

Effects of spring–summer temperature on body mass of chamois

MARCO RUGHETTI* AND MARCO FESTA-BIANCHET

Département de Biologie, Université de Sherbrooke, Sherbrooke, Québec J1K 2R1, Canada

* Correspondent: marco.rughetti@usherbrooke.ca

Environmental change, including global warming, can lead to directional changes over time in phenotypic traits such as sex- and age-specific body mass. We evaluated the potential short-term effects of a series of hot and dry springs and early summers on mass of yearling chamois (*Rupicapra rupicapra*) in 2 populations in the western Alps. Yearling mass decreased in both populations over the study period, but much of this decline seemed to originate from a sharp drop in 2003, after which body mass remained low. Our analysis suggested that this decrease was caused by the additive effects of warm springs and summers over the first 2 years of life. The mass of adult chamois also decreased over time. These results suggest that ongoing warming in the Alps could be a selective pressure on the life history and reproductive strategies of wild ungulates.

Key words: body mass, *Rupicapra rupicapra*, temperature, weather, yearlings

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Environmental changes, especially global climate change, may affect the life histories and reproductive strategies of wild species through both ecological and evolutionary mechanisms (Gienapp et al. 2007; Ozgul et al. 2009; Pettorelli et al. 2007). The effects of environmental changes and density dependence on population dynamics are a central issue in ecology (Gaillard et al. 2000; Gordon et al. 2004). These effects may be partly determined by changes in phenotype, such as age- and sex-specific mass (Clutton-Brock and Coulson 2002; Coulson et al. 2001; Toïgo et al. 2006), which is typically correlated with fitness-related life-history traits such as mating success, fecundity, and longevity (Coltman et al. 2005; Mousseau and Roff 1987; Roff and Mousseau 1987).

Most large mammals are considered to be capital breeders because they rely partly on accumulated body reserves to satisfy the energy needs of reproduction (Festa-Bianchet et al. 1998) and individual body mass affects both reproduction and survival (Gaillard et al. 2000). Body mass is a combination of body condition and body size (Taillon et al. 2011; Toïgo et al. 2006). Body condition reflects short-term changes in muscle mass and in the accumulation of fat reserve, whereas structural size depends mostly upon environmental conditions during growth (Festa-Bianchet et al. 2000; Rughetti and Festa-Bianchet 2011b).

Environmental condition can affect the body mass of large herbivores (Clutton-Brock and Coulson 2002; Toïgo et al. 2006). Typically, spring–summer vegetation productivity has strong effects on body mass of adults and growth of juveniles (Herfindal et al. 2006a; Pettorelli et al. 2007; Toïgo et al.

2006). Juveniles are more sensitive than older animals to environmental conditions, because they are undergoing body growth (Gaillard et al. 2000). In temperate climates, temperature has a strong direct effect on plant phenology and vegetation productivity (Chuine and Cour 1999; Linderholm 2006). Consequently, it can indirectly affect ungulate body mass, interacting with precipitation, population density, and winter harshness (red deer [*Cervus elaphus*—Myrsterud et al. 2008] and moose [*Alces alces*—Herfindal et al. 2006a]).

Over the last century, the average temperature in the Alps has increased by 1.1°C; more than double the global average (Böhm et al. 2001). Yearly minimum temperatures have warmed by about 2°C (Beniston et al. 1997). For mountain ungulates these changes in environmental condition may have short-term ecological consequences on body mass. Over the long term, they may become directional selective pressures. Understanding how environmental condition such as temperature affect body mass is of fundamental importance, because ecological and evolutionary pressures on mass can rapidly modify life-history traits and reproductive strategies (Coltman et al. 2003).

Here we evaluate the potential ecological and short-term effects of a series of hot and dry springs and early summers on body mass of chamois (*Rupicapra rupicapra*) in 2 populations in the western Alps. We first focused our analyses on yearlings,



because environmental effects are usually more evident in individuals that have not completed body growth (Gordon et al. 2004). We then tested if observed changes in yearling mass persisted among adult chamois and whether they were caused by changes in structural size or in body condition.

