The number of parameters in each model (K), R^2 values, ΔAICs and Akaike model weights are shown. The most parsimonious model for each site is displayed in bold. 'Sex' represents sex-specific model intercepts.

Figure 4 Temporal variation in observed and fitted juvenile body mass. Fitted juvenile body mass predictions of best models for males (red) and females (black) and observed body mass data in the three study populations. Lines are predictions and points are observed data for years used in modelling (i.e. years for which there are no missing data for any predictor). R^2 shown.

Figure 5 Model averaged standardised predictor effect sizes. Akaike model averaged standardised predictor coefficients calculated from all body mass models within the top model set for each site (see Table 1 for full model selection table).

Figure 6 Modelled effects of temperature and population density on juvenile body mass. Modelled effects of **a)** mean growing season temperature and **b)** population density on change in juvenile body mass since 1983 in Adamello (black), Presanella (red) and Brenta (green). Solid lines are predictions of the most parsimonious body mass model for each site, with other predictors set to mean values. Dashed lines are 95% confidence intervals calculated from 1000 bootstrapped replicates [59].

The modelled effects of NDVI are much weaker than the effects of density and temperature, and are generally positive (Table 1, Figure 5). Only in Brenta is there strong evidence for an influence of vegetation productivity and phenology; a strong, lagged, positive effect of INDVI is present in all top models and there is some evidence for a lagged, positive effect of peak NDVI. In Adamello and Presanella, NDVI effects are generally weaker and inconsistent, although there is some support for a positive effect of long growing seasons in Presanella and, surprisingly, for a negative effect of INDVI in Adamello.

Discussion

Pronounced long-term body mass declines were identified in all three populations. Models of juvenile body mass performed well in explaining these declines (Figure 4). However, the poor performances of residual models show that deviations from the general trends (i.e. years in which juveniles are particularly heavy or particularly light relative to the trend) cannot be explained as accurately. Mass declines appear to be linked most strongly to increases in growing season temperatures and population density; temperature and/or density have the strongest negative effects on body mass and deviations from yearly trend in all sites (Table 1, Figure 5). In comparison, there is no evidence of a strong negative effect of vegetation productivity or phenology on body mass, suggesting that body mass declines were not mediated by vegetation change as indexed by NDVI. Our results provide an interesting contrast to the majority of studies to date, which have implicated changes in food availability and quality as the most likely cause of body size declines [7].

Growing season temperature appears to be strongly linked to mass declines in all three populations (Table 1, Figures 5 and 6). However, despite significant temperature change (Figure 2a), there has been no consistent change in either vegetation productivity or phenology (Figure 3). Furthermore, there is no relationship between temperature and any NDVI metric. As such, we find no evidence for our first putative driver of mass change: that climate change has affected body mass via effects on resource productivity or phenology. Instead, our results provide support for our second putative driver: that climate change could be directly affecting chamois behaviour or physiology, limiting their ability to acquire resources. In another alpine ungulate, the ibex (*Capra ibex*), temperatures above 15-20 °C result in heat discomfort in males, reducing the time they can spend foraging [31]. In ungulates, behavioural changes, such as allocating less time to foraging, play an important role in thermoregulation because they can be more energetically efficient than autonomic thermoregulation [60,61]. Higher daily temperatures during spring and summer may have led to juvenile chamois spending more time resting and less time foraging than in the past, reducing their ability to store energy reserves and invest in growth. Indeed, chamois, like many ungulates, reduce their feeding activity during the hottest period of the day [62]. Furthermore, chamois spend less time foraging when it is hotter, independent of time of day [63]. Our results suggest that temperature affects the ability of juveniles to acquire resources themselves rather than via lagged effects on their mothers (Figure 5). It is possible that juvenile ungulates are more susceptible to higher temperatures due to having higher relative metabolic demands than adults [64,65]. Whilst we did not find any evidence for sex-specific environmental effects on body mass, that mass declines in juvenile males are consistently more pronounced than in females (Figure 1) suggests that, even in a relatively monomorphic ungulate species, a more energetically demanding growth phase could make males more susceptible to environmental stressors [20].

