ORIGINAL RESEARCH

Is horn length crucial for Alpine chamois?

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Abstract

Animal weapons are one of the most studied morphological traits, particularly in Artiodactyla. Since in polygynous species males with larger weapons tend to be more successful in gaining access to females, researchers have traditionally focused on horn size. However, in species with limited horn size, weapon size has been assumed to have a reduced or null effect on life history traits. We examined the effect of intrinsic and extrinsic factors on the length of the second and third segments of Alpine chamois horns (*Rupicapra rupicapra*) in a population living in a poor environment. Our aim was to test how environmental conditions affected weapon growth and whether compensatory growth occurred. We showed that horn length was isometric to body size, although male horns grew more quickly. Ecological factors such as snow and forage availability affected weapon length, though mildly. No sign of compensatory growth was detected. We inferred that chamois mainly use horns as armament in intrasexual interactions. However, horn length was not a key element since horn growth remained isometric, at least under suboptimal ecological conditions. In species without extreme weapons, the handicap caused by longer horns is likely not compensated by an increase in individual fitness.

Introduction

The study of animal weapon evolution has highlighted that specific circumstances have to fall into place before species launch into an arms race (Stankowich, 2012). The understanding of these conditions reveals much about weapon function and ontogeny, including why in a number of species their size and shape have been emphasised, while in some others they have not (Emlen, 2014).

Although a few non-ungulate mammal lineages show impressive male weapons, the vast majority of sexually selected weapons have arisen within the taxon Pecora (Emlen, 2008). Recently, a study showed a single evolutionary origin of Pecoran weapons, which likely share a common cellular origin derived from neural crest stem cells (Wang et al., 2019). Given the common origin but the notable differences in size and shape of weapons found in the different Pecoran species, an important effect of alternative sources of selection (e.g. sexual selection, foraging, defence) and of environmental conditions should be considered. The use of horns and antlers as ornament and armament has been documented by field studies on behaviour, life history and reproductive biology (Stankowich, 2012). Males with the largest weapons are generally the largest and in best condition (Coltman et al., 2002; Vanpé

et al., 2007). Consequently, they are more likely to gain access to females (Bartoš & Bahbouh, 2006; Bergeron et al., 2010) and usually achieve the highest reproductive success (Malo et al., 2005; Preston et al., 2003). Following this approach, researchers who have studied species with modest weapons have analysed the intrinsic (e.g. Côté et al., 1998) and extrinsic (e.g. Chirichella et al., 2013) factors affecting weapon growth. However, such studies have often failed to provide a full understanding of the actual benefits associated with larger weapons in these species. Only recently researchers have assumed that, in these species, weapon size has a reduced or null effect on life history traits, for example individual survival (Corlatti et al., 2017; Douhard et al., 2020), thus suggesting to downscale the role of size.

Another gap is evident in literature: researchers have focused on male weapons and have seldom investigated the ecological mechanisms associated with weapon growth in females. However, a comparison of weapon growth between the sexes may help to understand the role and evolution of this trait. For instance, a comparative study on the effects of environmental factors may help us understand whether female weapons have evolved primarily either as defence against predators or as armaments for intrasexual interactions (Stankowich, 2012; Stankowich & Caro, 2009).

By assuming the crucial role of size, several studies have focused on compensatory growth, that is the mechanism whereby an individual can compensate a lack of growth caused by challenging periods by increasing resource allocation to weapons when environmental conditions improve (Jobling, 2010; Metcalfe & Monaghan, 2001).

By presuming that horn size is less important in species without extreme weapons, we predicted that, in these species, weapon growth would be only slightly affected by environmental conditions. Accordingly, we expected that the individuals which experienced reduced horn growth during the first years of their life did not invest energy in compensatory growth of the subsequent horn segments since the total horn length might not play a pivotal role in individual reproductive success. Rupicaprini are morphologically less differentiated species within Bovids, and are characterised by low sexual dimorphism and relatively small weapon size in both sexes (Geist, 1966). Moreover, in genus *Rupicapra,* it was reported that body weight was likely the most important attribute, rather than horn size, in determining dominance (Locati & Lovari, 1991). Therefore, Rupicaprini are an ideal case study to disentangle the role of horn length when this secondary sexual trait does not reach extreme dimensions. Based on our hypothesis, we examined annual weapon length and compensatory growth by using a large dataset of Alpine chamois (*Rupicapra rupicapra*) living in an area characterised by suboptimal and limiting conditions (i.e. siliceous area – Chirichella et al., 2013).