MATERIALS AND METHODS

Study area.—We studied chamois in the Comprensorio Alpino Verbano Cusio-Ossola (VCO2) in northern Piedmont, Italy (727 km²; 46°N, 8°E), and in the adjacent Ticino Canton in Switzerland (2746 km²; 46°N, 9°E). Narrow valleys and steep mountains dominated all landscapes. Snow cover at the bottom of the valleys (850–1,000 m elevation) usually lasted from December to March. Beech (*Fagus sylvatica*) forests, predominant at the bottom of the valley, were replaced by conifers (*Picea abies*, *Abies alba*, and *Larix decidua*) as elevation increased, and by alpine pastures at higher elevations. Roe deer (*Capreolus capreolus*) and wild boars (*Sus scrofa*) were present mainly below 1,200 m elevation. Red deer were abundant in both study areas.

Chamois data.—We obtained data on sex, age, and body mass (eviscerated and partially eviscerated for VCO2, and only eviscerated for Ticino Canton) for 756 yearlings and 1,409 adults chamois harvested in VCO2 from 1996 to 2008 and for 4,374 yearling and 18,459 adults chamois harvested in the 6 hunting districts of Ticino from 1993 to 2009. Age of individuals can be determined with precision by counting horn annuli (Schroder and Elsner-Schack 1985). Because in VCO2 some hunted chamois were eviscerated and others partially eviscerated (with heart, liver, and lungs), we 1st estimated the sex- and age-specific difference in mass then subtracted it from partially eviscerated chamois to estimate their eviscerated mass. In VCO2 hunting begins in early September and normally ends in early October. In Ticino hunting starts in the 1st week of September and the harvest plan is mostly completed after 3 weeks. Harvest date was transformed to Julian date with day 1 on 1 September. Although total ground counts were conducted yearly in VCO2, they do not provide reliable estimates of population density (Loison et al. 2006). No estimate of density was available for Ticino.

Weather.—We obtained data from 3 meteorological stations for Ticino and 1 for VCO2. We calculated the monthly mean temperature (°C) averaged from April to July and total precipitation (mm) over the same period. For Ticino we averaged values across stations. We selected the April–July period because for chamois in our study areas late pregnancy and the birth seasons are in April (Rughetti and Festa-Bianchet 2011a), whereas May–July is the main period of lactation for kids and body mass increase for yearlings. In alpine habitats, vegetation growth begins in April, peaks in July, then decreases (Pettorelli et al. 2007). Temperatures follow a similar pattern. Yearly weather in Ticino and VCO2 was strongly correlated (temperature: $r = 0.81$, $t_{12} = 4.88$, $P < 0.001$; precipitation: $r = 0.85$, $t_{12} = 5.74$, $P < 0.001$), therefore

we used indexes obtained for Ticino because of the longer time series.

Statistical analysis.—To test for a temporal trend in yearling mass over time, we fit a mixed model for each population setting sex and year of harvest as fixed effects. To examine the effects of climatic variables on yearling mass, we fit a mixed model for each population separately. Because temperature and precipitation during the 1st (kid) and 2nd (yearling) year of life were not correlated (all $P \geq 0.12$), we considered them as independent variables and set them as explanatory fixed effects in the same model.

Yearling mass should directly reflect resource availability, because it responds to the combined effects of population density and vegetation productivity (Garel et al. 2011). Because from 2003 onward, yearling body mass decreased substantially, we expected that adult chamois harvested before 2003 would be heavier than those harvested later. To test this hypothesis we fit a mixed model for each population, with adult mass as response variable. We set age as a fixed effect with quadratic and cubic effects to account for the nonlinear change of mass with age (Rughetti and Festa-Bianchet 2011b). Year of harvest was a fixed effect with 2 levels: before 2003, and from 2003 onward.