Population density also appears to be strongly linked to mass declines in juvenile chamois, providing support for our third putative driver: that changes in density affect per-capita resource availability (Table 1, Figures 5 and 6). The study populations have grown substantially following the implementation of stricter controls on hunting. As a result, increased intra-specific competition for resources may have led to reduced rates of per-capita food intake. Additionally, climate change may have affected chamois survival or fecundity, contributing to this population growth. Density dependence in body mass has been detected in a range of ungulate species (e.g. [27,36,66]) and even specifically in juvenile chamois [52]. At high latitudes and in alpine regions, this effect is most likely to manifest during winter, when snow cover reduces forage availability and increases forage patchiness, resulting in higher levels of agonistic interactions among individuals [67,68]. It is also possible that density dependence could be mediated by overgrazing; however, no changes in NDVI consistent with overgrazing, such as decreases in peak NDVI or INDVI [69], were detected. Overgrazing can also encourage the colonisation of grazing-tolerant, less palatable species [70], which might not result in detectable changes in productivity. However, such changes would not alter our finding that increases in density appear to have influenced body mass via changes in per-capita resource availability. As with temperature, the effect of density in the year of shooting appears most important (Figure 5), suggesting that competition for forage following weaning, rather than a lagged influence of competition on mothers in the previous year, has a stronger influence on juvenile mass. Indeed, intra-specific competition for resources is most likely to result in the displacement of subordinate individuals, such as juveniles, from food patches [71-73]. Previously, the importance of lagged effects on juvenile condition has been stressed (e.g. [56,58]). However, our findings are consistent with recent work on juvenile chamois showing that environmental conditions during the second year of life, which influence the ability of juveniles to acquire resources directly, have an important effect on investment in growth and energy storage [37,52]. Only in Brenta is there no evidence for density dependence in body mass (Figures 5 and 6). Brenta is calcareous, harbouring a more nutrient-rich plant community [74], so forage availability could be less limiting here than in the other populations. A hunting regime maintaining this population below its carrying capacity, and limiting the effect of resource competition on mass, could also contribute to the less pronounced mass declines observed in Brenta (Figure 1).

There was no evidence for a strong role of vegetation productivity or phenology in the observed long-term mass declines (Table 1, Figure 5). Given that NDVI is only a proxy for vegetation productivity, it remains possible that other changes in vegetation quality and phenology have had more of an effect than suggested here. As with overgrazing, it is possible that warmer temperatures in spring and summer could lead to increases in the abundance of less palatable species [75], or reductions in the protein content of the species present [76], changes which NDVI might not detect. Although they do not appear to play a strong role in mass declines, there is some evidence that vegetation productivity and phenology influence variation in juvenile body mass. This is particularly the case in the calcareous area, Brenta, where there is strong evidence that productive growing seasons (in terms of INDVI and maximum NDVI) have positive effects on juvenile body mass (Table 1, Figure 5). This is consistent with findings from another calcareous Alpine area, where long growing seasons have been linked to higher juvenile chamois body mass [52]. In our study, it is intriguing that the relative importance of environmental factors should vary among neighbouring areas that differ predominantly only in their geological substrate. These differences may arise because calcareous vegetation, whilst being more nutrient-rich, varies more in quality in response to environmental variation than siliceous vegetation [74,77]. The variation in substrate in this study area has previously been shown to mediate differences in reproductive strategy, body mass [38] and horn length [37]; this study further highlights the importance of considering geological variation in studies of animal morphology, physiology and life history.

Conclusions

We have detected strong links between recent environmental change and negative temporal body mass trends in juvenile chamois. Increases in both temperature, due to climate change, and population density, due to stricter controls on hunting, appear to be driving the mass declines. Since we found no evidence for an effect of changing resource productivity or phenology on body mass, the observed patterns may not be mediated by changes in vegetation. We propose that heightened thermoregulatory demands and intra-specific competition, to both of which juveniles are particularly susceptible, could be responsible. These findings add an interesting contrast to the large number of studies implicating climate-mediated changes in resource productivity or phenology as drivers of declines in animal body size. Interestingly, our findings highlight that changes in management could ameliorate negative impacts of climate change. For example, future increases in hunting offtake could reduce the intensity of resource competition, counteracting negative impacts of temperature warming on body mass. This study further highlights the importance of considering management when examining the influence of environmental change on species, which is an increasingly important focus of ecological research (e.g. [63,78,79]). Future reductions in body size are likely to have far-reaching effects on the functioning and productivity of ecosystems [7,8]; decreases in juvenile body condition could result in reduced survival of juveniles and depressed population growth rates. An increasing focus on the links between climate, management, body condition and demography will shed light on the influence of anthropogenic and climate change on populations.

Competing interests

The authors declare that they have no competing interests.

Authors’ contributions

TM, MA, SW and PS conceived the study. TM analysed the data and, with SW and PS, wrote the manuscript. MA and RC provided the data. All authors contributed to revisions and approved the final manuscript.

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References

1. Parmesan C, Yohe G: **A globally coherent fingerprint of climate change impacts across natural systems.** *Nature* 2003, **421:**37–42.

2. Menzel A, Sparks TH, Estrella N, Koch E, Aasa A, Ahas R, Alm-Kubler K, Bissolli P, Braslavska O, Briede A, Chmielewski FM, Crepinsek Z, Curnel Y, Dahl A, Defila C, Donnelly A, Filella Y, Jatcza K, Mage F, Mestre A, Nordli O, Penuelas J, Pirinen P, Remisova V, Scheifinger H, Striz M, Susnik A, Van Vliet AJH, Wielgolaski FE, Zach S: **European phenological response to climate change matches the warming pattern.** *Glob Chang Biol* 2006, **12:**1969–1976.

