

## The role of geological substrate for horn growth in ungulates: a case study on Alpine chamois

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**Abstract** Ecological factors such as environmental and climatic conditions affect the growth of ornaments in ungulates. Studies about their influence can reveal key information on individual life histories and detect the events that can have important evolutionary consequences. Among the ecological factors commonly thought to play a role in such ecological processes, researches have so far neglected the possible influence of the geological feature which may either promote or restrain the early investment in horn growth. This study takes into consideration a broad range of ecological factors that are expected to affect horn growth and analyses how the substrate (calcareous *versus* siliceous) could modify the horn size in 1,685 yearling Alpine chamois (*Rupicapra rupicapra*) which were legally shot during 5 consecutive years in Central-Eastern Italian Alps. Interestingly, we found shorter horns in chamois shot on siliceous than on calcareous substrate, irrespective of the sex, showing how the substrate (and related ecological conditions) may affect horn growth. The substrate interacted with two ecological factors in shaping the horn size, i.e. aspect and snow cover. Differences between horn lengths recorded for chamois shot on these two substrates were less pronounced where South-facing slopes prevailed. During an average winter (about 100 days with more than 10 cm of snow on the ground) chamois horns were longer in individuals using calcareous areas, although the increase of number of

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days with more than 10 cm of snow on the ground had a stronger impact in reducing horn length in calcareous environment. We demonstrated that substrate, and related ecological conditions, influence horn growth. In ungulate species where ornament size is related to reproductive success, environmental factors, such as geological feature, can thus cause evolutionary consequences in the expression of ornaments and individual fitness.

**Keywords** *Rupicapra rupicapra* · Horn growth · Geological substrate · Precipitation · Snowfall · Temperature

## Introduction

In polygynous mammals, well-developed weaponry favours male reproductive success conferring advantages in intrasexual competition and are often preferred by females (Andersson 1994). Environmental conditions and related food availability are responsible for affecting the body condition of ungulates, which is strongly related with antler and horn size (*Rupicapra pyrenaica*, Pérez-Barbería et al. 1996; *Oreamnus americanus*, Côté et al. 1998; *Capra ibex*, von Hardenberg et al. 2004; *Ovis canadensis*, Festa-Bianchet et al. 2000, 2004; *Cervus elaphus hispanicus*, Gaspar-López et al. 2008). These traits are thus affected by several non-genetic factors such as habitat, winter harshness, and, more in general, environmental conditions. Nievergelt (1966) showed remarkable differences in the horn growth of Alpine ibex (*Capra ibex*) males living in different ecological contexts, and more recent papers confirmed these findings in other ungulate species (Fandos 1995; Pérez-Barbería et al. 1996; Jorgenson et al. 1998; Festa-Bianchet et al. 2000, 2004; Kruuk et al. 2002; Ciuti and Apollonio 2011). Previous studies showed that climatic factors such as rainfall (Pérez-Barbería et al. 1996; Giacometti et al. 2002; Von Hardenberg et al. 2004), temperatures (Schmidt et al. 2001; Giacometti et al. 2002), and winter conditions (Mysterud et al. 2005) influence horn and antler growth by modifying the food availability. Researchers also showed an indirect effect of population density on weapon growth, due to intra-specific competition for resources (Jorgenson et al. 1998; Mysterud et al. 2005; Schmidt et al. 2001).

Among the ecological factors commonly thought to affect growth and size of horns, researchers have neglected the possible influence of the geological feature, and associated soil composition and ecological conditions, which may either promote or restrain the early investment in growth of these traits. Characteristics of soil, though, are important features that could affect vegetation communities and forage quality, and, consequently, growth rate and size of weapons in ungulates. As Geist and Bayer (1988) reported, Vogt's (1948) first showed that grasses, compared to foliage, forbs and some browse were lower in protein, and especially in mineral content. Vogt (1948) also showed that the chemical composition of forage greatly affected the antler size in both red deer (*Cervus elaphus*) and roe deer (*Capreolus capreolus*). Pastures on calcareous substrates have a higher grazing value than pastures on siliceous substrates due to nitrogen-richness (Rameau et al. 1993), better quality of grassland communities (Cavallero et al. 2007) and high species richness (Michalet et al. 2002). Thus, herbivores grazing on calcareous substrate may be expected to be in comparatively better conditions and to exhibit larger secondary sexual traits. In this respect, regional differences (i.e. large scale) in white-tailed deer antler size (*Odocoileus virginianus*) were found to be likely due to differences in soil fertility (Strickland and Demarais 2000).

Horns and antlers of ungulates represent one of the most evident examples of secondary sexual traits in vertebrates and have been object of interest since Darwin (1859, 1871) developed his theory of sexual selection. In ungulates, siring success is affected by male's age, social rank, body and weapon size (Pemberton et al. 1992; Coltman et al. 2002; Mainguy et al. 2009). Size of horns and antlers was found to be related to mating success in many ungulate species, such as red deer (Kruuk et al. 2002), fallow deer (*Dama dama*; Ciuti and Apollonio 2011), and feral sheep (*Ovis aries*; Preston et al. 2001). Antler size in cervids was also correlated with sperm quantity and quality (Malo et al. 2005). However, in some ungulate groups there are no firm evidences that horn size influences male mating success, as recently shown for rupicapinae in mountain goats (*Oreamnos americanus*; Mainguy et al. 2009). It is thus important to disentangle all factors that may affect horn growth in rupicaprinae and might mask potential correlations between horn size and mating success. The analysis of ecological factors influencing horns growth and size can provide key information for the study of individual life histories (e.g. von Hardenberg et al. 2004), and for a deeper understanding of population dynamics in large herbivores (e.g. Toigo et al. 2006; Bergeron et al. 2008).