To benefit from homogeneous environmental conditions over a long temporal scale, we selected a relatively small study area. In so doing, we were able to focus on seasonal meteorological conditions and forage availability (short temporal scale), which are typically the main factors affecting horn growth (Carvalho et al., 2020). We implemented a multivariate analysis on a horn length dataset considering a large set of potential explanatory variables. We investigated the influence of these variables on horn growth, also estimating their effect on the actual horn length. Our hypothesis was that environmental conditions affect horn growth in a species without extreme weapons, though their consequences, in terms of actual horn length, would be negligible from a biological point of view. Moreover, we investigated potentially different patterns of growth between females and males. To this end, in the second step of our analysis, we fitted models including only the predictor variables reported to be significant by the first set of models and, for each variable, we distinguished the effect on females and males.

Materials and methods

Study area

Data collection was performed in the area surrounding the Adamello-Presanella Massif (51 847 ha; 46°020N; 10°380E, East-central Alps, Italy), a typical Alpine environment characterised by a substrate of siliceous rocks. Elevations ranged from 517 m to 3558 m a.s.l. in the Presanella Massif. The tree line was located at c. 2000 m a.s.l., above which the area was mainly composed of Alpine meadow plants, especially *Festuca*

scabriculmis and *Carex curvula* (Adamello Brenta Nature Park – unpublished report), and rocky slopes. The climate is transitional from semi-continental to Alpine. The average temperatures ranged between -8.1 and $8.5°C$ during winter and between 5 and $30.3°C$ during summer. Snowfall mostly occurred from November to April.

Red deer (*Cervus elaphus*) and roe deer (*Capreolus capreolus*) were the most abundant ungulate species in the study area, though they rarely use the areas above the tree line, that is the areas mostly used by chamois. Mouflon (*Ovis aries musimon*) and Alpine ibex (*Capra ibex*), which may potentially use chamois areas, were limited to few small sites. Potential terrestrial predators included a small population of brown bears (*Ursus arctos*) and occasionally lynx (*Lynx lynx*) and wolves (*Canis lupus*). The golden eagle (*Aquila chrysaetos*) typically preys upon small kids, but its influence on Alpine chamois populations was estimated to be negligible.

For management purposes, the area was divided into 16 hunting management units (HMUs, 3145.18 ± 619.67 ha, mean $\pm$ SE). Every summer, that is after the birth period and prior to the hunting season, chamois population density was estimated by means of block counts in all HMUs. During the period of data collection (2005–2011), chamois density was 14.5 ind./km^2 and remained relatively stable. Each year, this population was hunted with rifles from mid-September to mid-December. Hunting was regulated through licenses issued by local wildlife boards and quotas were set for specific sex- and age- classes. During the data collection, the yearly average hunting bag was 563.7 chamois (range 411–693; mean percentage: 28.2 females, 34.7 males, 37.0 yearlings).

Data collection and analysis

From 2005 to 2011, we recorded body weight (eviscerated) of each culled chamois and measured the length of the first two left horn segments (L2: for the detailed definition of the segment see Corlatti et al., 2015) of 1560 yearlings and L2 and L3 (i.e. the third horn segment) of 499 chamois ≥2 years of age. In addition, the fourth (L4, 660 individuals) and fifth (L5, 559 individuals) horn segments of chamois ≥3 years of age were measured. Weight was recorded by means of a digital balance to the nearest 0.1 kg, while the left horn length was measured on the front side by using a flexible ruler to the nearest 0.5 mm.