3. van de Pol M, Vindenes Y, Saether B-E, Engen S, Ens BJ, Oosterbeek K, Tinbergen JM: **Effects of climate change and variability on population dynamics in a long-lived shorebird.** *Ecology* 2010, **91:**1192–1204.

4. Musolin DL: **Insects in a warmer world: ecological, physiological and life-history responses of true bugs (*Heteroptera*) to climate change.** *Glob Chang Biol* 2007, **13:**1565–1585.

5. Ozgul A, Childs DZ, Oli MK, Armitage KB, Blumstein DT, Olson LE, Tuljapurkar S, Coulson T: **Coupled dynamics of body mass and population growth in response to environmental change.** *Nature* 2010, **466:**482–U485.

6. Ozgul A, Tuljapurkar S, Benton TG, Pemberton JM, Clutton-Brock TH, Coulson T: **The Dynamics of Phenotypic Change and the Shrinking Sheep of St. Kilda.** *Science* 2009, **325:**464–467.

7. Gardner JL, Peters A, Kearney MR, Joseph L, Heinsohn R: **Declining body size: a third universal response to warming?** *Trends Ecol Evol* 2011, **26:**285–291.

8. Sheridan JA, Bickford D: **Shrinking body size as an ecological response to climate change.** *Nat Clim Change* 2011, **1:**401–406.

9. Guthrie RD: **Rapid body size decline in Alaskan Pleistocene horses before extinction.** *Nature* 2003, **426:**169–171.

10. Bickford D, Howard SD, Ng DJJ, Sheridan JA: **Impacts of climate change on the amphibians and reptiles of Southeast Asia.** *Biodivers Conserv* 2010, **19:**1043–1062.

11. Bergmann C: **Ueber die Verhältnisse der Wärmeökonomie der Thiere zu ihrer Grösse (Concerning the relationship of heat conservation of animals to their size).** *Gottinger Studien* 1847, **3:**595–708.

12. Mayr E: **Geographical character gradients and climate adaptation.** *Evolution* 1956, **10:**105–108.

13. Ashton KG, Tracy MC, de Queiroz A: **Is Bergmann's rule valid for mammals?** *Am Nat* 2000, **156:**390–415.

14. Meiri S, Dayan T: **On the validity of Bergmann's rule.** *J Biogeogr* 2003, **30:**331–351.

15. Freckleton RP, Harvey PH, Pagel M: **Bergmann's rule and body size in mammals.** *Am Nat* 2003, **161:**821–825.

16. Teplitsky C, Mills JA, Alho JS, Yarrall JW, Merila J: **Bergmann's rule and climate change revisited: Disentangling environmental and genetic responses in a wild bird population.** *Proc Natl Acad Sci U S A* 2008, **105:**13492–13496.

17. Husby A, Hille SM, Visser ME: **Testing Mechanisms of Bergmann's Rule: Phenotypic Decline but No Genetic Change in Body Size in Three Passerine Bird Populations.** *Am Nat* 2011, **178:**202–213.

18. Coltman DW, O'Donoghue P, Jorgenson JT, Hogg JT, Strobeck C, Festa-Bianchet M: **Undesirable evolutionary consequences of trophy hunting.** *Nature* 2003, **426:**655–658.

19. Allendorf FW, England PR, Luikart G, Ritchie PA, Ryman N: **Genetic effects of harvest on wild animal populations.** *Trends Ecol Evol* 2008, **23:**327–337.

20. Clutton-Brock TH, Guinness FE, Albon SD: *Red deer. Behavior and ecology of two sexes.* USA & Edinburgh: University of Chicago & Edinburgh University Press; 1982.

21. Gaillard JM, Festa-Bianchet M, Delorme D, Jorgenson J: **Body mass and individual fitness in female ungulates: bigger is not always better.** *Proc R Soc London B Biol Sci* 2000, **267:**471–477.

22. Stewart KM, Bowyer RT, Dick BL, Johnson BK, Kie JG: **Density-dependent effects on physical condition and reproduction in North American elk: an experimental test.** *Oecologia* 2005, **143:**85–93.

23. Loison A, Langvatn R, Solberg EJ: **Body mass and winter mortality in red deer calves: disentangling sex and climate effects.** *Ecography* 1999, **22:**20–30.

24. Pettorelli N, Weladji RB, Holand O, Mysterud A, Breie H, Stenseth NC: **The relative role of winter and spring conditions: linking climate and landscape-scale plant phenology to alpine reindeer body mass.** *Biol Lett* 2005, **1:**24–26.

25. Pettorelli N, Pelletier F, von Hardenberg A, Festa-Bianchet M, Cote SD: **Early onset of vegetation growth vs. rapid green-up: Impacts on juvenile mountain ungulates.** *Ecology* 2007, **88:**381–390.