Part of the variation in weapon size in ungulates has been shown to have a genetic basis (Kruuk et al. 2002), but related individuals also often show similarity due to shared environmental factors (Kruuk and Hadfield 2007). Such shared environmental effects may also result in an association between the fitness of an individual and its phenotype. For example, a study on red deer found that the relationship between antler size and fitness was largely due to an environmental covariance between the two rather than a genetic covariance (Kruuk et al. 2002). This study highlights the need to carefully consider which ecological factors are involved and their effect as this can have important consequence for trait evolution.

Unlike cervids' antlers, which are renewed every year, the early development of permanent horns is a critical life-step for bovids. Given that the majority of horn growth occurs during the first years of life in several species (see for example *O. americanus* Festa-Bianchet and Côté 2008 and *Rupicapra rupicapra* Rughetti and Festa-Bianchet 2011), it is important to determine the factors affecting such an early investment because horn size can foster future individual success. Alpine chamois (*R. rupicapra*) is an ideal case study for disentangling investment on weapons (Garel et al. 2009; Rughetti and Festa-Bianchet 2010; Rughetti and Festa-Bianchet 2011). About 60–70 % of horn growth takes place in the first 1.5 years of life in both males and females (Bassano et al. 2003; Rughetti and Festa-Bianchet 2010; Rughetti and Festa-Bianchet 2011).

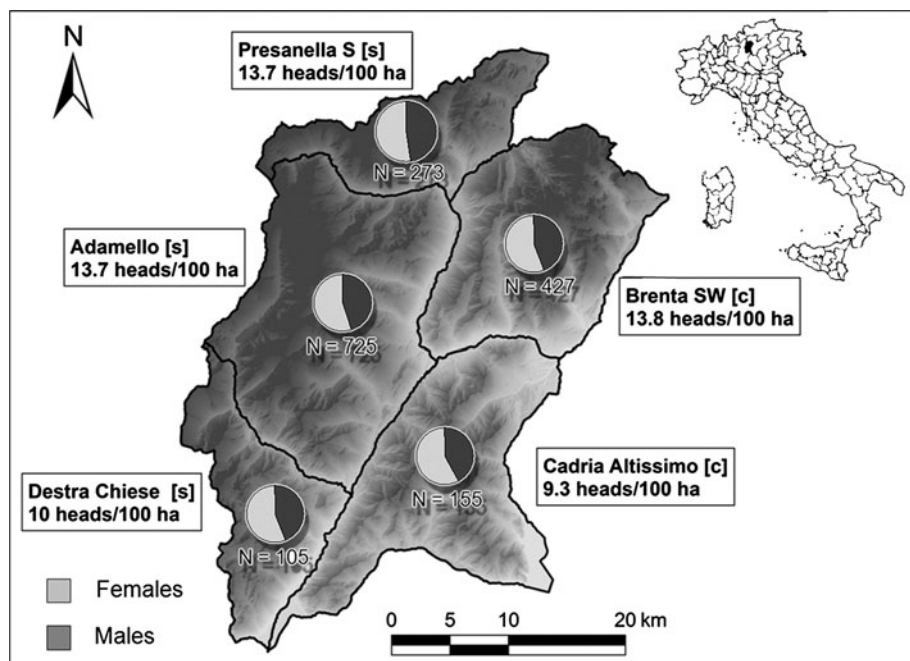
In this study we analysed the variation of horn size of 1,685 yearling Alpine chamois legally shot in autumn–winter (when about 1.5 y.o.) during 5 consecutive years in the central-eastern Italian Alps. By controlling for age (the same for the whole sample), we assessed the influence on horn growth of a broad range of ecological factors such as elevation, aspect, climate (rainfall, snow cover, temperature, winter harshness), along with other factors such as sex and population density and we analysed whether the geological substrate (calcareous *versus* siliceous) can affect such an early investment in Alpine chamois. Our analysis, performed in a relatively small area with fairly homogeneous climatic characteristics and different substrate types, enabled us to investigate for the first time the relationship between each substrate and growth rate and size of weapons in an ungulate species.

