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Is chamois hybridization in the northern Dinaric Mountains an important factor for horn development?

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The Dinaric region is the natural habitat of the Alpine chamois *Rupicapra rupicapra rupicapra* and Balkan chamois *Rupicapra rupicapra balcanica*. Recently confirmed, these two subspecies hybridize in the contact zone on Mts Velebit, coastal Croatia. Patterns of horn development in chamois can differ within populations and subspecies, and are mostly influenced by genetic structure, sex and resource availability. These factors control the direct ability of energy allocation to secondary sexual traits with diverse outcomes. This is the first study to investigate the horn growth patterns of Alpine and Balkan chamois populations and their admixed progeny. We explored the differences in horn growth and compensatory patterns among populations as a function of genetic background, separately for females and males. A significantly different pattern of horn development was detected in the hybrid population showing higher rates of initial horn growth – until 2.5 years, and much lower compensation rates in the first 4.5 years of life in both sexes in comparison to other chamois populations. Interestingly, differences in growth patterns were more expressed among males. Higher initial horn growth and low compensation rates in the hybrid population can be explained by both non-genetic and genetic factors, but may suggest an effect of heterosis, i.e. the occurrence of hybrid vigour. Therefore, this situation could reveal the extent to which life history patterns and evolutionary consequences can shape important traits of population outlook/vigour, such as horn size, in different chamois populations.

Keywords: compensatory growth, crossbreeding, horn growth patterns, hybrid vigour, *Rupicapra rupicapra*

Horn development in bovids is continuous throughout the animal's life (Bubenik and Bubenik 1990). It can be influenced by non-genetic factors, such as physiological condition (Santiago-Moreno et al. 2004, Toledano-Díaz et al. 2007), environmental factors (Chirichella et al. 2013, Douhard et al. 2016), selective harvesting (Garel et al. 2007, Rughetti and Festa-Bianchet 2014), and by the genetic basis (von Hardenberg et al. 2007).

Hybridization can produce variation in morphological traits, which can be associated with sexual selection. Hybrid morphology is typically depicted as intermediate, although in reality, hybrid populations are highly variable and show a wide range of phenotypes (Ackermann et al. 2010). The direct effect of ungulate hybridization on horn/antler growth is still unclear, although some authors have reported differences in horn length and shape in hybrid lineages (Giacometti et al. 2004, Loehr et al. 2008, Grobler et al. 2011, Vaz Pinto et al. 2016). In the genus *Rupicapra*, the influence of hybridization on horn development has been poorly investigated (Iacolina et al. 2018). As regards Caprinae, Blyth (1869) recorded hybrids between chamois and domestic goat *Capra hircus*, and provided pictures of a hybrid horn shape, although further attempts to produce a hybrid failed.

Chamois (genus *Rupicapra*) are slightly dimorphic mountain ungulates, showing small variation in horn growth, with the males having slightly longer horns than females (Bassano et al. 2003). About 60–70% of horn growth takes place in the first 1.5 year of life in both sexes (Rughetti and Festa-Bianchet 2010). During this period, the chamois rapidly increases its skeletal size, including the bony core – and thus horn size. Several authors have discussed the reasons for such an early investment in horn size of wild caprine species (Mangel and Stamps 2001, Toïgo et al. 2013)

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and the related abilities to allocate energy reserves, though the extent to which horn size can improve individual success and survival is yet to be elucidated. In northern chamois *Rupicapra rupicapra*, variations in ornament size seems to be unrelated to reproductive success (Corlatti et al. 2012) and the role of chamois horns is still unclear.

It has been shown that various patterns of compensatory horn growth mechanisms of Rupicaprini can occur between populations due to taxonomic affiliation (Massei et al. 1994, Pérez-Barbería et al. 1996, Bassano et al. 2003). Corlatti et al. (2015) found difference in the rates of compensatory growth between distant populations of Alpine chamois *Rupicapra rupicapra rupicapra* and suggested the contribution of genetic differentiation and environmental conditions as possible factors in horn development. These factors are 'engraved' on the surface of the permanent horns in bovids, and thus can reveal important information about the life history of individuals.

The Dinaric region is the natural habitat of both the northern subspecies of chamois: Alpine and Balkan chamois *Rupicapra rupicapra balcanica* (Masini and Lovari 1988). Alpine chamois inhabits the northern Dinaric Mountains, whereas the central and southern areas are inhabited by Balkan chamois (Corlatti et al. 2011). Prompted by a publication on the successful translocation of both Alpine and Balkan chamois specimens to the Mts Velebit, coastal Croatia (Frković 2008), Šprem and Buzan (2016) found the existence of Alpine and Balkan chamois haplotypes, thereby classifying the Mts Velebit as a hybridization zone between the subspecies.