26. Toïgo C, Gaillard JM, Van Laere G, Hewison M, Morellet N: **How does environmental variation influence body mass, body size, and body condition? Roe deer as a case study.** *Ecography* 2006, **29:**301–308.

27. Mysterud A, Yoccoz NG, Stenseth NC, Langvatn R: **Effects of age, sex and density on body weight of Norwegian red deer: evidence of density-dependent senescence.** *Proc R Soc London B Biol Sci* 2001, **268:**911–919.

28. Yom-Tov Y, Yom-Tov S, MacDonald D, Yom-Tov E: **Population cycles and changes in body size of the lynx in Alaska.** *Oecologia* 2007, **152:**239–244.

29. Laternser M, Schneebeli M: **Long-term snow climate trends of the Swiss Alps (1931–99).** *Int J Climatol* 2003, **23:**733–750.

30. Parker KL, Robbins CT, Hanley TA: **Energy expenditures for locomotion by mule deer and elk.** *J Wildl Manage* 1984, **48:**474–488.

31. Aublet JF, Festa-Bianchet M, Bergero D, Bassano B: **Temperature constraints on foraging behaviour of male Alpine ibex (*Capra ibex*) in summer.** *Oecologia* 2009, **159:**237–247.

32. Luterbacher J, Dietrich D, Xoplaki E, Grosjean M, Wanner H: **European seasonal and annual temperature variability, trends, and extremes since 1500.** *Science* 2004, **303:**1499–1503.

33. Sinervo B, Mendez-de-la-Cruz F, Miles DB, Heulin B, Bastiaans E, Cruz MVS, Lara-Resendiz R, Martinez-Mendez N, Calderon-Espinosa ML, Meza-Lazaro RN, Gadsden H, Avila LJ, Morando M, De la Riva IJ, Sepulveda PV, Rocha CFD, Ibarguengoytia N, Puntriano CA, Massot M, Lepetz V, Oksanen TA, Chapple DG, Bauer AM, Branch WR, Clobert J, Sites JW: **Erosion of Lizard Diversity by Climate Change and Altered Thermal Niches.** *Science* 2010, **328:**894–899.

34. Kearney M, Shine R, Porter WP: **The potential for behavioral thermoregulation to buffer “cold-blooded” animals against climate warming.** *Proc Natl Acad Sci U S A* 2009, **106:**3835–3840.

35. Stuble KL, Pelini SL, Diamond SE, Fowler DA, Dunn RR, Sanders NJ: **Foraging by forest ants under experimental climatic warming: a test at two sites.** *Ecol Evol* 2013, **3:**482–491.

36. Kjellander P, Gaillard JM, Hewison AJM: **Density-dependent responses of fawn cohort body mass in two contrasting roe deer populations.** *Oecologia* 2006, **146:**521–530.

37. Chirichella R, Ciuti S, Grignolio S, Rocca M, Apollonio M: **The role of geological substrate for horn growth in ungulates: a case study on Alpine chamois.** *Evol Ecol* 2013, **27:**145–163.

38. Mason THE, Chirichella R, Richards SA, Stephens PA, Willis SG, Apollonio M: **Contrasting life histories in neighbouring populations of a large mammal.** *PLoS One* 2011, **6:**e28002.

39. Mason THE, Stephens PA, Willis SG, Chirichella R, Apollonio M, Richards SA: **Intraseasonal variation in reproductive effort: young males finish last.** *Am Nat* 2012, **180:**823–830.

40. Oftedal OT: **Body size and reproductive strategy as correlates of milk energy output in lactating mammals.** *Acta Zool Fenn* 1984, **171:**183–186.

41. Wu ZH, Huang NE, Long SR, Peng CK: **On the trend, detrending, and variability of nonlinear and nonstationary time series.** *Proc Natl Acad Sci U S A* 2007, **104:**14889–14894.

42. Jonzen N, Hedenstrom A, Hjort C, Lindstrom A, Lundberg P, Andersson A: **Climate patterns and the stochastic dynamics of migratory birds.** *Oikos* 2002, **97:**329–336.

43. Skogland T: **The effects of density-dependent resource limitations on the demography of wild reindeer.** *J Anim Ecol* 1985, **54:**359–374.

44. Fryxell J: **Food limitation and demography of a migratory antelope, the white-eared kob.** *Oecologia* 1987, **72:**83–91.

45. Sinclair AR, Dublin H, Borner M: **Population regulation of Serengeti Wildebeeest: a test of the food hypothesis.** *Oecologia* 1985, **65:**266–268.

46. Tucker CJ, Pinzon JE, Brown ME, Slayback DA, Pak EW, Mahoney R, Vermote EF, El Saleous N: **An extended AVHRR 8-km NDVI dataset compatible with MODIS and SPOT vegetation NDVI data.** *Int J Remote Sens* 2005, **26:**4485–4498.

