



## Horn growth patterns in Alpine chamois



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### ABSTRACT

The analysis of horn growth may provide important information about the allocation of metabolic resources to secondary sexual traits. Depending on the selective advantages offered by horn size during intra- and inter-specific interactions, ungulates may show different investment in horn development, and growth variations within species may be influenced by several parameters, such as sex, age, or resource availability. We investigated the horn growth patterns in two hunted populations of Alpine chamois (*Rupicapra r. rupicapra*) in the Central Italian Alps. We tested the role of individual heterogeneity on the growth pattern and explored the variation in annulus length as a function of different factors (sex, age, hunting location, cohort). We then investigated the mechanisms underlying horn growth trajectories to test for the occurrence of compensatory or recovery growth and their potential differences between sexes and populations. Annulus length varied as a function of sex, age of individuals and, marginally, hunting location; no effect of cohort or individual heterogeneity was detected. Male and female chamois showed compensatory horn growth within the first 5½ years of life, though the partial convergence of horn trajectories in chamois suggests that this mechanisms would best be described as 'recovery growth'. Compensation rates were greater in males than in females, while only compensatory growth rates up to 2½ years of age were different in the two populations. Besides confirming the sex- and age-dependent pattern of horn development, our study suggests that the mechanism of recovery growth supports the hypothesis of horn size as a weakly selected sexual trait in male and female chamois. Furthermore, the greater compensation rates in horn growth shown by male chamois possibly suggest selective effects of hunting on age at first reproduction, while different compensation rates between populations may suggest the occurrence of some plasticity in resource allocation to sexual traits in relation to different environments.

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### 1. Introduction

Horns are secondary sexual characteristics displayed by either one or both sexes in bovids and their evolution reflects intra- and inter-specific interactions, although intra-sexual competition among males is thought to be the main evolutionary driver (Geist, 1966).

Horn development is continuous throughout an animal's life and it can be influenced by a number of different factors that may

reveal important information about the life history of individuals. In some species, males may invest in conspicuously larger horns than do females to secure higher potential for competition and higher reproductive success (e.g. bighorn rams, *Ovis canadensis*: Coltman et al., 2002; Alpine ibex, *Capra ibex*: Willisch et al., 2015) whereas in other species mating success does not seem to rely upon horn size (e.g. mountain goat, *Oreamnos americanus*: Mainguy et al., 2009; Northern chamois, *Rupicapra rupicapra*: Corlatti et al., 2012) and horn dimorphism is smaller (Lovari and Scala, 1984; Côté et al., 1998). Age also plays a key role in horn development, as the growth rate normally decreases throughout the animal's life (but see Bunnell, 1978; Koubek and Hrabe, 1983). The extent of this reduction, however, appears to be species-specific: where horn size is expected to confer substantial mating advantages, males tend not to compensate for shorter horn growth in early life

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(Willisch et al., 2015), while other species – for example some *Rupicaprina* (Côté et al., 1998) – may show a compensatory mechanism of horn growth, i.e. the ‘capacity to grow abnormally rapidly after a period of reduced growth’ (Jobling, 2010), which is expected to reduce the variance in total horn length within populations. In turn, fast-growing weapons are expected to involve important costs in terms of survival (Mangel and Stamps, 2001); recent studies, however, suggest that this relationship is controversial (e.g. Bergeron et al., 2008; Toïgo et al., 2013) and that individual heterogeneity may be an important factor determining fitness components (Toïgo et al., 2013). Individual heterogeneity, i.e. the occurrence of high-quality and low-quality individuals with different abilities to allocate energy reserves, may in fact trigger a positive co-variation between fitness components (i.e. horn growth and survival) that, consequently, would make it difficult to detect costs (van Noordwijk and de Jong, 1986), as seen in the Alpine ibex (Toïgo et al., 2013).

Cohort effect is also expected to influence a number of life history traits through environmental factors that may impact on maternal care and therefore, in the long term, on adult growth rate and phenotypic quality (Toïgo et al., 1999). Furthermore, horn development may be affected by space- or time-dependent variations in environmental parameters such as precipitations (Chirichella et al., 2013), temperature (Giacometti et al., 2002) or food availability (Festa-Bianchet et al., 2004).