In this study, we explored the horn metrics of culled chamois from three distinct populations in the Dinaric region, with the aim to better understand the non-genetic and genetic factors that may affect the lengths of the first five horn segments and the circumferences of the second and third annuli ring. Based on the genetic structure of chamois in the northern Dinaric Mountains (Šprem and Buzan 2016), the investigated populations were divided into three groups, according to their genetic background (i.e. origin): Alpine population (Gorski Kotar), hybrid population (Mts Velebit) and Balkan population (Mt Biokovo and Mt. Prenj).

We predicted that:

1) the length of horn segments and the circumference sizes differ among populations;
2) compensation rates differ among populations due to the unique situation in the northern Dinaric Mountains which includes the presence of two subspecies, their hybrids, and their mutual contact in a geographically small area.

Material and methods

Study area

The Dinaric massif stretches from Slovenia in the northwest to Albania in the southwest with a total length of 645 km. The area is characterized by a moderate rainy and humid-boreal climate with a Mediterranean influence (Vukelić 2012). The high level of ecological diversity on Dinaric Mountains is represented by numerous forms of vegetation – mountain and sub-mountain pasture, meadows, small plateaus, rock creeps, breaches of rocks, tall herbs, low marshes, springs and bare rocks (Redžić 2007). The Dinaric massif is a highly heterogeneous area, covering an elevation range from sea level to 2115 m, with an upper forest limit mainly lying above 1400 m.

Samples of chamois horns were collected in four areas: three in Croatia (Gorski Kotar, Mts Velebit and Mt Biokovo) with a total area of 51 401 ha, and one in Bosnia and Herzegovina (Mt Prenj) with a total area of 34 504 ha (Fig. 1). The study populations inhabit diverse habitats (in terms of forest cover, elevation, substrate, aspect, slope etc.) and seasonal migrations have been recorded to occur even to sea level for the populations from Mts Velebit and Mt Biokovo (B. Šabić pers. comm.). Population size is estimated by census, mostly performed by hunter field observations twice a year (spring and autumn).

While populations of Gorski Kotar (*R. r. rupicapra*) and Mt Prenj (*R. r. balcanica*) have not experienced any translocations, and therefore represent 'clean' populations of two subspecies, on Mts Velebit chamois were translocated in two turns in 1970s. The first translocation occurred in 1974, with Balkan chamois from the Mt Prenj in Bosnia and Herzegovina, and the second in 1978, with Alpine chamois from Kamnik Alps in Slovenia (Frković 2008). The chamois were also introduced to Mt Biokovo by several successive translocations from 1964 to 1967 with total of 48 Balkan chamois from the Mt Prenj (Šabić 2014), which allowed us to combine the data of two populations (Mt Biokovo and Mt Prenj), since they share a common origin. The largest population can be found on Mts Velebit, with an estimated 860 individuals, followed by Balkan chamois population on Mt Biokovo, with an estimated 380 individuals. The population of Alpine chamois in Gorski Kotar numbers around 280 individuals (Šprem et al. 2015, Anonymous 2018), while the smallest population of virtually extinct Balkan chamois can be found on Mt Prenj, with an estimated 50 individuals (Frković 2008).

Data collection

Horn growth data were recorded on 214 samples (135 from males and 79 from females) of chamois culled from 1990 to 2015: Alpine population - 71 samples, hybrid population - 44 samples and Balkan population - 99 samples. This sample set included horns of genotyped individuals analysed in a recent paper (Šprem and Buzan 2016), reinforced with samples of some additional individuals originated from the same areas. Horns originated from several collections, including museums and hunting lodges, but mostly from private trophy collections. We determined the age of chamois by counting the clearly separated annuli on their horns (Schröder and von Elsner-Schlack 1985). The length of the first two segments (L2) and circumferences on the L2 (L2C) and L3 (L3C) annuli rings were measured by means of a flexible ruler, while for the remaining segments (L3, L4, L5, L6), electronic calliper was used on the front side of the left horn (Fig. 2). Measures of annual segments represent the distance between each pair of complete annuli (Massei et al. 1994). We combined the lengths of the first two segments due to the hardly distinguishable annuli ring between them. Furthermore, we took into consideration only complete segments (i.e., L2 in animals of at least 1.5 years of age).