Male chamois are fully grown by age 5 years (Rughetti and Festa-Bianchet 2011b); therefore, to determine whether changes in adult mass were caused by changes in structural size or in body condition, we fit a mixed model setting as response variable the mass of males that were aged 5 years and older before 2003. Because this analysis only included males that had completed structural growth, mass of males harvested from 2003 onward could only be affected by changes in body condition. We set age and year of harvest (2 levels: before 2003, and from 2003 onward) as fixed effects. We performed this analysis only for adult males because the decline in body mass was less evident in females.

In all mixed models we accounted for variability of year of harvest and harvest date by setting them as random effects. For Ticino, hunting district also was set as a random effect to account for variability between hunting areas. Model selection was based on the Akaike information criterion corrected for small sample size (AIC_c—Burnham and Anderson 2002). We calculated AIC weights as a measure of support for a given model. AIC weights estimate the probability that a model is the best in a set of candidate models (Burnham and Anderson 2002). We 1st created a general model accounting for the effects of sex, temperature, and precipitation as a yearling, their 1st-order interactions, and temperature and precipitation as kid. We did not include higher-order interactions to avoid complex models of uncertain biological meaning. We then ran all models with all possible combinations of explanatory variables from the general model and ranked them by AIC weight. Because no single model was clearly superior (AIC weight > 0.9), we averaged all models within <4 AIC_c units of the model with the lowest AIC_c (Burnham and Anderson 2002) and calculated parameter estimates and confidence intervals.

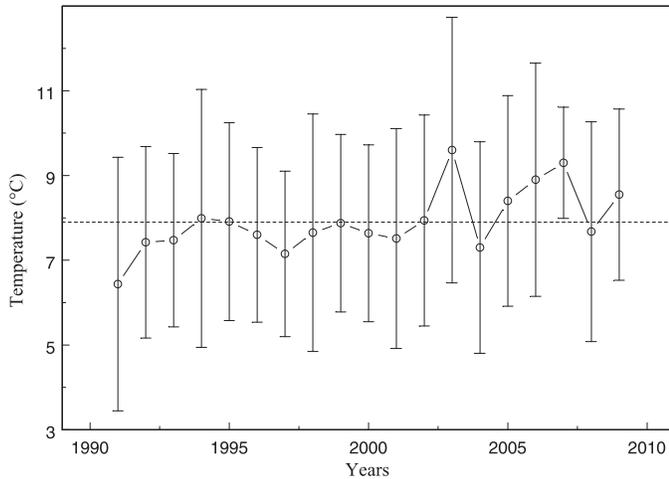


FIG. 1.—Average April–July temperatures with standard error (*SE*) from 1991 to 2009 for Ticino, Switzerland. The horizontal line indicates the average temperature over the study period.

All statistical analyses were performed using R, version 2.12.1 (R Development Core Team 2009).

RESULTS

The years 2003–2009 were on average warmer and drier than previous years (temperature: $F_{1,15} = 9.58, P = 0.007$; precipitation: $F_{1,15} = 11.37, P = 0.004$). Average temperature from 1993 to 2002 was 7.6°C; from 2003 to 2009 it was 8.5°C. Total April–July precipitation from 1993 to 2002 was 834 mm; from 2003 to 2009 it was 603 mm. The spring–summer of 2003 was 1.7°C warmer than the study period average (Fig. 1), and years 2005–2009 were on average 0.9°C warmer than the study period average.

Yearling mass decreased over time in both populations and for both sexes (Table 1; Fig. 2). There seemed to be a sudden decline in 2003, after which yearling chamois remained small

TABLE 1.—Mixed model of mass as a function of sex and year of harvest (continuous variables) for yearling chamois (*Rupicapra rupicapra*) harvested in Comprensorio Alpino Verbano Cusio-Ossola (VCO2), Piedmont, Italy ($n = 756, 1996–2008$), and in Ticino, Switzerland ($n = 4,769, 1993–2009$). Year of harvest (variance: Ticino = 0.10 and VCO2 = 0.00), harvest date (variance: Ticino = 0.02 and VCO2 = 0.13), and district (for Ticino only; variance = 1.00) were included as random effects. Residual variance: Ticino = 5.11 and VCO2 = 6.28. *CI* = confidence interval.