47. Pettorelli N, Vik JO, Mysterud A, Gaillard JM, Tucker CJ, Stenseth NC: **Using the satellite-derived NDVI to assess ecological responses to environmental change.** *Trends Ecol Evol* 2005, **20:**503–510.

48. EEA: *Corine land cover 2006 (CLC2006) 100m - version 2/2010.* 2010.

49. Beck PS, Atzberger C, Høgda KA, Johansen B, Skidmore AK: **Improved monitoring of vegetation dynamics at very high latitudes: A new method using MODIS NDVI.** *Remote Sens Environ* 2006, **100:**321–334.

50. Burnham KP, Anderson DR: *Model selection and multimodel inference: a practical information-theoretic approach.* 2nd edition. New York: Springer; 2002.

51. Richards SA: **Dealing with overdispersed count data in applied ecology.** *J Appl Ecol* 2008, **45:**218–227.

52. Garel M, Gaillard JM, Jullien JM, Dubray D, Maillard D, Loison A: **Population abundance and early spring conditions determine variation in body mass of juvenile chamois.** *J Mammal* 2011, **92:**1112–1117.

53. Linderholm HW: **Growing season changes in the last century.** *Agr Forest Meteorol* 2006, **137:**1–14.

54. Crawley MJ: *Herbivory: the dynamics of animal-plant interactions.* Oxford: Blackwell; 1983.

55. R Development Core Team: *R: A language and environment for statistical computing.* Vienna, Austria: R Foundation for Statistical Computing; 2011.

56. Côté SD, Festa-Bianchet M: **Birthdate, mass and survival in mountain goat kids: effects of maternal characteristics and forage quality.** *Oecologia* 2001, **127:**230–238.

57. Weladji RB, Holand O: **Global climate change and reindeer: effects of winter weather on the autumn weight and growth of calves.** *Oecologia* 2003, **136:**317–323.

58. Bonenfant C, Gaillard JM, Klein F, Loison A: **Sex- and age-dependent effects of population density on life history traits of red deer *Cervus elaphus* in a temperate forest.** *Ecography* 2002, **25:**446–458.

59. Efron B, Tibshirani R: **Statistical Data Analysis in the Computer Age.** *Science* 1991, **253:**390–395.

60. Dussault C, Ouellet JP, Courtois R, Huot J, Breton L, Larochelle J: **Behavioural responses of moose to thermal conditions in the boreal forest.** *Ecoscience* 2004, **11:**321–328.

61. Maloney SK, Moss G, Cartmell T, Mitchell D: **Alteration in diel activity patterns as a thermoregulatory strategy in black wildebeest (*Connochaetes gnou*).** *J Comp Physiol A Neuroethol Sens Neural Behav Physiol* 2005, **191:**1055–1064.

62. Ruttimann S, Giacometti M, McElligott AG: **Effect of domestic sheep on chamois activity, distribution and abundance on sub-alpine pastures.** *Eur J Wildl Res* 2008, **54:**110–116.

63. Mason THE, Stephens PA, Apollonio M, Willis SG: **Predicting potential responses to future climate in an alpine ungulate: inter-specific interactions exceed climate effects.** *Glob Chang Biol* 2014. In press.

64. Hudson RJ: *Body size, energetics, and adaptive radiation.* Boca Raton, Florida: CRC Press, Inc.; 1985.

65. Solberg EJ, Jordhoy P, Strand O, Aanes R, Loison A, Saether BE, Linnell JDC: **Effects of density-dependence and climate on the dynamics of a Svalbard reindeer population.** *Ecography* 2001, **24:**441–451.

66. Forchhammer MC, Clutton-Brock TH, Lindstrom J, Albon SD: **Climate and population density induce long-term cohort variation in a northern ungulate.** *J Anim Ecol* 2001, **70:**721–729.

67. Weckerly FW: **Social bonding and aggression in female Roosevelt elk.** *Can J Zool* 1999, **77:**1379–1384.

68. Espmark Y: **Social behaviour of roe deer at winter feeding stations.** *Appl Anim Ethol* 1974, **1:**35–47.

69. Hilker T, Natsagdorj E, Waring RH, Lyapustin A, Wang Y: **Satellite observed widespread decline in Mongolian grasslands largely due to overgrazing.** *Glob Chang Biol* 2014, **20:**418–428.

70. Fernandez-Gimenez ME, Allen-Diaz B: **Testing a non-equilibrium model of rangeland vegetation dynamics in Mongolia.** *J Appl Ecol* 1999, **36:**871–885.

71. Veiberg V, Loe LE, Mysterud A, Langvatn R, Stenseth NC: **Social rank, feeding and winter weight loss in red deer: any evidence of interference competition?** *Oecologia* 2004, **138:**135–142.

72. Shi J, Dunbar R: **Feeding competition within a feral goat population on the Isle of Rum, NW Scotland.** *J Ethol* 2006, **24:**117–124.