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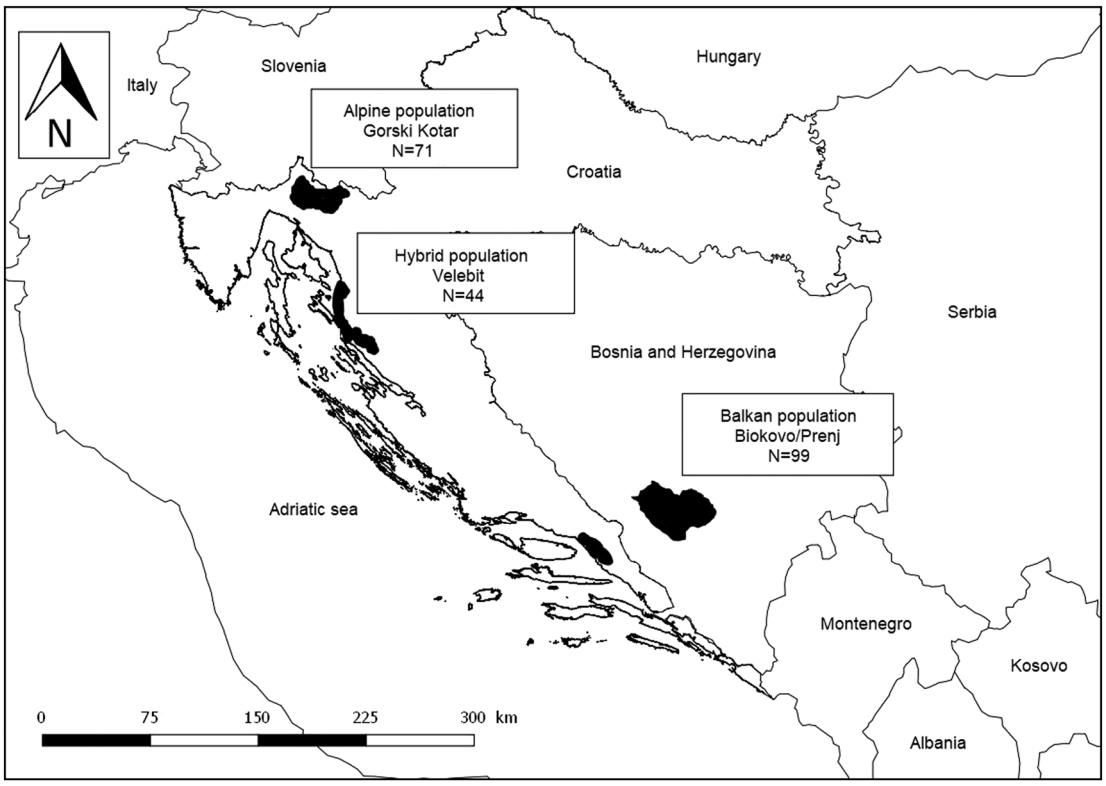


Figure 1. Map of the study area (Gorski Kotar region, Mts Velebit, Mt Biokovo / Mt Prenj) and sample size (N).

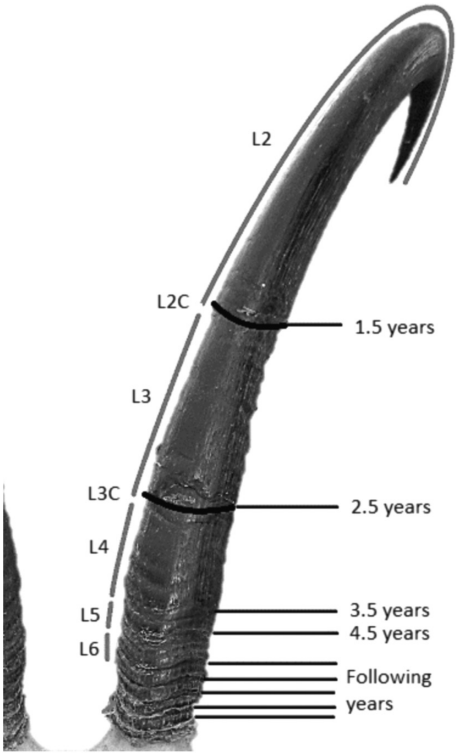


Figure 2. Horn growth pattern of chamois: the left side of the horn L2, L3, L4, L5 and L6 represent the length of measured segments while L2C and L3C represent the circumferences at the end of L2 and L3 segment. On the right side, age estimation by annuli rings.

Data analysis

We performed geographical analyses of study area using Digital elevation model over Europe (EU-DEM) to gain an insight into habitat heterogeneity among populations with a different genetic background. We also applied three types of Copernicus web service high-resolution layers to obtain land use data (forests, imperviousness and other land). Other land was characterized as open areas, including grassland and wetlands. Geology data was obtained from the website of the Croatian Geological Survey.