	Estimate	SE	<i>t</i>	<i>CI</i> _{0.025}	<i>CI</i> _{0.975}
Ticino					
Intercept	231.753	40.964	5.658	153.473	323.724
Sex (male)	86.368	32.354	2.669	23.630	152.898
Year	-0.109	0.020	-5.315	-0.155	-0.069
Sex (male)*year	-0.043	0.016	-2.658	-0.076	-0.012
VCO2					
Intercept	384.174	58.061	6.617	244.884	517.795
Sex (male)	0.391	0.185	2.108	0.018	0.752
Year	-0.184	0.029	-6.349	-0.251	-0.114

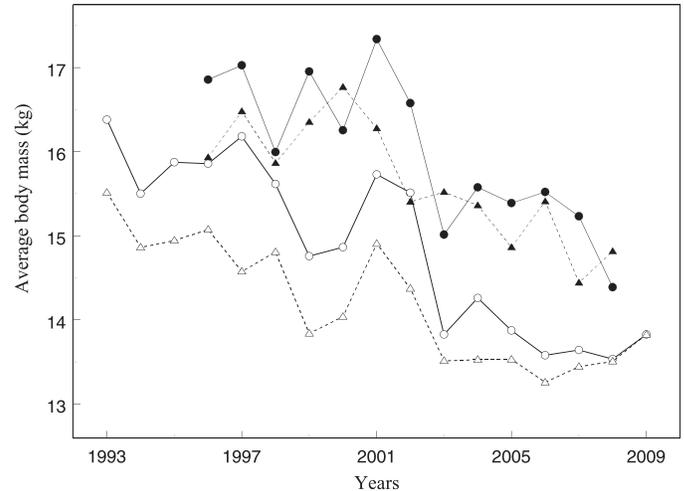


FIG. 2.—Yearly average eviscerated body mass of yearling male (circles) and female (triangles) chamois harvested in Comprensorio Alpino Verbano Cusio-Ossola (VCO2), Piedmont, Italy ($n = 756, 1996–2008$, solid symbols), and in Ticino, Switzerland ($n = 4,769, 1993–2009$, open symbols). In VCO2, standard error (*SE*) ranges from 0.36 to 0.93 kg for male mass and from 0.27 to 0.96 kg for females. In Ticino, *SE* ranges from 0.14 to 0.37 kg for males and from 0.15 to 0.37 kg for females.

(Fig. 2). After accounting for sex, yearling body mass from 2003 onward was lower than in previous years for both Ticino (estimate = -0.128, $SE = 0.018, t = -7.017, P < 0.001$) and VCO2 (estimate = -0.183, $SE = 0.028, t = -6.624, P < 0.001$). In Ticino, mean mass before 2003 was 15.6 kg ± 2.5 *SD* for males and 14.5 ± 2.5 kg for females. In 2003–2009 it declined by 12% to 13.8 ± 2.5 kg for males and by 7% to 13.5 ± 2.6 kg for females. In VCO2, mean mass in 1996–2002 was 16.7 ± 2.6 kg for males and 16.1 ± 2.6 kg for females, declining in 2003–2008 by 9% to 15.2 ± 2.3 kg for males and by 6% to 15.1 ± 2.6 kg for females. After removing the difference in body mass before and after 2003 (Ticino: estimate = -0.681, $SE = 0.273, t = -2.496, P = 0.013$; VCO2: estimate = -0.777, $SE = 0.369, t = -2.107, P = 0.035$), the effect of year of harvest as a continuous response variable was significant in Ticino only for males (estimate = -0.047, $SE = 0.031, t = -1.554, P = 0.121$; sex [male]: estimate = -0.045, $SE = 0.016, t = -2.811, P = 0.005$). It was not significant in VCO2 (estimate = -0.090, $SE = 0.054, t = -1.651, P = 0.09$).