## Materials and methods

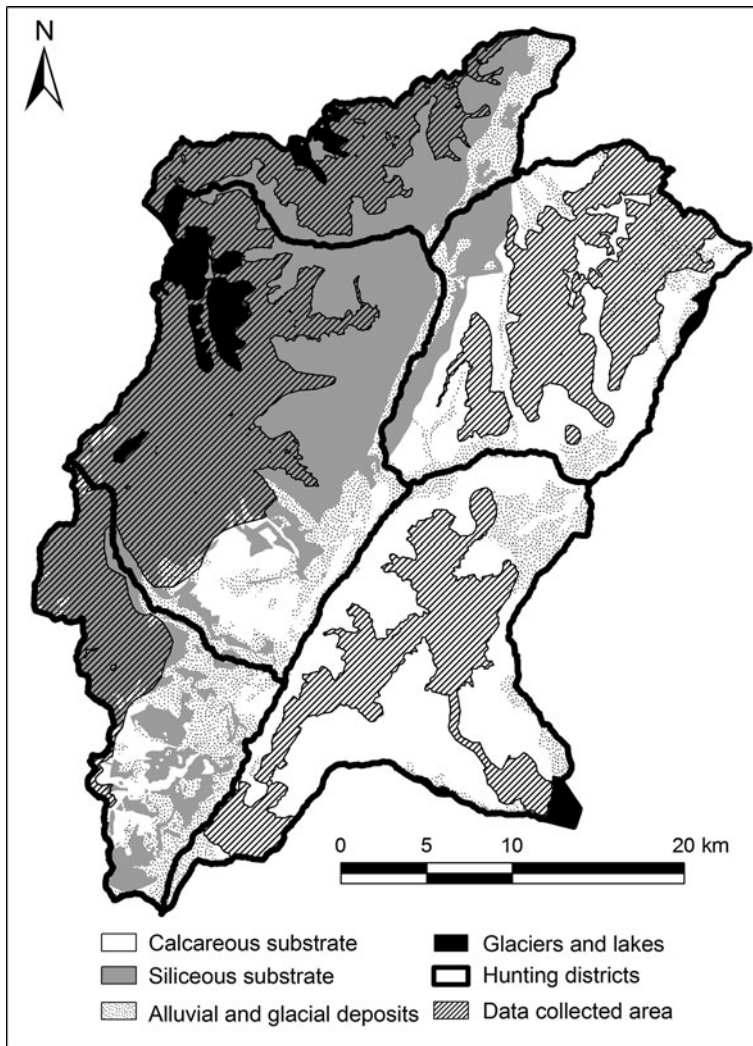
### Study area

This study was carried out in the Central-Eastern Alps (Fig. 1), in a 121,906 ha-wide area of the Trento Province (46°02'N; 10°38'E), Italy. Two macro areas were recognizable within the study site (Fig. 2): the Adamello-Presanella Massif (51,847 ha), characterized by siliceous rocks, and the Brenta and Cadria Altissimo Massif (70,059 ha), characterized by calcareous and sedimentary rocks (mainly limestone and dolomite). As a consequence of the different geological features of these two macro areas, soil composition accounts for the natural development of different plant associations, with special regard to meadows above the tree line. Typical meadows covering the calcareous substrate were mainly composed by *Sesleria albicans* and *Carex firma*, whereas meadows covering the siliceous substrate were composed by *Festuca scabriculmis* and *Carex curvula* (Adamello Brenta Nature Park—official data). Red deer and roe deer were abundant but rarely used the areas above the tree line (2,000 m a.s.l.), which were usually populated by the Alpine chamois. In contrast, mouflon (*Ovis orientalis musimon*) and Alpine ibex, which potentially used chamois areas, were limited to few and small spots, the two species having been respectively introduced and reintroduced in the recent past only.

The study area was subdivided into 5 hunting districts (Fig. 1) where chamois hunting with rifles was allowed from mid-September to mid-December. The 5 hunting districts



**Fig. 1** Map of the study area (Province of Trento, Central-Eastern Alps, Italy). The 5 hunting districts (substrate type: [s] = siliceous, [c] = calcareous) where 1,685 yearling chamois were legally shot during 5 consecutive years are shown in the digital elevation model of the study area (darker colours correspond to higher elevation above sea level). Chamois density (heads/100 ha) and sample size (N chamois shot) are shown for each hunting district. Sample size split according to sex is indicated by the pie charts



**Fig. 2** Map of the study area (Province of Trento, Central-Eastern Alps, Italy) showing geological features (Trento Province Official data; geological categories were reduced by authors) and locations of chamois data collection. The 5 hunting districts where 1,685 yearling chamois were legally shot during 5 consecutive years are shown on the map

were further subdivided into 68 municipal reserves (hunting management units). Every summer, i.e. after the birth period and prior to the hunting season, population density was estimated by means of block count census in all municipal reserves of the five hunting districts. Hunting was regulated through licenses issued by local wildlife boards. Hunting quotas in each district were set for specific sex-age classes. During this study (2005–2009), yearling quota represented 22 % of the planned hunting bag in each hunting district and 88 % of the quota was met. The inspection by wildlife managers of each chamois shot was mandatory in each municipal reserve.

## Data collection and analyses

From 2005 to 2009, we measured the left horn length of 1,685 yearling Alpine chamois shot during 5 consecutive hunting seasons (Fig. 1). The left horn length was measured to the nearest 0.5 millimetres on the front side by 2 researchers using a flexible ruler. Repeated measures ( $n = 3$ ; Palmer 1994) were taken on a subsample of 50 horns in order to test (Paired-Samples *t* Test) the absence of data collector effect. An error lower than 3.5 % was considered negligible for secondary sexual traits in ungulates (Kruuk et al. 2003). We ascertained that hunting mortalities differed among hunting districts by means of ANOVA analysis, in order to exclude any potential bias due to a heterogeneous distribution of mortalities in the 5 hunting districts through time.

Kids of chamois were usually born in May (Schröder 1971) and yearling Alpine chamois were about 16–19 months old when shot and measured (depending on the shooting day through the hunting season). Thus, yearling chamois had experienced two summers and one winter since they were born. Accordingly, we considered a large number of ecological factors potentially able to influence the horn growth during their life. The complete list of these predictor variables is reported in Table 1. We also considered some ecological factors of the period before the birth of sampled chamois, which are supposed to affect the body condition of the mothers during late pregnancy, and of the kids (Table 1). ArcGIS 9.3 (ESRI inc. 1999–2008) was used to associate predictor variables to the location of the shooting place of each sampled chamois.

We built a correlation matrix (Pearson correlation coefficient,  $r_p$ ) within each sub-group of variables potentially able to predict horn length to avoid collinearity (Sokal and Rohlf 1995). Highly correlated variables ( $r_p > 0.7$ ) were examined by means of Pearson correlation coefficient (Table 1) in order to select the one that was better correlated with the response variable (i.e., left horn length).