Following our predictions, we assessed the influence of the origin of chamois, i.e. differences among populations, in segment lengths (L2–L6) and on L2C and L3C of the left horn. We fitted generalised linear models (GLMs) with the genetic background as a single predictor for each analysed response variable to test for the existence of various horn growth patterns among the three populations. We analysed female and male horns separately, on the basis of existing knowledge about the different dynamics of the horn growth between both sexes (Bassano et al. 2003, Corlatti et al. 2015).

To confirm the prediction of possible various compensation rates among the investigated populations, we ran multiple linear regressions among subsequent segments (i.e. L3–L2, L4–L3, L5–L4, L6–L5) and subsequent circumferences (i.e. L3C–L2C) with the origin of chamois as a fixed factor, separately for males and females. All statistical analyses were performed using base functions of RStudio software, ver. 1.1.423 (RStudio Team 2016). Package 'ggplot2' was used for data visualization.

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Table 1. Terrain and habitat characteristics processed from EU – DEM and Croatian Geological Survey.

Population	Environmental factors (mean)				
	Aspect	Elevation m	Slope°	Limestone %	Open areas %
Alpine population	168.5 (SE)	818	14.1	~ 65	11.8
Balkan population	166.8 (SE)	1310	20.8	~ 90	60.4
'Hybrid' population	251.6 (SW)	366	16.9	> 90	85.0

Results

The geographical analyses using EU–DEM and geological data confirmed our prediction of habitat heterogeneity. We found expressed differences among population sites, where the area of Mts. Velebit stood out by the lowest mean elevation (366 m), highest percentage of open areas (85%) and limestone substrate (>90%). On the contrary, Gorski Kotar appeared to be characterized predominantly by forested areas (88%) with a higher mean elevation (818 m) and notably lower percentage of limestone soil (65%; Table 1).

The origin of individuals, i.e. from population of 'pure' Alpine chamois, population of 'pure' Balkan chamois, or population where introgression of genes of both subspecies had occurred in the past (thereafter 'hybrid population'), had a significant effect on the L2 horn segment growth, L2C and L3C for males ($p < 0.001$). The longest L2 segments were found in the hybrid population ('hybrid' versus Balkan: ß = –2.012, SE = 0.464, t = –4.332, $p < 0.001$; 'hybrid' versus Alpine: ß = –2.023, SE = 0.475, t = –4.264, $p < 0.001$; Fig. 3a). No significant differences were found for the remaining segments (i.e. L3, L4, L5, L6; $p > 0.05$; Fig. 3a). The largest L2C were found in males of the hybrid