The best models ($\Delta AIC_c < 4$ —Burnham and Anderson 2002) were very similar for VCO2 and Ticino (Table 2). Temperatures as yearling and kid were always the most important explanatory variables for yearling mass (Table 2). Warm spring–summer temperatures during the first 2 years of life reduced yearling mass in both populations (Tables 2 and 3; Fig. 3). The average estimates of additional weather parameters were not different from zero, suggesting a weak effect on yearling mass variability over time (Table 3). Adult chamois harvested before 2003 were heavier than those shot from 2003 onward (Table 4; Figs. 4 and 5). After accounting for age, for the subsample of males aged 5 years and older and fully grown before 2003, those shot from 2003 onward were lighter than

TABLE 2.—Model selection for the effects of temperature as yearling (Ty), temperature as kid (Tk), precipitation as yearling (Py), precipitation as kid (Pk), and sex on the body mass of yearling chamois (*Rupicapra rupicapra*) harvested in Comprensorio Alpino Verbano Cusio-Ossola (VCO2), Piedmont, Italy ($n = 756$, 1996–2008), and in Ticino, Switzerland ($n = 4,769$, 1993–2009). The table reports number of parameters (Np), differences in Akaike's information criterion corrected for small sample size (ΔAIC_c) between each model and the model with the lowest AIC_c , and the Akaike weights (w_s) of each model. Only models with $\Delta AIC_c < 4$ are reported. An x indicates term included. Null model: Ticino, $\Delta AIC_c = 41.160$; VCO2, $\Delta AIC_c = 10.051$.

Ty	Tk	Sex	Py	Pk	Sex*Ty	Ty*Py	Sex*Py	Np	ΔAIC_c	w
Ticino										
x	x	x			x			9	0.000	0.236
x	x	x	x		x			10	1.764	0.098
x	x	x						8	1.793	0.096
x	x	x		x	x			10	1.911	0.091
x	x	x	x		x		x	11	3.137	0.049
x	x	x	x		x	x		11	3.436	0.042
x	x	x	x					9	3.574	0.039
x	x	x	x	x	x			11	3.680	0.037
x	x	x		x				9	3.693	0.037
VCO2										
x	x	x						7	0.000	0.115
x	x	x		x				8	0.833	0.076
x	x	x	x				x	9	1.024	0.069
x	x	x			x			8	1.550	0.053
x	x	x	x					8	1.746	0.048
x	x	x	x	x			x	10	1.793	0.047
x	x							6	2.256	0.037
x	x	x		x	x			9	2.386	0.035
x		x		x				7	2.425	0.034
x	x	x	x	x				9	2.517	0.033
x	x	x	x			x	x	10	2.844	0.028
x	x	x	x		x		x	10	3.022	0.025
x	x	x	x	x		x	x	11	3.259	0.023
x	x			x				7	3.260	0.023
x	x	x	x		x			9	3.303	0.022
x	x	x	x			x		9	3.563	0.019
x	x	x	x	x	x		x	11	3.799	0.017
x	x		x					7	3.972	0.016

those harvested before 2003 for both Ticino (estimate = -1.022 , $SE = 0.301$, $t = -3.390$, $P = 0.0007$, $n = 2947$) and VCO2 (estimate = -1.821 , $SE = 0.625$, $t = -2.910$, $P = 0.004$, $n = 167$).

DISCUSSION

Our analyses produced 3 main results. First, body mass of yearling chamois decreased over the study period, mostly because it dropped suddenly in 2003, and never recovered. Second, this decrease seemed related to the additive effects of warm spring–summer temperatures over the first 2 years of life. Finally, the mass of adult chamois also decreased after 2003, likely because of a decline in body condition.