We analysed the variation of the left horn length by fitting Linear Mixed Effect models with the REML method. We considered the hunting district as a random factor in our models to avoid pseudo-replication of data. We used the Akaike information criterion (AIC; Symonds and Mousalli 2011; Burnham et al. 2011) to select the best predicting model. To avoid retention of overly complex models (i.e., models having additional parameters that result in a minimal increase of fit), we excluded models that were only more complex versions of those with a lower AIC value (Richards et al. 2011). Akaike weight  $w_i$  for a given model  $i$  of a set of  $n = R$  models was computed as follows:  $w_i = \exp(-0.5 \Delta AIC_i) / \sum_{r=1}^R \exp(-0.5 * \Delta AIC_r)$ , which quantifies the probability that the model is the best approximating one. AIC approach might penalize the models in relation to the number of predictor variables (Greven and Kneib 2010), as the number of predictors is not assessable because of the random effect. Accordingly, both Gelman and Hill (2007) and Bolker et al. (2009) advocated the use of the deviance information criterion (DIC). Hence, we checked our model selection also by DIC approach (see “Appendix”). We performed parameter estimation for the most parsimonious model. We estimated  $R^2$  following Magee (1990) to describe the way models fitted the observed data as follows:  $R^2 = 1 - \exp(-2/n(\log L_M - \log L_0))$ , where  $n$  is the number of observations,  $\log L_M$  is the standard log-likelihood of the model (which includes fixed and random effects) and  $\log L_0$  is the standard log-likelihood of the intercept-only model. Statistical analyses were performed using R version 2.14.1 (R Development Core Team 2011); all means were reported with standard errors.

**Table 1** Candidate variables potentially able to predict the variability of horn length in yearling Alpine chamois

| Factor                              | Unit of measurement and description   | Variables included in model selection [f = fixed factor; c = covariate] | Predicted link with horn length  | Supporting examples in ungulates                                 |
|-------------------------------------|---|---|--|--|
| Sex                                 | –   | Females, males [f]  | Horns are expected to be shorter in females.   | Pérez-Barbería et al. (1996)                                     |
| Soil                                | –   | Siliceous, calcareous [f]   | Horns are expected to be shorter on siliceous soil due to lower quality of meadows (Duchaufour 1989, 1997; Gensac 1990; Rameau et al. 1993). | None   |
| Snow cover (Nov–Apr) <sup>b</sup>   | Days—number of days with more than 10 cm of snow on the ground from November to April | Snow cover (November–April) [c]   | Horns are expected to be shorter as higher energy expenditure for locomotion is required due to snow cover and snow depth.                   | Parker et al. (1984)   |
| Snow cover (Mar–Apr) <sup>a,b</sup> | Days—number of days with more than 10 cm of snow on the ground in March–April         | –   |  |  |
| Snow depth (Nov–Apr) <sup>a,b</sup> | cm—average snow cover for the whole period November–April                             | –   |  |  |
| Rain (Apr–May I) <sup>b</sup>       | mm—total precipitation during late pregnancy–birth period                             | Rain Apr–May I [c]  | Horns are expected to be longer as more abundant precipitations improve forage availability (indirect effect driven by mothers' care).       | Oftedal (1984); Gómez (2004)                                     |
| Rain (Jun–Jul I) <sup>b</sup>       | mm—total precipitation during early lactation period                                  | Rain Jun–Jul I [c]  |  |  |
| Rain (Aug–Sept I) <sup>b</sup>      | mm—total precipitation during late lactation period                                   | Rain Aug–Sept I [c]   |  |  |
| Rain (Apr–May II) <sup>b</sup>      | mm—total precipitation during spring when chamois were 1 y.o.                         | Rain Apr–May II [c]   | Horns are expected to be longer as more abundant precipitations improve forage quality and quantity  | Côté et al. (1998); Lesage et al. (2000); Gendreau et al. (2005) |

Table 1 continued

| Factor   | Unit of measurement and description   | Variables included in model selection [f = fixed factor; c = covariate] | Predicted link with horn length   | Supporting examples in ungulates |
|--|---|---|---|----------------------------------|
| Rain (Jun–Jul II) <sup>b</sup>                     | mm—total precipitation during late spring-early summer when chamois were 1 y.o. | Rain Jun–Jul II [c]   |   |                                  |
| Rain (Aug–Sept II) <sup>b</sup>                    | mm—total precipitation during late summer when chamois were 1 y.o.              | Rain Aug–Sept II [c]  |   |                                  |
| Max winter temperature (Dec–Feb) <sup>b</sup>      | °C—average maximum temperatures during the coldest months of the year           | Max temperature Dec–Feb [c]   | Horns are expected to be longer as lower energy expenditure for thermoregulation is required due to higher winter temperature | Mysterud et al. (2005)           |
| Min winter temperature (Dec–Feb) <sup>a,b</sup>    | °C—average minimum temperatures during the coldest months of the year           | –   |   |                                  |
| Mean winter temperature (Dec–Feb) <sup>a,b</sup>   | °C—average temperatures during the coldest months of the year                   | –   |   |                                  |
| Max spring temperature (Mar–May I) <sup>a,b</sup>  | °C—average maximum temperatures during the pre-birth period                     | –   |   | Toigo et al. (1999)              |
| Min spring temperature (Mar–May I) <sup>a,b</sup>  | °C—average minimum temperatures during the pre-birth period                     | –   |   |                                  |
| Mean spring temperature (Mar–May I) <sup>b</sup>   | °C—average temperatures during the pre-birth period                             | Mean temperature Mar–May I [c]  |   |                                  |
| Max spring temperature (Mar–May II) <sup>a,b</sup> | °C—average maximum temperatures during the only spring experienced by animals   | –   |   | Toigo et al. (1999)              |
| Min spring temperature (Mar–May II) <sup>a,b</sup> | °C—average minimum temperatures during the only spring experienced by animals   | –   |   |                                  |