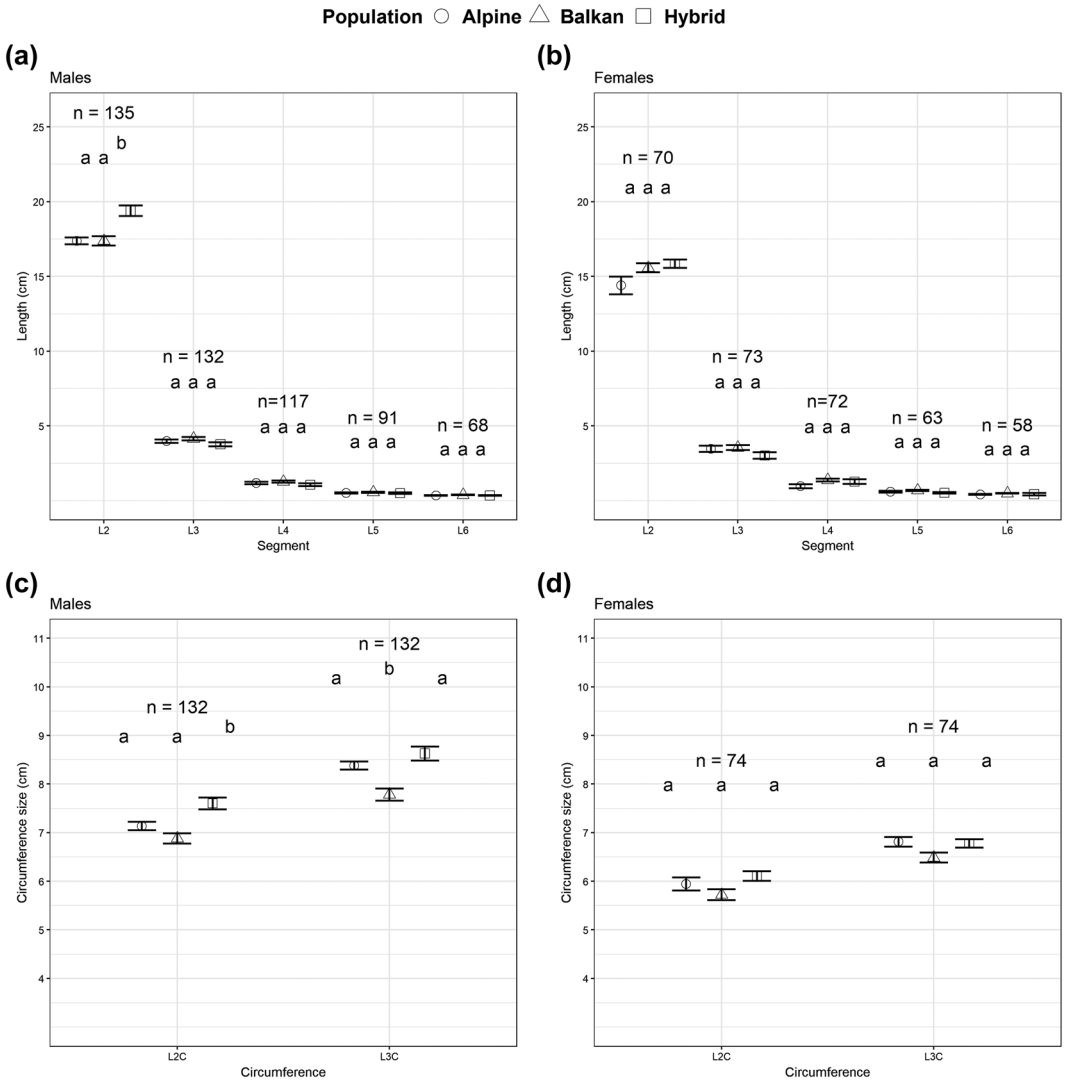


Figure 3. Means and standard deviations of annulus length (in cm) and circumference (in cm) as a function of age (L2 and L2C corresponding to age 1.5 year, etc.), sex (males – left plot, females – right plot), and population (Alpine population *R. r. rupicapra* – circle, Balkan population *R. r. balcanic*) – triangle, 'hybrid' population – square). Means sharing a letter above points are not significantly different ($p > 0.05$).

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population ('hybrid' versus Alpine: ß = –0.467, SE: 0.167, t = –2.791, p = 0.006; 'hybrid' versus Balkan: ß = –0.719, SE: 0.164, t = –4.384, p < 0.001; Fig. 3c), while males of the Balkan population had significantly smaller L3C (Balkan versus Alpine: ß = 0.595, SE: 0.152, t = 3.921, p < 0.001; Balkan versus 'hybrid': ß = 0.844, SE = 0.184, t = 4.590, p < 0.001; Fig. 3c). No significant differences among populations were found in the case of females (p > 0.05; Fig. 3b, d).

The pairwise analysis of subsequent segment lengths revealed the occurrence of compensatory growth between L3 and L2 for males in the Alpine population (males: ß = –0.229, SE = 0.067, t = –3.389, p = 0.003; Fig. 4a) and both sexes in Balkan population (males: ß = –0.149, SE = –0.149, t = –3.402, p = 0.001; females: ß = –0.214, SE = 0.082, t = –2.609, p = 0.013; Fig. 4a–b).

On the contrary, in the hybrid population the pairwise analysis of subsequent segment lengths revealed no compensatory growth between L3 and L2 in males and females (p > 0.05; Fig. 4a–b).

The relationship between L4 and L3 length for males of the Alpine and the Balkan population showed a significantly positive relationship (Alpine: ß = 0.528, SE = 0.080, t = 6.598, p < 0.001; Balkan: ß = 0.373, SE = 0.073, t = 5.068, p < 0.001; Fig. 4c). On the contrary, the relationship between the L4 and L3 segments in males of the hybrid population was not significant (p > 0.05; Fig. 4c). In females, an increase in the rate of growth between L4 and L3 was significant only in the Alpine population (ß = 0.405, SE = 0.119, t = 3.403, p = 0.003; Fig. 4d).

Males in all populations showed a significantly positive relationship between the L5 and L4 segments (Alpine: ß = 0.159, SE = 0.049, t = 3.280, p < 0.001; Balkan: ß = 0.170, SE = 0.060, t = 2.834, p = 0.007; Fig. 4e), with the hybrid population showing the highest growth acceleration (ß = 1.666, SE = 0.463, t = 3.596, p = 0.003; Fig. 4e). On the contrary, the highest growth acceleration in females between the L5 and L4 segments was found in the Alpine population (ß = 0.426, SE = 0.047, t = 8.914, p < 0.001; Fig. 4f), followed by the Balkan population (ß = 0.209, SE = 0.061, t = 3.413, p = 0.002; Fig. 4f), while in hybrid population relationship wasn't significant (p > 0.05; Fig. 4f).