Ciais et al. (2005) reported a strong decrease in plant primary productivity across Europe in 2003 relative to previous years. The unusually warm July was proposed as the main cause of this reduction, although there is some debate as to whether water limitation or high temperatures had the strongest effect on plant productivity (Reichstein et al. 2007). In our study sites, unusually warm temperatures also were recorded in 2005, 2006, 2007, and 2009 (Fig. 1). Examination of our data

suggests that high spring–summer temperatures in 2003–2009 were the main cause of reduction in yearling mass. Although reduced plant productivity in 2003 could explain low yearling body mass that year, the persistence of low mass in subsequent years was likely because of continuing similar environmental conditions. Our analysis suggests an additive effect of high temperatures experienced over the first 2 summers of life on the mass of yearlings in autumn (Table 2). That result confirms the importance of environmental conditions during early growth for large herbivores (Forchhammer et al. 2001; Nussey et al. 2007). A decline in mass also was evident in adults. In large herbivores, female body condition often affects offspring mass, mostly at high population density when females reduce maternal care (Festa-Bianchet and Jorgenson 1998). Therefore, the reduction in adult female mass could reinforce the negative effect of high temperatures on yearling mass.

These results are important for 2 main reasons. First, they support earlier suggestions that sport harvests are unlikely to have a strong selective effect on chamois phenotypic traits (Rughetti and Festa-Bianchet 2010, 2011b). Instead, it seems that directional change in environmental conditions may be responsible for a strong decrease in the mass of Alpine

TABLE 3.—Average parameter estimates from models within 4 Akaike’s information criterion corrected for small sample size (AIC_c) units of the model with the lowest AIC for the mass of yearling chamois (*Rupicapra rupicapra*) harvested in Comprensorio Alpino Verbano Cusio-Ossola (VCO2), Piedmont, Italy ($n = 756$, 1996–2008), and in Ticino, Switzerland ($n = 4,769$, 1993–2009). Mass was a function of temperature as yearling (Ty), temperature as kid (Tk), precipitation as yearling (Py), and precipitation as kid (Pk). *CI* = confidence interval.

	Estimate	SE	CI _{0.025}	CI _{0.975}
Ticino				
Intercept	22.000	2.800	16.500	27.500
Ty	-0.472	0.232	-0.927	-0.018
Tk	-0.523	0.183	-0.883	-0.163
Sex (male)	1.430	0.860	-0.253	3.120
Py	0.0005	0.0012	-0.0018	0.0027
Pk	0.00006	0.00023	-0.00050	0.00038
Sex (male)*Ty	-0.126	0.101	-0.324	0.072
Ty*Py	0.00004	0.00010	-0.00024	0.00017
Sex (male)*Py	0.00002	0.00005	-0.00013	0.00009
VCO2				
Intercept	23.600	3.480	16.800	30.500
Ty	-0.514	0.174	-0.855	-0.172
Tk	-0.465	0.204	-0.866	-0.065
Sex (male)	0.200	0.992	-1.750	2.150
Py	-0.00054	0.00203	-0.00452	0.00345
Pk	-0.00039	0.00062	-0.00083	0.00161
Sex (male)*Ty	-0.022	0.078	-0.176	0.132
Ty*Py	0.00001	0.00017	-0.00032	0.00034
Sex (male)*Py	0.00046	0.00076	-0.00103	0.00196

chamois. Second, examination of our data suggests that ongoing warming in the Alps could lead to changes in life history and reproductive strategies of mountain ungulates through an effect on body growth and adult mass. These effects