We randomly distributed the culled chamois within the single HMUs in which they were killed and associated with them the random coordinates and the corresponding characteristics. In our analysis, we considered individual characteristics of the culled chamois (sex, weight, harvest data) and a large number of ecological factors (Tables S1 and S2), which were potentially able to influence the yearling growth during their life. In particular, we considered the environmental features of the corresponding HMU: chamois density, elevation, slope, aspect, proportion of open areas, the vegetation green-up corresponding to the pregnancy period as well as to the seasons during which horns grew. The latter was estimated by using the

Normalised Difference Vegetation Index (NDVI), which is widely used to depict vegetation green-up in mountain ungulates (Bischof et al., 2012; Brivio et al., 2019; Hamel et al., 2009; Mason et al., 2014, 2017; Pettorelli et al., 2007). NDVI was acquired by the Moderate-resolution Imaging Spectroradiometer (MODIS) on board of the AQUA satellite (16-day composites from daily data recorded at a 250 × 250 m pixel size). Following Pettorelli et al. (2007), we calculated 4 different NDVI measures: the average NDVI values during May, the average NDVI values throughout summer, the NDVI slope between early May and early July, and the maximal slope between any two consecutive bimonthly NDVI values from early May to early July.

In addition, we considered weather data: seasonal amount of precipitation, and the minimum, maximum and mean temperature during the pregnancy period and the seasons during which horns grew (as a kid and as a yearling). To estimate the impact of snow, we used average snow depth and the number of days with snow cover deeper than 10 cm, for both measures we considered data of the winter corresponding to the pregnancy period and the winter when the chamois were a kid. Finally, we considered the average mean value of the North Atlantic Oscillation index (NAO) referred to different time windows: the year, the season (winter) and the winter months (Dec., Jan., Feb., Mar.) experienced by the culled chamois as a kid. Moreover, we also considered the yearly average of NAO index referred to the year experienced by the mother when pregnant.

Since the set of explanatory variables might include collinear predictors and the number of parameters may exceed those potentially predicted with our sample size (i.e. failed convergence), we applied a Random forest analysis (randomForest-package in R). In so doing, the importance of the parameters was ranked according to a certain number ($n = 500$) of randomly generated decision trees so as to select the better predictors and remove the collinear ones (Tables S1 and S2). The collinearity and multicollinearity among all predictor variables were evaluated by means of the Pearson correlation matrix and the Variance Inflation Factor (VIF), with thresholds set at | r_p| = 0.7 and VIF = 3, respectively (Zuur et al., 2009). This procedure enabled to reduce the amount of the potential explanatory variables from 52 to 14 for the L2 segment and from 26 to 8 for the L3 segment.

To assess the effects of these intrinsic and extrinsic variables on horn size, we modelled L2 and L3 length separately, by using Generalised Additive Mixed Models (GAMMs), with a Gaussian distribution, implemented within the mgcv package (version 1.8-10) in R. In both cases, we firstly implemented models (L2a and L3a models) considering only the non-collinear factors selected by the Random forest analysis (Tables S1 and S2). Secondly, we fitted models (L2b and L3b model) including only the predictor variables reported to be significant by L2a and L3a models. For each variable, we distinguished the effect on females and males (by adding the 'by sex' function in the script). In all the models, to consider spatial autocorrelation, we included a spatial correlation structure by using the corExp function as the exponential structure resulted to be the best option based on the minimum AIC

criterion (Zuur et al., 2009). We detected no violation of independence owing to temporal autocorrelation. We built GAMMs in which culling date effect was included as a linear predictor. Aspect effect was modelled as a cyclic cubic regression spline to consider the circularity of this variable, whereas the effect of all other continuous predictor variables was modelled as natural cubic spline functions. The optimal roughness of the smoothing terms was determined by minimising the generalised cross-validation value. When the actual degrees of freedom (edf) of a predictor variable were = 1 and the graphical inspection confirmed a linear relationship with the response variable, we refitted the model by omitting the smoothing function. We confirmed the global goodness-of-fit (i.e. homoscedasticity, normality of errors and independence) of each model by visual inspection of residuals (Zuur et al., 2009).

To investigate the fine-scale occurrence of compensatory growt in subsequent annulus, we performed multiple linear regressions between subsequent segments in a pairwise manner (i.e. L4–L3, L5–L4), separately for males and females.