73. Thouless C: **Feeding competition between grazing red deer hinds.** *Anim Behav* 1990, **40:**105–111.

74. Gensac P: **Plant and soil groups in the alpine grasslands of the Vanoise Massif, French Alps.** *Arctic Alpine Res* 1990, **22:**195–201.

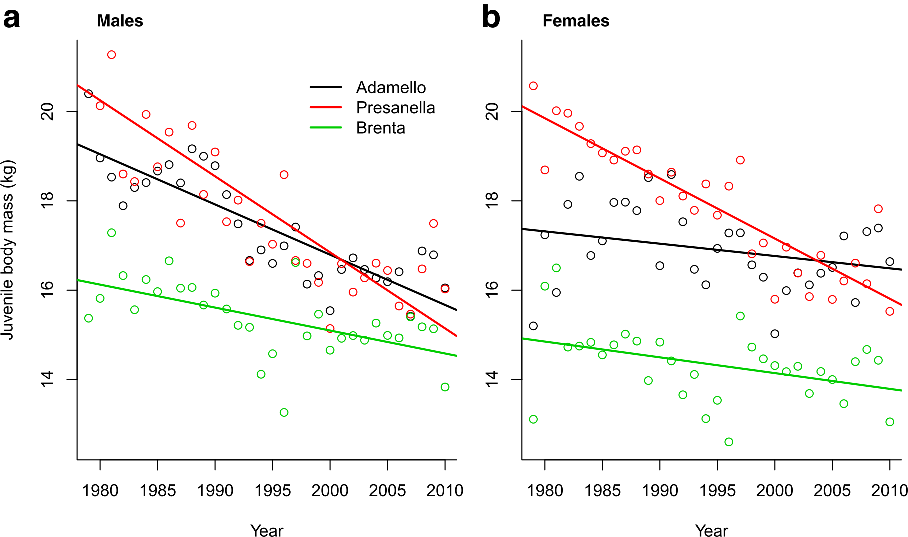
75. Sage RF, Kubien DS: **Quo vadis C4? An ecophysiological perspective on global change and the future of C4 plants.** *Photosynth Res* 2003, **77:**209–225.

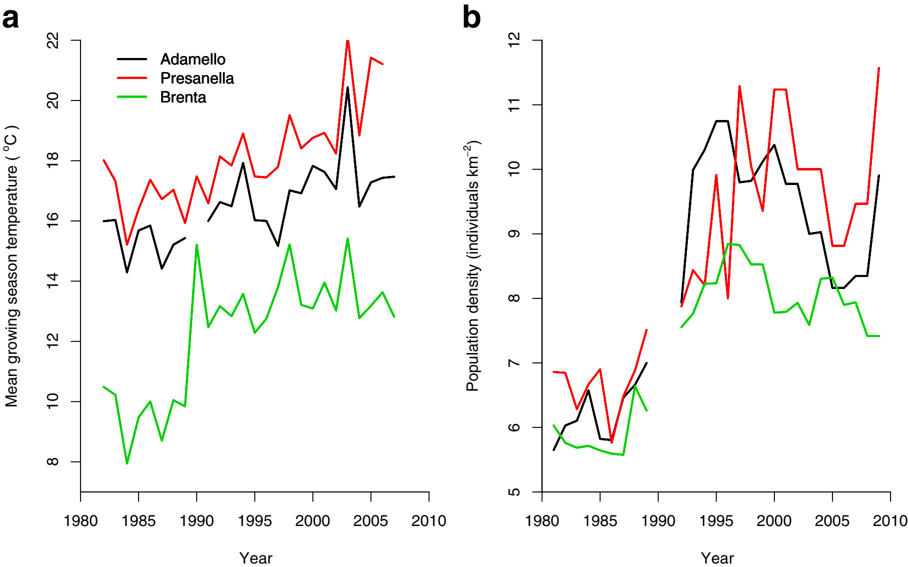
76. Barbehenn RV, Chen Z, Karowe DN, Spickard A: **C3 grasses have higher nutritional quality than C4 grasses under ambient and elevated atmospheric CO2.** *Glob Chang Biol* 2004, **10:**1565–1575.