When considering relationship between L6 and L5 segment, males of the Alpine and Balkan populations showed a significantly positive relationship (Alpine: ß = 0.369, SE = 0.077, t = 4.751, p < 0.001; Balkan: ß = 0.279, SE = 0.064, t = 4.356, p < 0.001; Fig. 4g), which was not the case in the hybrid population (p > 0.05; Fig. 4g). In females, significant relationship was found only in the Alpine population (ß = 0.399, SE = 0.070, t = 5.641, p < 0.001; Fig. 4h).

The pairwise analysis of L3C and L2C revealed that horn circumferences grow gradually in the early stages of chamois life (first 3 years), which was confirmed by the significantly positive relationship between L3C and L2C for both sexes in all three populations: Alpine (males: ß = 0.832, SE = 0.071, t = 11.727, p < 0.001; females: ß = 0.568, SE = 0.107, t = 5.299, p <0.001); Balkan - with most expressed compensatory rates for females (males: ß = 0.630, SE = 0.134, t = 4.692, p < 0.001; females: 0.862, SE = 0.058, t = 14.661, p < 0.001); and hybrid - with highest growth acceleration for males (males: ß = 1.101, SE = 0.084, t = 12.999, p < 0.001; females: ß = 0.569, SE = 0.174, t = 3.269, p = 0.005) (Fig. 5a–b).

Discussion

Reaching up to 10% in size, the longest segments (L2) and the largest circumferences (L2C and L3C) were found in the male hybrid population. When comparing the Alpine and Balkan populations, no differences were detected, despite the expectation for longer segments in the Balkan population based on horn development data of Alpine (Bassano et al. 2003) and Balkan chamois (Massei et al. 1994). Moreover, the great differences in compensation rates among populations are the most surprising result. Particularly, this is the first evidence of the absence of compensatory growth between the L3 and L2 segments in chamois horns. In general, the hybrid population showed much lower compensation rates in the first 4.5 years of life than other populations.

The findings reported here could support the claims of Chirichella et al. (2013) for Alpine chamois yearlings, indicating the importance of environmental factors on chamois horn development. Chamois culled on Mts Velebit inhabit significantly lower elevations than other populations. For example, the area inhabited by the hybrid population (mean = 396 m) is almost 1100 meters lower on average than for the Balkan population (mean = 1310 m). Furthermore, on Mts Velebit, chamois inhabitancy is predominantly on the south-facing slopes, with a high percentage of calcareous substrate in limestone form, which could indirectly increase the rates of horn growth (Chirichella et al. 2013). Consequently, there is an obvious difference in solar radiation, air temperature and vegetation forms between populations. Body condition of ungulates, which is strongly correlated with weapon size, is under direct influence of environmental factors and related food availability (Pyrenean chamois *Rupicapra pyrenaica*: Pérez-Barberìa et al. 1996; mountain goat *Oreamnus americanus:* Côté et al. 1998; bighorn sheep *Ovis canadensis*: Festa-Bianchet et al. 2000; Alpine ibex *Capra ibex*: Büntgen et al. 2014). Accordingly, we strongly believe that the specific climatic conditions in the study area also contributed to the evident differences in horn growth, although due to the irrelevance of available data for statistical modelling, we weren't able to draw clear conclusions. Better habitat suitability, according to the favourable environmental conditions of Mts Velebit, may have allowed chamois to allocate more energy resources to horn development, compared to other populations where poorer nutrition and a harsher environment resulted in a lesser investment in horn growth, with energy allocated for other important vital processes (Mason et al. 2014).

Taking genetic data into account (Šprem and Buzan 2016), together with differences in horn growth among populations, it seems possible that low genetic diversity and higher inbreeding coefficient (F_{IS}) may negatively affect horn development in terms of smaller circumferences or shorter segments in both Alpine and Balkan populations. A genetic study showed that relatively outbred red deer have greater lifetime breeding success (LBS) than their more inbred counterparts, which is an evidence that heterosis might influence overall fitness in both sexes (Slate et al. 2000). Theoretically,