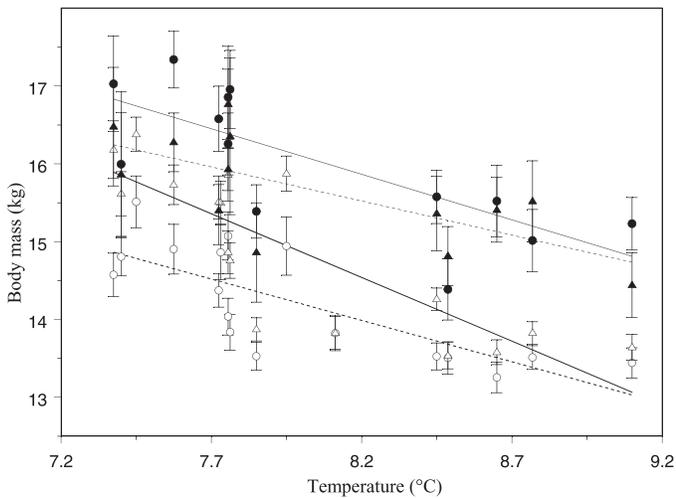


FIG. 3.—Eviscerated body mass with standard errors (SEs) in relation to spring–summer temperature for yearling male (circles) and female (triangles) chamois harvested in Comprensorio Alpino Verbano Cusio-Ossola (VCO2), Piedmont, Italy ($n = 756$, 1996–2008, solid symbols), and in Ticino, Switzerland ($n = 4,769$, 1993–2009, open symbols). Temperatures were averaged over the first 2 years of life of each cohort.

TABLE 4.—Mixed model of mass as a function of sex, age, and year for adult chamois (*Rupicapra rupicapra*) harvested in Comprensorio Alpino Verbano Cusio-Ossola (VCO2), Piedmont, Italy ($n = 1,409$, 1996–2008), and in Ticino, Switzerland ($n = 18,459$, 1993–2009). Year was set as a 2-level factor: for Ticino 1996–2002 and 2003–2009; for VCO2 1993–2002 and 2003–2008. Year of harvest (variance: Ticino = 0.11 and VCO2 = 0.13), harvest date (variance: Ticino = <0.001 and VCO2 = 0.01), and district (for Ticino only; variance = 1.13) were included as random effects. Residual variance: Ticino = 9.71 and VCO2 = 11.50. *CI* = confidence interval.

	Estimate	SE	t	CI _{0.025}	CI _{0.975}
Ticino					
Intercept	7.202	0.405	17.780	6.235	8.052
Sex (male)	4.890	0.049	99.750	4.790	4.977
Age	4.658	0.084	55.560	4.493	4.812
Age ²	-0.471	0.011	-42.540	-0.492	-0.449
Age ³	0.014	<0.001	33.090	0.013	0.015
Year (2003–2009)	-0.522	0.174	-3.000	-0.904	-0.131
VCO2					
Intercept	12.568	0.578	21.753	11.387	13.735
Sex (male)	5.854	0.187	31.287	5.477	6.232
Age	3.438	0.278	12.369	2.895	4.004
Age ²	-0.349	0.039	-9.042	-0.425	-0.271
Age ³	0.010	0.002	6.751	0.007	0.013
Year (2003–2008)	-1.044	0.276	-3.784	-1.6781	-0.302

can best be monitored and understood through long-term studies of marked known-age animals (Clutton-Brock and Sheldon 2010).

Our results agree with previous studies of other large herbivores (Herfindal et al. 2006b; Pettorelli et al. 2007; Solberg et al. 1999) reporting that warm temperature in spring reduces body mass, likely by affecting plant phenology. In