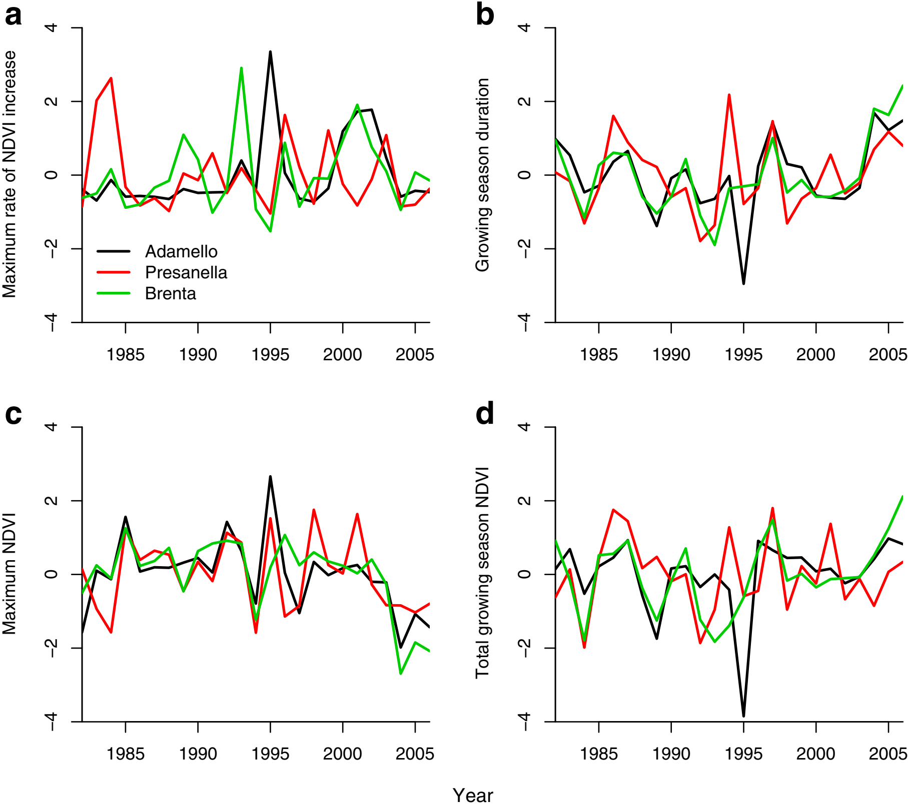
77. Michalet R, Gandoy C, Joud D, Pages JP, Choler P: **Plant community composition and biomass on calcareous and siliceous substrates in the northern French Alps: Comparative effects of soil chemistry and water status.** *Arctic Antarctic Alpine Res* 2002, **34:**102–113.

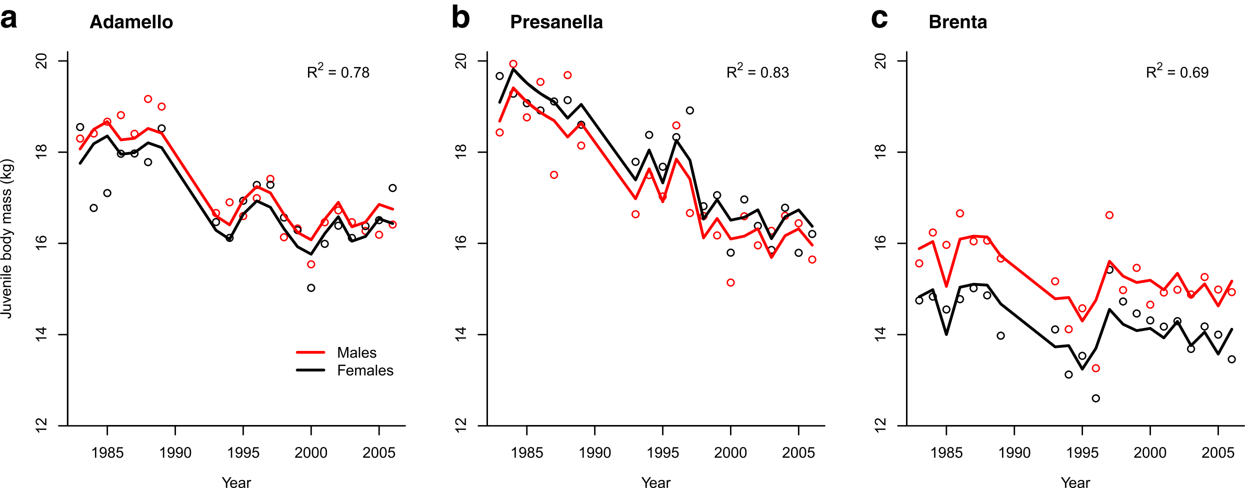
78. Brodie J, Johnson H, Mitchell M, Zager P, Proffitt K, Hebblewhite M, Kauffman M, Johnson B, Bissonette J, Bishop C: **Relative influence of human harvest, carnivores, and weather on adult female elk survival across western North America.** *J Appl Ecol* 2013, **50:**295–305.