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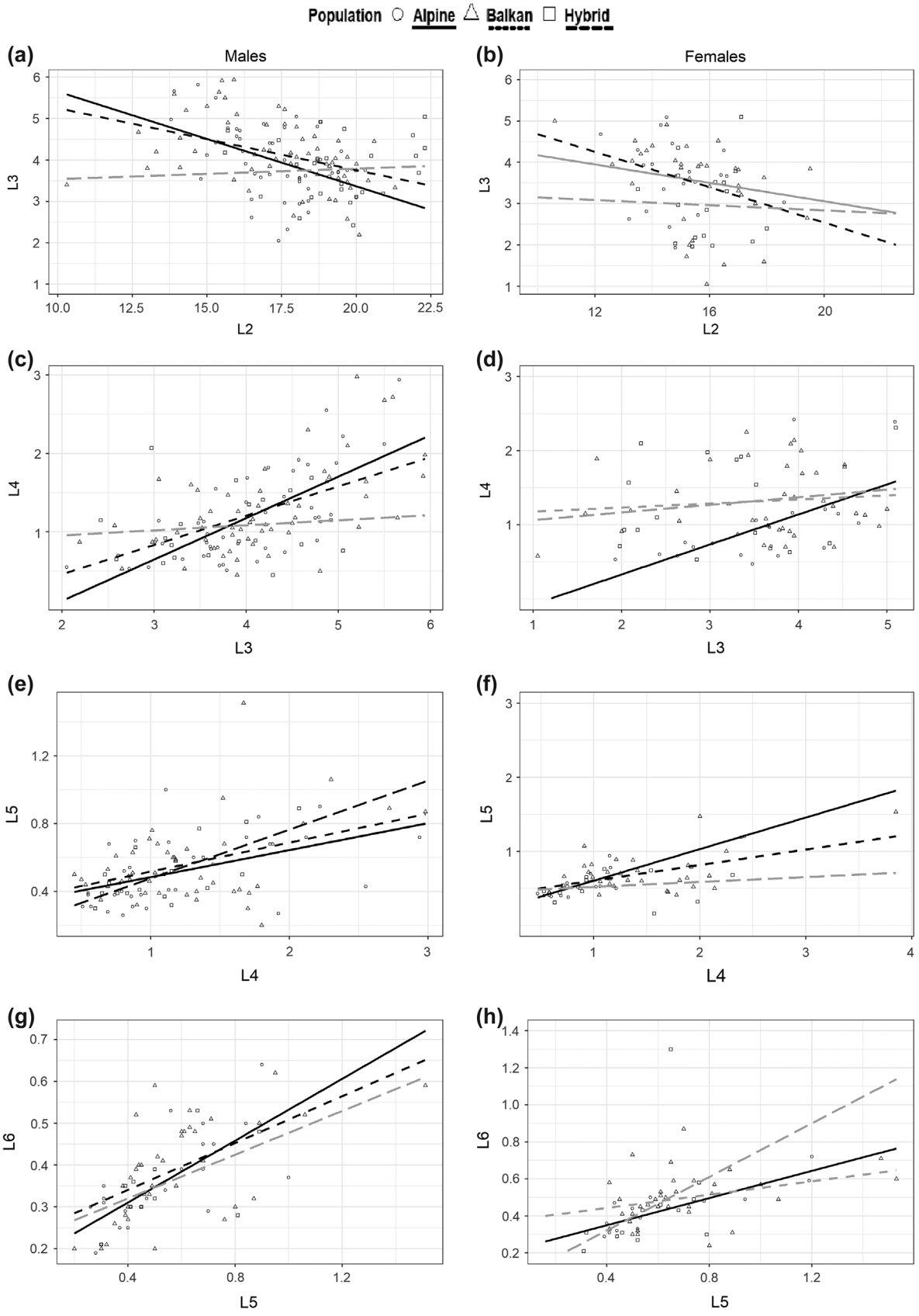


Figure 4. The relationship between subsequent segments for males (a, c, e, g) and females (b, d, f, h) of three different chamois populations. The regression lines marked in grey showing not significant relationship.