Results

L2a model reported that the following factors exerted a significant effect on L2 growth: sex, culling date, individual empty weight, NDVI slopes increasing from May to July of the first (i.e. during pregnancy, birth period and early gestation) and the second (i.e. when the sampled individuals were yearlings) year, number of snowy days during the winter before and after birth, maximum NDVI increase during the second year, and average HMU aspect ($R^2 = 0.46$; Table 1). L2b model, which analysed these significant factors by separating the outcomes between the sexes, found out an isometric relationship between weight and horn growth: horn length increased with increasing body weight, with a stronger effect in males than in females ($R^2 = 0.46$; Fig. 1 and Table S3). Based on the body weight recorded for the culled individuals, the model estimated an L2 length range of 66.3 mm (126.7–192.9 mm) and 35.9 mm (min–max = 115.3–151.2 mm) for males and females, respectively. The other factors exerted a weak influence on horn growth. Considering the factor with the strongest effect (i.e. number of snowy days – Fig. 2), the model estimated a range of only 5 and 10 mm in males and females, respectively. This corresponds to 3.5% of the mean L2 length for males and 8% for females.

L3a model investigated the presence of compensatory growth by considering the effect of intrinsic and extrinsic factors on L3 segment growth. However, we excluded it as we found a strong positive relationship between L2 and L3 segment length (Fig. 3). The environmental factors did not affect L3 segment growth ($R^2 = 0.84$–Table 2). The final model (L3b), which served to look for different patterns between sexes, suggested no difference between males and females ($R^2 = 0.84$, Table S4).

The fine-scale pairwise analysis of subsequent annulus length revealed that, in both sexes, compensatory growth did not occur between L4 and L3 as their relationship was significantly positive (males: estimate = 0.33, SE = 0.03, $t = 11.71$,

Table 1 Generalised Additive Mixed Model parameters estimated for the second horn segment (model L2a, see the text for further details) of Alpine chamois culled during 2005–2011 in the Adamello-Presanella Massif, Italy

Parametric coefficients	Estimate	SE	t value	P
Intercept	65.236	9.496	6.870	<0.001
Sex (male)	22.419	0.723	30.992	<0.001
Empty weight	2.493	0.165	15.110	<0.001
Julian date of the harvest	0.112	0.015	7.549	<0.001
Percentage of open areas inside HMU	−0.038	0.046	−0.814	0.416
Average of the mean temperature during autumn (kid)	0.259	0.343	0.756	0.450
Days with snow cover > 10 cm during winter (pregnancy)	−0.079	0.030	−2.595	0.010
Average of NDVI values during May (kid)	−3.641	4.409	−0.826	0.409
Maximum increase of NDVI (kid)	−0.904	105.214	−0.009	0.993
Slope of NDVI increase (kid)	2.807	1.409	1.992	0.047
Slope of NDVI increase (yearling)	4.630	1.741	2.660	0.008
Approximate significance of smooth terms	**edf**	**d.f.**	**F**	**P**
Average HMU aspect	1.264	8.000	0.444	0.049
Days with snow cover > 10 cm during winter (kid)	3.232	3.232	8.742	<0.001
Average of NDVI values during May (yearling)	1.622	1.622	0.484	0.436
Maximum NDVI increase (yearling)	2.784	2.784	2.953	0.024

HMU, hunting management units; NDVI, Normalised Difference Vegetation Index. For climatic and environmental variables, the individual's age during the referred period is reported in brackets. We assumed 1 May as the birthday for all individuals.
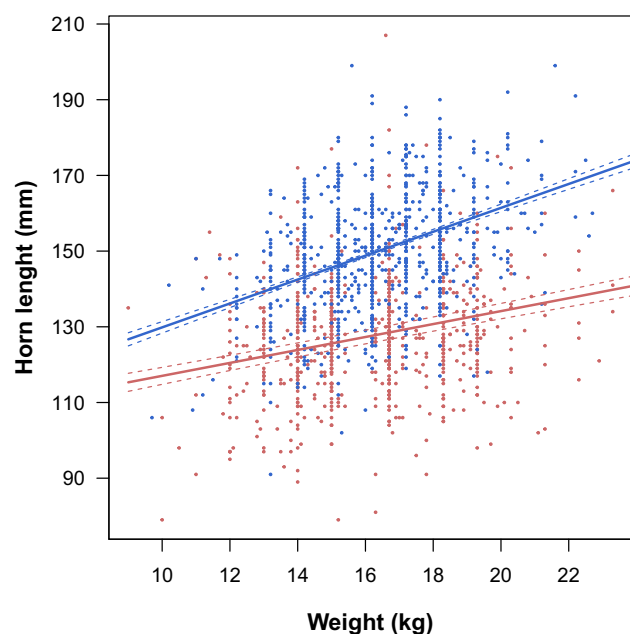