**Table 1** continued

| Factor  | Unit of measurement and description   | Variables included in model selection [f = fixed factor; c = covariate] | Predicted link with horn length  | Supporting examples in ungulates |
|---|---|---|--|----------------------------------|
| Mean spring temperature (Mar–May II) <sup>b</sup> | °C—average temperatures during the only spring experienced by animals                                 | Mean temperature Mar–May II [c]   |  |                                  |
| Max summer temperature (Jul I) <sup>b</sup>       | °C—average maximum temperatures during the hottest months of the first year of life                   | Max temperature Jul I [c]   | Horns are expected to be shorter as higher summer temperatures decrease meadow quality.        | Crête and Courtois (1997)        |
| Min summer temperature (Jul I) <sup>a,b</sup>     | °C—average minimum temperatures during the hottest month of the first year of life                    | –   |  |                                  |
| Mean summer temperature (Jul I) <sup>a,b</sup>    | °C—average temperatures during the hottest month of the first year of life                            | –   |  |                                  |
| Max summer temperature (Jul II) <sup>b</sup>      | °C—average maximum temperatures during the hottest months of the second year of life                  | Max temperature Jul II [c]  | Horns are expected to be shorter as higher summer temperatures decrease meadow quality.        | Crête and Courtois (1997)        |
| Min summer temperature (Jul II) <sup>a,b</sup>    | °C—average minimum temperatures during the hottest month of the second year of life                   | –   |  |                                  |
| Mean summer temperature (Jul II) <sup>a,b</sup>   | °C—average temperatures during the hottest month of the second year of life                           | –   |  |                                  |
| Aspect (South to North)                           | –1 < aspect < 1—average aspect of the municipal reserve (n = 68) where chamois were shot <sup>c</sup> | Aspect [c]  | Horns are expected to be shorter in north facing slopes due to lower solar radiation exposure. | Jonas et al. (2008)              |
| Maximum elevation                                 | m a.s.l.—maximum elevation of the municipal reserve (n = 68) where chamois were shot                  | Maximum elevation [c]   | Horns are expected to be shorter as higher altitudes reduce forage availability.               | Mysterud et al. (2005)           |
| Mean elevation <sup>a</sup>                       | m a.s.l.—average elevation of the municipal reserve (n = 68) where chamois were shot                  | –   |  |                                  |

**Table 1** continued

| Factor                     | Unit of measurement and description                                      | Variables included in model selection [f = fixed factor; c = covariate] | Predicted link with horn length  | Supporting examples in ungulates                 |
|----------------------------|--|---|--|--|
| Hunting date               | Number of days after the beginning of the hunting season (7th September) | Hunting date [c]  | Horns are expected to be longer at the end of hunting season (due to horn growth during autumn-early winter) | Pérez-Barbería et al. (1996)                     |
| Chamois population density | Number of heads per 100 ha   | Chamois population density [c]  | Horns are expected to be shorter as higher is population density (limited food resources due to competition) | Gaillard et al. (1998); Post and Stenseth (1999) |

<sup>a</sup> Variable not included in model selection due to collinearity

<sup>b</sup> Five weather stations and snow-gauges supplied data on temperatures, precipitations and depth of snow cover (Forecasts and Organization Office—Civil Protection and Infrastructures Department—Trento Province, official data). These covariates were associated according to municipal reserve considering the weather station closest to the reserve

<sup>c</sup> Originally expressed within the 0–360° range, it was cosine transformed, therefore assuming values from –1 (south facing slopes) to 1 (north facing slopes)

## Results

The temporal distribution of hunting mortalities did not differ among the 5 hunting districts (ANOVA:  $F_{4,1684} = 0.775$ ,  $p = 0.508$ ). We tested for data collector effect on measurement of left horn lengths. The average measurement error was lower than 0.8 % for both measurers. No differences were reported between data collected by the 2 collectors (Paired-Samples  $t$  Test:  $t_{(2)49} = 0.41$ ,  $p = 0.79$ ).

The top 10 Linear Mixed Effect models predicting horn length in yearling chamois are reported in Table 2. The most parsimonious model (AIC = 13,963.9,  $R^2 = 0.62$ ) had 92 % probability to be the best approximating one. Parameter estimates of the best predicting model are reported in Table 3. Males had longer horns ( $n = 929$ ,  $153.36 \pm 0.58$  mm) than females ( $n = 756$ ,  $130.14 \pm 0.59$  mm). Horns were recorded to be longer for chamois shot on calcareous substrate than on siliceous ones, for both females (siliceous substrate:  $n = 502$ ,  $127.76 \pm 0.68$  mm; calcareous substrate:  $n = 254$ ,  $133.74 \pm 1.04$  mm) and males (siliceous substrate:  $n = 601$ ,  $150.68 \pm 0.89$  mm; calcareous substrate:  $n = 328$ ,  $157.11 \pm 0.98$  mm).

The number of days with more than 10 cm of snow cover recorded from November to April of the chamois first year of life had a negative effect on their horn length: the more days of snow cover, the shorter the horns (Table 3). Spring rainfalls recorded in April–May I (i.e. during late pregnancy of mothers, birth period, and early gestation) and those recorded in April–May II (i.e. when sampled individuals were 1 y.o.) positively affected horn growth (Table 3), with longer horns recorded when higher precipitations occurred. Mean temperatures recorded in spring (March–May I) were included in the best model even though without a clear effect on horn length (Table 3), while spring mean temperatures recorded in the second year of life of chamois negatively affected their horn length. The average maximum temperatures recorded in July during the 1st and 2nd year of life of sampled chamois negatively affected horn length (Table 3), while the average maximum temperature recorded in winter (Dec.–Feb.) positively affected horn growth.

As the aspect value decreased (i.e. the shooting occurred in a municipality where the average mountainside faced the South), the horn length increased (Table 3). The higher the maximum elevation of the municipal reserve where the sample was shot, the shorter the horn (Table 3). The date also played a role in the model: the later into the hunting season a chamois was shot, the longer the horn. Finally, population density had a negative effect on horn size (Table 3).

Only 2 two-way interactions were included in the best predicting model (Table 2). Environmental variables such as snow cover (number of days with more than 10 cm of snow on the ground) and aspect had effects on horn length that varied according to substrate (Table 3). During an average winter (about 100 days with more than 10 cm of snow on the ground) chamois horns were recorded to be longer in individuals using calcareous areas than in individuals using siliceous areas (Fig. 3). As the number of days with more than 10 cm of snow cover increased, the horn length of chamois shot in areas with calcareous substrate decreased (Fig. 3). Differences between horn lengths recorded for chamois shot on the two substrates were less pronounced where South-facing slopes prevailed. Chamois shot on calcareous substrate had indeed longer horns than those shot on siliceous ones, when North-facing slopes prevailed (Fig. 3).