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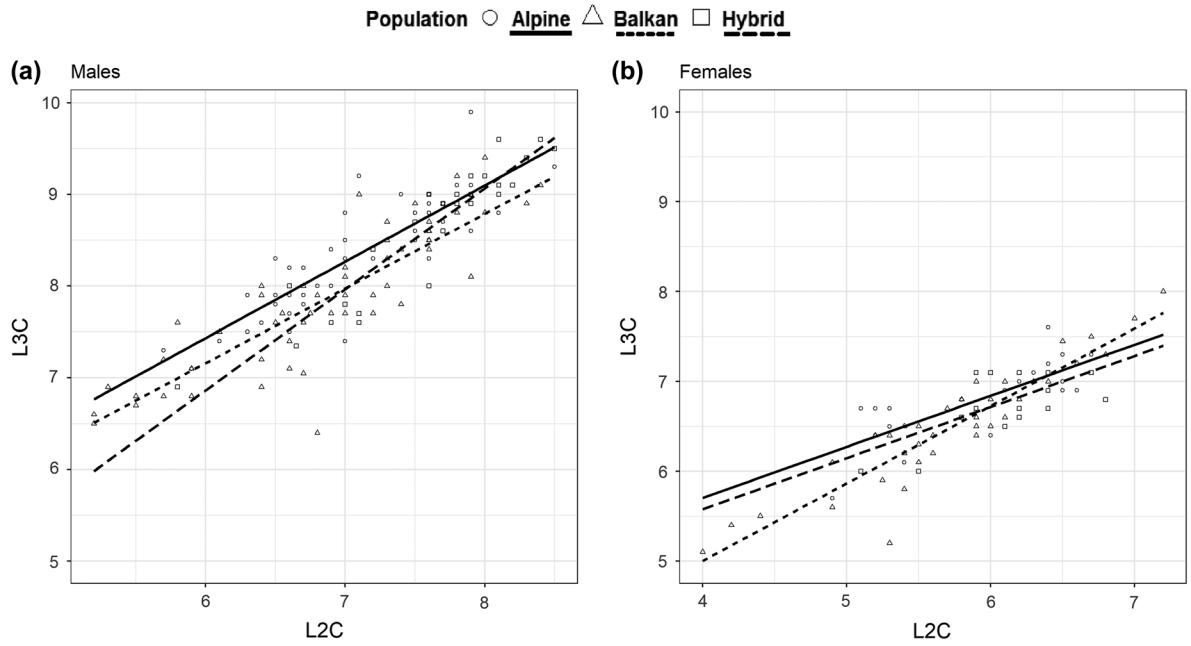


Figure 5. The relationship between circumference (in cm) for L3C and L2C of three different chamois populations: males (a), females (b).

heterosis, also called hybrid vigour, can be expressed indirectly through higher horn growth rates, presumably due to increased heterozygosity for loci with overdominance (Lippman and Zamir 2006, Keller and Taylor 2010). Although several authors have recorded hybridization between chamois subspecies (Crestanello et al. 2009, Zemanová et al. 2015), exact reflection on horn development is still unclear. It is possible that the hybrid population differs not only in horn size, but also in other morphological and phenotypic traits, such as skull and body morphometry, body mass, fur coloration, etc. Unfortunately, such data are lacking (Iacolina et al. 2018). However, Giacometti et al. (2004) found longer horns of hybrids between Alpine ibex and domestic goat, while Loehr et al. (2008) showed that coat darkness is associated with greater horn growth, which influenced social dominance and mating behaviour in a mountain sheep hybrid lineage.

With the exception of the environmental and genetic factors, which may have affected horn development examined here, several other factors may have contributed to differences in horn growth patterns among the investigated populations, since our data originate from hunted populations. Douhard et al. (2016) showed that under strong selective harvest, the horn length of Stone's sheep rams *Ovis dalli stonei* became shorter for a given base circumference. In contrast, under lower hunting pressure (<10% of population), there were no changes in horn length. The first harvest of chamois on Mts Velebit following the translocations (1974–1978) started in 1996, while harvest on Mt Biokovo began only ten years after translocation (Šabić and Lalić 2005). It is possible that the 20-year period without harvest of chamois on Mts Velebit resulted in better condition of the animals and, indirectly, better quality of their traits. In the case of chamois, Rughetti and Festa-Bianchet (2010) did not find differences in horn length between hunted and protected (non-hunted) Alpine chamois populations, while Corlatti et al. (2017) showed that selection through culling can be strongly sex-biased in weekly dimorphic species, depending on hunters' preferences and hunting regulations.

Although there is no evidence that longer horns in chamois may affect siring success, Locati and Lovari (1991) suggested that in Apennine chamois *Rupicapra pyrenaica ornata* dominant males had longer horns and were older than their competitors. In addition, several studies on other species have observed the relationship between dominance and growth, such that dominant juveniles grow more rapidly than subordinate ones (Schluter 1995, Stamps and Krishnan 1995, Bergeron et al. 2010).

Considering the existing knowledge about the horn development in *Rupicaprinae*, this unique situation might contribute to important knowledge how life history patterns can shape different populations. Different compensatory rates of horn growth found in the hybrid population suggest that hybridization may play a significant role in horn shaping, although influence of non-genetic factors should not be neglected and may be the predominant drivers in determining horn growth process. Therefore, up-following research should be implemented to provide more relevant information about wide set of environmental factors, closely related to the investigated populations. Finally, it would be worth investigating the coherence of body mass and horn development to identify differences in compensatory growth rates and tradeoffs in relation to environmental and genetic factors.

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