Figure 1 Relationship between L2 horn segment and weight of Alpine chamois culled during 2005–2011 in the Adamello-Presanella Massif, Italy. The continuous lines (blue for males, red for females) represent the values predicted by the best Generalised Additive Mixed Model (model L2b, see the text for more details). The predictions are given according to the mean of all other covariates in the model. The broken lines are the estimated standard errors. The dots, blue for males ($N = 852$) and red for females ($N = 708$), represent the raw data. Male data points on the x axis are offset (+0.2 kg) to avoid the overlap with female points and allow a more comprehensive visualisation of results.

$P < 0.001$; females: estimate $= 0.25$, SE $= 0.03$, $t = 8.60$, $P < 0.001$). The relationship between L5 and L4 was not significant in males (estimate $= -0.01$, SE $= 0.03$, $t = -0.37$, $P = 0.71$) and slightly negative in females (estimate $= -0.05$, SE $= 0.02$, $t = -2.13$, $P = 0.03$).

Discussion

We found that male and female chamois horn length was significantly affected by snow cover and food availability. The influence of these variables was consistent with the previous knowledge on horn growth in chamois (Chirichella et al., 2013) and, generally, in other bovids (Carvalho et al., 2020; Festa-Bianchet, 2004; Giacometti et al., 2002). However, the magnitude of such influence, assessed by using the measures predicted by the best model, was scarce. This resulted in weak differences in horn growth, even when the environmental conditions reached the most extreme values. In fact, the environmental factor with the strongest effect on chamois horn growth (i.e. snow cover experienced by the kid during its first winter) caused a maximum variation of 0.5 and 1.0 cm in males and females, respectively. Our analyses were sensitive enough to detect the effects of environmental conditions on horn growth. However, these effects had no notable impact on the actual weapon size. The effect was stronger in females than in males, a result which may be unexpected in polygynous species since males are generally thought to have higher advantages from longer horns, at least in terms of reproductive success. The linearity of the relationships between horns and weight, found for both males and females, indicated that these biometric measures were actually isometric during the first 2 years of life.
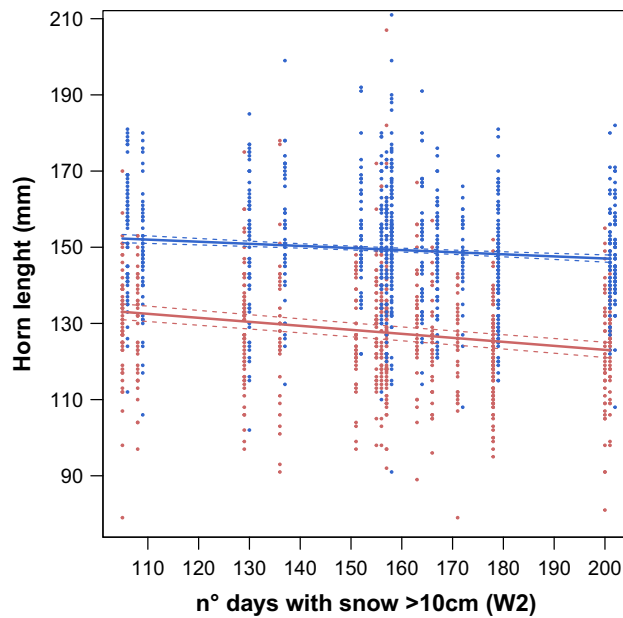
Figure 2 Relationship between snow cover and L2 horn segment of Alpine chamois culled during 2005–2011 in the Adamello-Presanella Massif, Italy. The continuous lines (blue for males, red for females) represent the values predicted by the best Generalised Additive Mixed Model (model L2b, see the text for more details). The predictions are given according to the mean of all other covariates in the model. The broken lines are the estimated standard errors. The dots, blue for males (*N* = 852) and red for females (*N* = 708), represent the raw data. W2 = winter conditions experienced by the individual as a kid. Male data points on the x axis are offset (+1.0 cm) to avoid the overlap with female points and allow a more comprehensive visualisation of results.