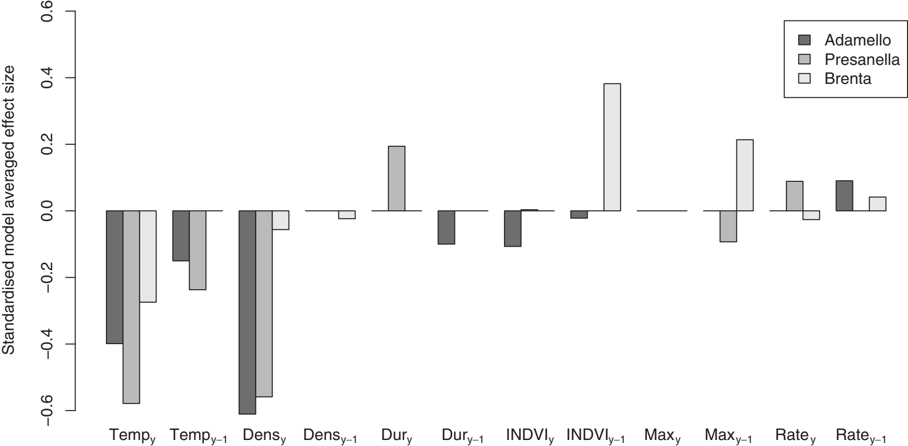
79. Juillet C, Choquet R, Gauthier G, Lefebvre J, Pradel R: **Carry-over effects of spring hunt and climate on recruitment to the natal colony in a migratory species.** *J Appl Ecol* 2012, **49:**1237–1246.

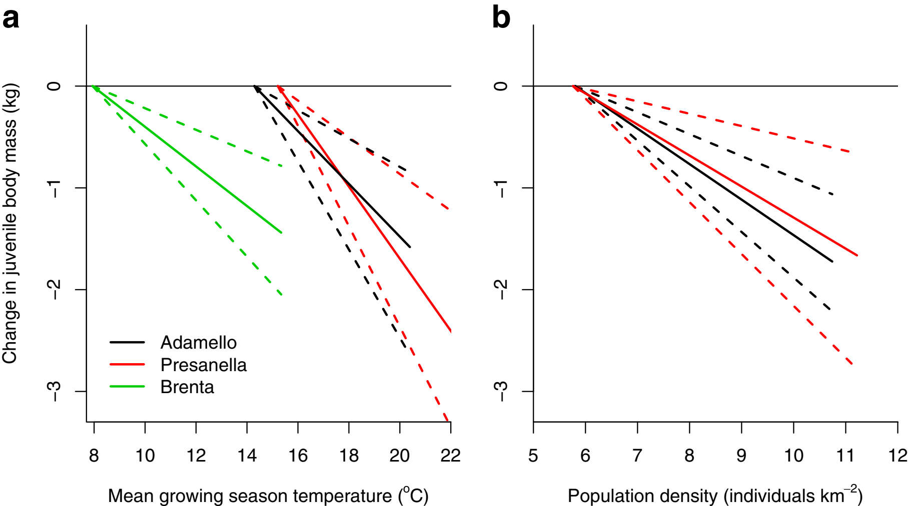

a
Males
b
Females
Adamello
Presanella
Brenta
Juvenile body mass (kg)
14
16
18
20
1980
1985
1990
1995
2000
2005
2010
Year


a
Adamello
Presanella
Brenta
Mean growing season temperature (°C)
8
10
12
14
16
18
20
22
1980
1985
1990
1995
2000
2005
2010
Year
b
Population density (individuals km^{-2})
5
6
7
8
9
10
11
12
1980
1985
1990
1995
2000
2005
2010
Year


a
b
c
d
Maximum rate of NDVI increase
Growing season duration
Maximum NDVI
Total growing season NDVI
Adamello
Presanella
Brenta
4
2
0
−2
−4
1985
1990
1995
2000
2005
Year


a
Adamello
R^2 = 0.78
Males
Females
b
Presanella
R^2 = 0.83
c
Brenta
R^2 = 0.69
Juvenile body mass (kg)
12
14
16
18
20
1985
1990
1995
2000
2005
Year


Standardised model averaged effect size
0.6
0.4
0.2
0.0
−0.2
−0.4
−0.6
Adamello
Presanella
Brenta
Temp$_y$
Temp$_{y-1}$
Dens$_y$
Dens$_{y-1}$
Dur$_y$
Dur$_{y-1}$
INDVI$_y$
INDVI$_{y-1}$
Max$_y$
Max$_{y-1}$
Rate$_y$
Rate$_{y-1}$


a
b
Change in juvenile body mass (kg)
0
−1
−2
−3
8
10
12
14
16
18
20
22
Mean growing season temperature (°C)
Adamello
Presanella
Brenta
5
6
7
8
9
10
11
12
Population density (individuals km−2)

Addtional files provided with this submission:

Additional file 1. Annual variation in sample size of juvenile chamois (16k)
http://www.frontiersinzoology.com/content/supplementary/s12983-014-0069-6-s1.docx

Additional file 2. An illustration of the functional form describing intra-annual variation in NDVI (97k)
http://www.frontiersinzoology.com/content/supplementary/s12983-014-0069-6-s2.docx

Additional file 3. Variation in observed and fitted residuals of juvenile body mass temporal trends (85k)
http://www.frontiersinzoology.com/content/supplementary/s12983-014-0069-6-s3.docx