**Table 2** Top 10 linear mixed effect models predicting horn length in yearling chamois shot during 5 consecutive years in the Trento province, Italy

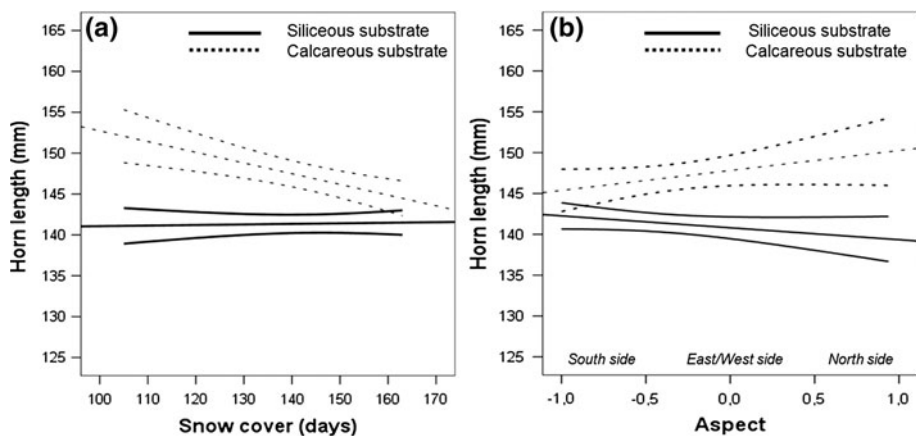
|              | Sex      | Substrate | Snow cover days | Rain Apr-May I | Rain Apr-May II | Rain Jun-Jul I | Rain Jun-Jul II | Rain Aug-Sep I | Rain Aug-Sep II | Max temperature Dec-Feb | Max temperature Jul I | Max temperature Jul II | Mean temperature Mar-May I | Mean temperature Mar-May II | Aspect   | Maximum elevation | Hunting day | Density  | Sex * Substrate | Sex * Snow cover days | Sex * Maximum elevation | Sex * Density | Substrate * Snow cover days | Substrate * Aspect | Substrate * Maximum elevation | Substrate * Density | Snow cover days * Aspect | Snow cover days * Density |
|--------------|----------|-----------|-----------------|----------------|-----------------|----------------|-----------------|----------------|-----------------|-------------------------|-----------------------|------------------------|----------------------------|-----------------------------|----------|-------------------|-------------|----------|-----------------|-----------------------|-------------------------|---------------|-----------------------------|--------------------|-------------------------------|---------------------|--------------------------|---------------------------|
|              | x        | x         | x               | x              | x               | x              | x               | x              | x               | x                       | x                     | x                      | x                          | x                           | x        | x                 | x           | x        | x               | x                     | x                       | x             | x                           | x                  | x                             | x                   | x                        | x                         |
| <i>AIC</i>   | 13963.90 | 13963.90  | 13963.90        | 13963.90       | 13963.90        | 13963.90       | 13963.90        | 13963.90       | 13963.90        | 13963.90                | 13963.90              | 13963.90               | 13963.90                   | 13963.90                    | 13963.90 | 13963.90          | 13963.90    | 13963.90 | 13963.90        | 13963.90              | 13963.90                | 13963.90      | 13963.90                    | 13963.90           | 13963.90                      | 13963.90            | 13963.90                 | 13963.90                  |
| $\Delta AIC$ | 0.00     | 0.00      | 0.00            | 0.00           | 0.00            | 0.00           | 0.00            | 0.00           | 0.00            | 0.00                    | 0.00                  | 0.00                   | 0.00                       | 0.00                        | 0.00     | 0.00              | 0.00        | 0.00     | 0.00            | 0.00                  | 0.00                    | 0.00          | 0.00                        | 0.00               | 0.00                          | 0.00                | 0.00                     | 0.00                      |
| $w_i$        | 0.91294  | 0.91294   | 0.91294         | 0.91294        | 0.91294         | 0.91294        | 0.91294         | 0.91294        | 0.91294         | 0.91294                 | 0.91294               | 0.91294                | 0.91294                    | 0.91294                     | 0.91294  | 0.91294           | 0.91294     | 0.91294  | 0.91294         | 0.91294               | 0.91294                 | 0.91294       | 0.91294                     | 0.91294            | 0.91294                       | 0.91294             | 0.91294                  | 0.91294                   |

x Terms included in each model, *AIC* akaïke information criterion;  $\Delta AIC$  difference in the *AIC* value between a given model and the most parsimonious one,  $w_i$  akaïke weight. See Table 1 for description of predictor variables

**Table 3** Coefficients ( $\beta$ ) and standard errors (SE) estimated by the best linear mixed effect model ( $AIC = 13,963.9$ ,  $w_i = 0.92$ ,  $R^2 = 0.62$ , see Table 2) predicting horn length in yearling chamois shot during 5 consecutive years in the Trento province, Italy

| Predictors                                     | $\beta$ | SE     |
|--|---------|--------|
| Intercept                                      | 198.349 | 10.380 |
| Sex [females]                                  | −23.345 | 0.773  |
| Substrate [siliceous]                          | −10.174 | 5.023  |
| Snow cover days (Nov–Apr)                      | −0.135  | 0.058  |
| Rain Apr–May I                                 | 0.037   | 0.019  |
| Rain Apr–May II                                | 0.014   | 0.011  |
| Mean temperature Mar–May I                     | −0.230  | 0.868  |
| Mean temperature Mar–May II                    | −0.768  | 0.554  |
| Max temperature Jul I                          | −0.242  | 0.172  |
| Max temperature Jul II                         | −0.224  | 0.140  |
| Max temperature Dec–Feb                        | 1.033   | 0.331  |
| Aspect   | −0.436  | 0.178  |
| Maximum elevation                              | −0.005  | 0.001  |
| Hunting day                                    | 0.072   | 0.016  |
| Density  | −1.342  | 0.321  |
| Substrate [siliceous] $\times$ snow cover days | 0.071   | 0.042  |
| Substrate [siliceous] $\times$ aspect          | 1.664   | 1.183  |