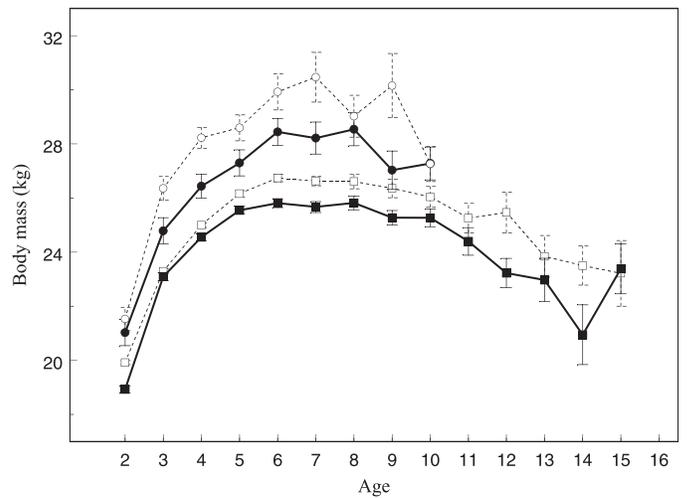


FIG. 4.—Average age-specific eviscerated body mass with standard errors (SEs) for 381 and 404 adult male chamois shot in Comprensorio Alpino Verbano Cusio-Ossola (VCO2), Piedmont, Italy, from 1996 to 2002 (open circles and dashed lines) and from 2003 to 2008 (solid circles and lines) and for 7,408 and 3,842 adult male chamois shot in Ticino, Switzerland, from 1993 to 2002 (open squares and dashed lines) and from 2003 to 2008 (solid squares and lines).

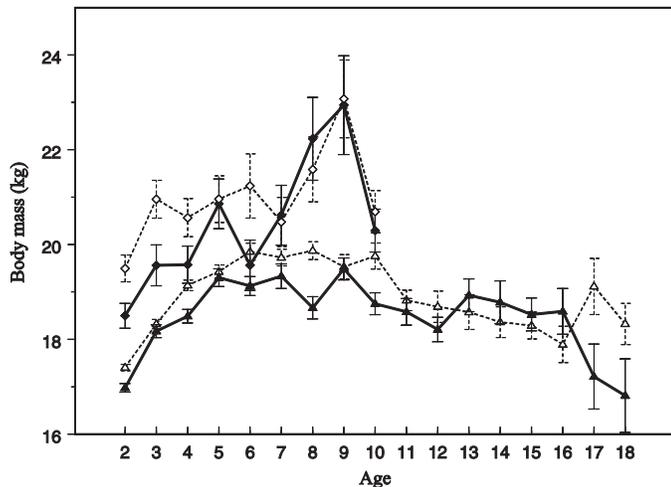


FIG. 5.—Average age-specific eviscerated body mass with standard errors (SEs) for 298 and 326 adult female chamois shot in Comprensorio Alpino Verbano Cusio-Ossola (VCO2), Piedmont, Italy, from 1996 to 2002 (open diamonds and dashed lines) and from 2003 to 2008 (solid diamonds and lines) and for 4,258 and 2,951 adult female chamois shot in Ticino, Switzerland, from 1993 to 2002 (open triangles and dashed lines) and from 2003 to 2008 (solid triangles and lines).

mountain ungulates, warm temperatures reduce the growth of mountain goats (*Oreamnos americanus*) and bighorn sheep (*Ovis canadensis*) juveniles by accelerating plant development and shortening the period of availability of growing vegetation with high nutritional quality (Pettorelli et al. 2007). For yearling chamois in the French Alps (Garel et al. 2011), an early onset of green-up led to heavier juveniles, although no temporal trend was reported. The poor foraging conditions in spring and early summer suggested by small yearling mass after 2003 also seemed to reduce the mass of adult chamois (Figs. 4 and 5), possibly leading to lower survival and population growth, as shown for other chamois populations (Loison et al. 1999).

The decline in mass in 2003–2009 by fully grown males that did not experience high temperatures in early life was likely caused mostly by a reduction in body condition rather than in structural size. That decline in body mass may have reflected a short-term response to poor food quality and quantity caused by high temperature. Although we observed an ecological response of chamois body mass to high temperature, persistent high temperatures in future years could act as an evolutionary pressure with long-term effects on the life history of mountain ungulates (Ozgul et al. 2009).

Our analyses could not account for changes in population density. Population density often affects the mass of young ungulates (Bonenfant et al. 2009). Unfortunately, there are no reliable data on changes in density of the populations that we studied. Over the study period in Ticino (for which we have the largest sample), however, the age structure of harvested males indicated an increase in older age classes, whereas the number of harvested adults decreased, suggesting a reduction in hunting pressure. Lower harvest rate may allow an increase

in density, which could partly explain the reduction in mass through increased intraspecific competition. The sudden decline in mass in 2003–2009, however, was more likely caused by a sudden decrease in resource availability than to a gradual increase in population density.

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