Figure 3 Relationship between L2 and L3 horn segments of Alpine chamois culled during 2005–2011 in the Adamello-Presanella Massif, Italy. The continuous lines (blue for males, red for females) represent the values predicted by the best Generalised Additive Model (model L3b, see the text for more details). The broken lines are the estimated standard errors. The dots, blue for males (*N* = 366) red for females (*N* = 133), represent the raw data.

Our best model on L3 length showed that this segment was not affected by environmental conditions, though it was highly, positively and linearly related to L2 segment length in both males and females. This result was in contrast with other researches' findings (Corlatti et al., 2015; Rughetti & Festa-Bianchet, 2010), which supported the presence of compensatory growth in chamois. The positive relationship between L4 and L3 confirmed the absence of compensatory growth in the studied population. Since the other horn segments are typically millimetric in chamois (see Corlatti et al., 2015 for more details about the segments' length), L2, L3 and L4 length is pivotal in determining the total horn length in this species. Thus, no other mechanism of compensatory growth might be expected in chamois. It is worth noting that, compared to other studies, our analysis was implemented in an area with demanding environmental conditions and considering several ecological factors simultaneously. These differences might affect the final outcome and surely stressed the need to implement a comparative study investigating horn length in several areas and under different environmental conditions.

Why is horn growth in male yearlings about twice as fast as in females? We can conjecture that males begin to interact
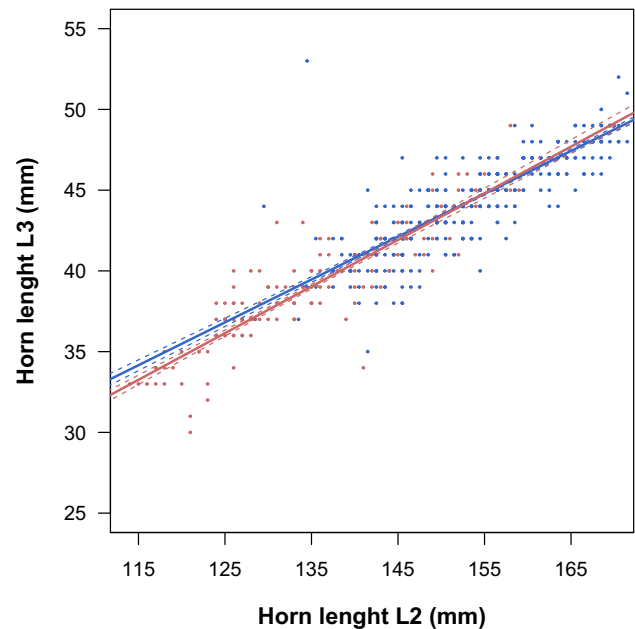
within the bachelor groups and have to use the weapons – likely as an armament – earlier than females. Locati and Lovari (1990) reported sex differences in patterns of aggressive behaviour in Apennine chamois (*Rupicapra pyrenaica ornata*), which are likely related to the different degrees of gregariousness between the sexes. The body target areas selected by females and males during interactions were significantly different, with females selecting more often low-risk districts and males preferring body regions with the greatest risk of lethal injury. These authors explained this behaviour, as well as the hooked horn tips of chamois, as initial signs of ritualisation. Our results on the lack of compensatory growth and the different development between the sexes seem to support Locati and Lovari's (1990) explanation about the ritualisation of aggressive interactions in chamois. A further study on the development of social behaviour in males and females by involving different species and populations of the *Rupicapra* genus may shed new light on this issue.