See Table 1 for description of predictor variables



**Fig. 3** Effect of snow cover (number of days with more than 10 cm of snow on the ground from November to April; *left chart*) and aspect on horn length (*right chart*) of  $n = 582$  yearling chamois shot in the calcareous substrate and  $n = 1,103$  yearling chamois shot in the siliceous substrate. Aspect (originally expressed within the  $0\text{--}360^\circ$  range) was cosine transformed, thus assuming values ranging from  $-1$  (i.e., south facing slopes) to  $1$  (i.e., north facing slopes). Linear relationships along with 95 % Confidence Intervals are reported on each graph

## Discussion

Horns were found to be longer in chamois shot in calcareous areas than in siliceous ones. The quality of meadows on a calcareous substrate is generally assumed to be higher than that of meadows on a siliceous one, due to the following reasons: (1) higher species richness (Cavallero et al. 2007; Grime 1979); (2) higher nutrient availability related to higher plant productivity (Duchafour 1989, 1997; Gensac 1990; Rameau et al. 1993); (3) the plant communities growing on siliceous substrate have structural characteristics that can also reduce digestion efficiency (Laca et al. 2001), and may negatively affect the energy intake of the animals feeding on them, with consequences on body size and the growth of weapons. Winnie et al. (2008) showed that the African buffalo modified spatial behaviour and foraging strategies according to the geologic substrate features (granite *versus* basalt) and to the corresponding differences in food quality and quantity. Indeed, granite areas are generally less fertile than areas characterized by other substrates, due to small nitrogen pools that tend to turn over slowly. Hence, Winnie et al. (2008) argued for the varying effects of different substrate on buffalo herd dynamics, distribution, and population dynamics.

We found two interactions between substrate type and both snow cover and aspect (i.e., mountain exposure). There were differences in horn length between substrate types in southern exposure but these became even more pronounced in northern exposures, with longer horns being recorded on calcareous substrate than on siliceous ones. Furthermore, we found that horn length decreased with increasing snow cover on calcareous substrates whereas it did not on siliceous substrates. As Michalet et al. (2002) argued, in damp conditions (high rainfall and/or deep soils and/or northern exposure) the calcareous substrate is more nitrogen rich than the siliceous one because of the higher amount of clay in the former (enhancing organic matter decomposition and thus nitrogen availability), whereas in dry conditions the calcareous substrate is less nitrogen-rich than siliceous one, because the mesh of the former induces a high water stress for plants. Thus, our results showed that horn length was positively affected by calcareous substrates especially in northern exposure, and that snow cover duration played an important role in that it reduced the positive effect of calcareous substrates. Geomorphic features of calcareous and siliceous areas vary to a considerable extent: limestone rocky areas are generally characterized by steep walls and herbaceous terraces, while siliceous areas are characterized by more even slopes with a homogeneous herbaceous cover. Calcareous environments are more likely to suffer from severe winters: thick and persistent snow cover causes a decrease in herbaceous growth, reducing the positive effect of the calcareous substrate (Michalet et al. 2002). As showed by Cavallero et al. (2007), vegetation communities growing on siliceous substrates in the Italian Alps show a higher resistance to winter conditions than vegetation of higher quality growing on calcareous substrate, ensuring constant trophic level availability in different environmental conditions. Michalet et al. (2002) found an increase in crude biomass and vegetation cover from calcareous to siliceous substrate. Moreover, opal silica improves plant resistance to mechanical stress and pathogens (Raven 1983). In the siliceous substrate we may expect more constant conditions whereas calcareous communities may display pronounced variability in plant biomass and quality. The environmental stress (i.e. snow cover) may induce different trade-offs between energy for maintenance activities and investment in horns in siliceous and calcareous areas.

Our findings showed that the geological substrate could also influence horn growth indirectly. We investigated the concurrence of a number of environmental and climatic variables (including some that had never been tested in chamois before) influencing the

early horn growth. Adverse environmental and climatic conditions (i.e. chamois shot in areas with higher snow cover and winter lower temperatures, with abundant northern slopes, and at higher elevations) negatively affected horn lengths in individuals of both sexes. Snow cover recorded in winter before the shooting negatively affected horn length, while higher winter temperatures had a positive effect. Harsh winters are generally thought to affect juvenile body conditions and survival by increasing the probability of starvation, through a combination of higher thermoregulatory costs and decreased forage availability due to deep snow cover (Forchhammer et al. 1998). Winters are harsher in north-facing mountainsides on account of lower solar radiation and this aspect may negatively affect horn growth, also in reason of the longer duration of snow cover (Jonas et al. 2008), as confirmed by the effect of the aspect in our best model. Another variable that influenced horn size was the average elevation of the municipal reserve where chamois were shot and where, supposedly, they had lived: the higher the elevation of such areas, the higher the probability to find snow cover. The height and persistence of snow cover were reported to affect the costs of locomotion (Parker et al. 1984) and availability of browsing (Post and Stenseth 1999). Snow cover was correlated with winter mortality of Alpine chamois (Jonas et al. 2008) and Pyrenean chamois (*Rupicapra pyrenaica*, Gonzalez and Crampe 2001). Similarly, as resources became scarce, young bighorn rams were reported to allocate an increasing proportion of resources to body growth, rather than to horn growth (Festa-Bianchet et al. 2004). Chamois using more elevated sites settle for suboptimal conditions, possibly as a pay off for a safer environment and a reduced intra-guild competition. It is well known that this species can live as low as 400 m above sea level (Apollonio et al. 2010), even though this implies a greater vulnerability to predators (e.g. wolves), that usually have a limited share of this ungulate in their diet in high altitude environments (Gazzola et al. 2005). In spite of the incoming winter harshness, we found an inertial horn growth during late autumn. The positive relationship between date of hunting, calculated as the number of days following the beginning of the hunting season (7th September), and horn length is consistent with a study on Cantabrian chamois (Pérez-Barbería et al. 1996), which showed an inertial horn growth (before the winter break) also in late autumn, especially in subadults.

In addition to the above described factors that contribute to exacerbate the winter conditions, several environmental factors recorded during both years of life of shot individuals as well as during the late pregnancy of mothers, influenced horn growth and size. For instance, abundant spring rainfalls were shown to favour horn growth through the increase of primary production (Lesage et al. 2000). Our results confirmed the importance of precipitations during this critical period of the year. In fact, the rainfalls recorded in April–May during both the late pregnancy of mothers and the first year of life of kids positively influenced horn growth. In mountain goats horn length increased along with the number of early-June faecal crude proteins due to the improved meadow quality (Gendreau et al. 2005). In regards to our study, rainfalls recorded in April–May I (late pregnancy–birth–early lactation) likely improved meadow quality and indirectly favoured horn growth in kids. This is in accordance with previous findings showing that an increase of meadow quality results in an improvement in mothers' milk quality (Côté and Festa-Bianchet 2001). As reported by Oftedal (1984), one major determinant of juvenile phenotypic quality in mammals is the quantity and quality of food resources available to the mother during lactation and the last third of gestation. Gómez (2004) confirmed the importance of maternal lactation (total milk production and milk protein percent weight) in relation to the length of secondary sexual traits. High temperatures recorded during the 1st and 2nd summer of life also seemed to concur in limiting horn growth, presumably on account of

decreasing productivity of meadows. The direct effect of higher summer temperature on weapon development has not been investigated so far. However, Crête and Courtois (1997) described the negative effect of this variable on moose (*Alces alces*) population dynamics (through suboptimal nutrition). As shown by our analyses on yearling chamois and unlike antlers in cervids, horn growth in bovids is a cumulative process able to reflect environmental and body conditions experienced throughout the individual's life history. Diverse environmental factors recorded during the first two years of life of shot individuals as well as during the late pregnancy of mothers, influence horn growth and size. Moreover, juvenile ungulates are more susceptible than adults to density-dependent resource limitations (Gaillard et al. 1998), and horns may be expected to be shorter in highly populated areas. In fact, high densities could negatively affect ungulate populations through increased forage competition (Post and Stenseth 1999).

Different ecological contexts (siliceous vs calcareous substrate) could provoke divergent evolutionary processes and lead to a clear-cut division between neighbouring chamois populations, such as those considered in this study (~20 km, see Fig. 2). Horns in both males and females are commonly associated either with intrasexual competition for breeding opportunities or with competition to attract mates (Clutton-Brock 2009). Our research highlights the interplay between a large-scale environmental factor (i.e. geological substrate) and evolutionary consequences: the selective advantage of possessing the best weapons may result in an increase of mating success. Sexual selection on performance traits, and, indirectly, their underlying morphology, may ultimately contribute to the evolution and maintenance of population dimorphism. In rupicaprinae, the variations in size of ornaments do not seem to be related to reproductive success. Mainguy et al. (2009) showed that horn length does not have evolutionary consequences and does not ultimately influence fitness in mountain goat. Actually, there are no evidences that long horns may affect siring success in Alpine chamois and further analyses are needed to understand the role of horns in rupicaprinae. However, our findings suggest that future research on ungulate species should consider a larger plethora of environmental factors to correctly understand evolutionary processes. The geological feature of the substrate should be included among the ecological factors influencing horn growth in ungulates since the expression of ornaments may affect the individual fitness and reproductive success.

Life histories, and specifically reproductive allocation, can be plastic with respect to the environment (Bardsen et al. 2011). Male chamois may suffer a substantial somatic cost during the rut (losing 28 % of body mass) and allocated differently resource to reproduction in areas with different substrates, as shown recently in our study site (Mason et al. 2011). Starting from these results, a comparative analysis of horn and body mass growth in different age classes could allow to assess if compensatory growth differs in relation to substrate and, in conclusion, to evaluate how life history patterns and related evolutionary consequences could vary across different populations.

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## Appendix

See Table 4.



**Table 4** Top 10 linear mixed effect models predicting horn length in yearling chamois shot during 5 consecutive years in the Trento province (Italy)

| Ranking using DIC | DIC       | Ranking using AIC | AIC       |
|-------------------|-----------|-------------------|-----------|
| 1                 | 13,838.49 | 1                 | 13,963.90 |
| 2                 | 13,842.10 | 2                 | 13,969.89 |
| 3                 | 13,843.70 | 3                 | 13,970.48 |
| 4                 | 13,849.77 | 5                 | 13,981.99 |
| 5                 | 13,850.73 | 6                 | 13,983.09 |
| 6                 | 13,858.57 | 4                 | 13,980.61 |
| 7                 | 13,864.53 | 7                 | 13,984.90 |
| 8                 | 13,874.66 | 9                 | 13,990.65 |
| 9                 | 13,896.05 | 10                | 13,999.74 |
| 10                | 13,896.11 | 8                 | 13,985.58 |

Models ranking was performed according to the Deviance Information Criterion *DIC*, and compared with the ranking computed by means of Akaike Information Criterion *AIC*. The best model was the same for both *AIC* and *DIC*

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