As we detected a limited effect of different environmental conditions in our study area, we can suppose that individuals did not invest a large amount of energy in horn growth. Conversely, it may be suggested that, at least under favourable conditions, chamois would invest in horn growth to increase their success as its cost did not seem particularly energy-demanding. However, even during years with favourable conditions, we did not detect a remarkable differential increase in horn size. A quick horn growth may not be a positive asset

Table 2 Generalised Additive Mixed Model parameters estimated for the third horn segment (model L3a, see the text for further details) of Alpine chamois culled during 2005–2011 in the Adamello-Presanella Massif, Italy

Parametric coefficients	Estimate	SE	*t* value	*P*
Intercept	2.965	1.213	2.443	0.015
Sex (male)	0.360	0.218	1.652	0.099
Length of second segment	0.272	0.007	38.527	<0.001
Average of NDVI values during summer (2 y.o.)	0.036	0.079	0.462	0.644
Percentage of open areas inside the HMU	−0.008	0.007	−1.19	0.235
Maximum NDVI increase (2 y.o.)	−14.103	20.053	−0.703	0.482
Slope of NDVI increase (2 y.o.)	−0.120	0.190	−0.630	0.529

Approximate significance of smooth terms	edf	d.f.	*F*	*P*
Average HMU aspect	0.0008	8	0	0.511
Days with snow cover > 10 cm during winter (yearling)	1.544	1.544	1.892	0.090

HMU, hunting management units; NDVI, Normalised Difference Vegetation Index. For climatic and environmental variables, the individual's age during the referred period is reported in brackets. We assumed 1 May as the birthday for all individuals.

from a biological viewpoint: long horns may break more easily than short ones, particularly if horn girth remains similar (Packer, 1983). Overall, our results suggested the importance of timing in horn ontogeny rather than energy investment to further their growth, likely because horn length does not play a pivotal role in interaction competitions. Locati and Lovari (1991) showed that body weight is one of the main clues affecting dominance in Apennine chamois, rather than horn length. In this light, some millimetres of horn length make little difference, whereas one or two kilograms of weight may be more important in a fight. Several studies on species without extreme weapons have focused on intrinsic and extrinsic factors affecting weapon growth, though they failed to understand the role and benefits of larger weapons in these species (Chirichella et al., 2013; Corlatti et al., 2017; Côté et al., 1998; Rughetti & Festa-Bianchet, 2010). Our findings support the conjecture that biological traits other than horn length (e.g. for chamois, running speed in rugged terrain) may play a key role in intra- and inter-sexual interactions in ungulates without extreme weapons (Corlatti et al., 2013; Locati & Lovari, 1991; Rughetti & Festa-Bianchet, 2010).

In conclusion, the arguments about the role of weapon size should be more cautious, especially in near-monomorphic species without extreme weapons. An analysis centred exclusively on size, regardless of shape and the actual use of secondary sexual traits, may lead to misleading conclusions. The role of horns in both males and females of species without extreme weapons, for example in Rupicaprini, was widely discussed without offering a thorough explanation also because these results were not paired with information about reproductive success. The study of chamois ethograms acknowledged the importance of horns as armaments in both sexes, though their length may not be relevant in this context, thus suggesting that other features may influence fighting ability (Locati & Lovari, 1991). A study recently proposed different hypotheses to explain how body size in Artiodactyla is positively correlated with the variation in male mating success (Cassini, 2020). Likewise, one should emphasise that, to fully understand the role of horns and their effect on individual fitness, a focus is needed not only on their size but also on their use, shape and the different drivers affecting their ontogenesis.

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Conflict of interests

We declare we have no competing interests.

Author contributions

SG, RC and MA conceived and designed the study. SG participated in data analysis and drafted the manuscript. FB conducted the statistical analyses and helped to draft the manuscript. RC collected field data. MA coordinated the study. All authors provided edits on the drafts of the manuscript and gave the final approval for publication.

Ethics

The work reported in this article includes information from individuals culled during yearly hunting activities. No animal

was either killed or captured to implement the analysis of this manuscript. The work reported in this article followed the guidelines for the ethical treatment of animals in research under UWA Ethics Committee approval (03/100/1456).

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Set of independent variables used to predict the variation of second horn segment (L2) length of Alpine chamois in the Adamello-Presanella Massif (Italy).

Table S2. Set of independent variables used to predict the variation of second horn segment (L3) length of Alpine chamois in the Adamello-Presanella Massif (Italy).

Table S3. Generalised Additive Mixed Model parameters estimated for the second horn segment (model L2b) of Alpine chamois culled during 2005-2011 in the Adamello-Presanella Massif, Italy.