As in other bovids, male and female chamois – a scarcely dimorphic ungulate dwelling on the mountain ranges of Europe and the near East – show differences in the pattern of horn growth, with the former having slightly longer horns than the latter (Lovari and Scala, 1984; Bassano et al., 2003). Additionally, the occurrence of a compensatory growth mechanism during the first years of life (Pérez-Barbería et al., 1996; Rughetti and Festa-Bianchet, 2010, 2011) should favour a reduced variation in total horn length, thus hinting at the pursuit of an ‘optimal’ horn size in both sexes (Rughetti and Festa-Bianchet, 2010). Pérez-Barbería et al. (1996) pointed out a positive effect of precipitation on horn growth and Couturier (1938) suggested differences in horn length between chamois populations living on different geological substrates, i.e. calcareous vs. siliceous; cf. Chirichella et al. (2013), who also called for an evaluation of potentially different patterns of compensatory growth across different environmental conditions.

Taking advantage of a sample of hunted individuals, in the present paper we first explore the variation in annual horn growth and total horn length as a function of different factors (including sex, hunting location and – for the annual growth – age, individual heterogeneity and cohort) in two populations of Alpine chamois (*R. r. rupicapra*). We then provide a detailed analysis of horn trajectories in both sexes, through pairwise comparisons of subsequent annulus lengths, to better understand the fine-scale mechanisms underlying the pursuit of an ‘optimal’ horn size. According to Jobling (2010), the convergence of growth trajectories may in fact occur not only through compensatory growth, but also in the absence of any compensatory response, i.e. through catch-up growth – ‘the convergence of growth trajectories of animals that have different growth histories’ – as well as through recovery growth, i.e. a combination of compensatory growth and catch-up growth (Jobling, 2010). Specifically, we explore if: (i) the convergence of horn trajectories in male and female chamois is the result of compensatory growth or of catch-up growth; further, we predict that: (ii) because females are expected to reach the asymptotic horn length at a slightly earlier age than males (Bassano et al., 2003), the compensation rates would be greater in the former than in the latter; (iii) because the reproductive allocation may vary depending on the environmental conditions (Mason et al., 2011), the rates of compensatory growth would differ between populations.

## 2. Materials and methods

### 2.1. Study area

The present study was conducted in the hunting district of Sondrio (Comprensorio Alpino di Sondrio, hereafter CA-So) that extends over approximately 78 km<sup>2</sup> in the Central Italian Alps (46°10' N, 09°52' E), ranging between 300 and 4000 m a.s.l. The climate is alpine-continental and shows mean yearly rainfalls of about 1000 mm and mean yearly temperatures between 11.5 °C at the bottom of the valley and 1.5 °C at 2000 m a.s.l. (Pelfini and Belloni, 1990). The CA-So is characterised by the presence of two separated mountain massifs extending from west to east, the south-facing Rhaetian Alps and the north-facing Orobian Alps, which differ in terms of climate, the former having a more xeric regime than the latter (Credaro and Pirola, 1975). In turn, different plant associations are found over the two massifs: above the treeline, meadows of Alpine sedge (*Carex curvula*) and Haller’s fescue (*Festuca halleri*) dominate the Rhaetian Alps, whereas meadows of coloured fescue (*Festuca varia*) dominate the Orobian Alps. Chamois are widely distributed over these massifs, though with different densities. The Rhaetian population shows lower densities (approx. 3 individuals/km<sup>2</sup>) than the Orobian one (approx. 8.5 individuals/km<sup>2</sup>), partly owing to differences in habitat suitability between the two areas (Ferloni, 2007). Average annual hunting bags of chamois amount to approx. 9% of the estimated population in the Rhaetian massif and to approx. 12% in the Orobian massif (Ferloni, 2007). Recent data showed the occurrence of a marked genetic differentiation between the two populations (Suchentrunk et al., 2011).

### 2.2. Data collection

Horn growth data were collected from 101 male and 93 female chamois  $\geq 3$  years of age legally shot in the CA-So during the hunting seasons (September–November) of 2009 and 2010: 28 males and 25 females were harvested on the Rhaetian massif, 73 males and 68 females were harvested on the Orobian massif. Chamois kids are normally born in May (Couturier, 1938) and because individuals were shot between the 5th and the 7th month of their current year of life, we indicated their age as 1.5, 2.5, 3.5 years etc. To avoid bias, the sample ( $N = 194$ ) did not include horns with broken/worn-out tips. The measures of the length of the first 6 growth annuli (i.e. segments up to 5½ years of age), for the longest horn of each animal, were taken by one of the authors (LC) during the annual trophy exposition, when hunters are obliged by law to provide the hunting authority with the clean skulls of all individuals shot over the hunting season (skulls are then returned to the owners). Age was estimated following Schröder and von Elsner-Schack (1985). In chamois, horn growth in the first and second year of life cannot be distinguished, therefore for our analysis we combined the first two segments (L2) measured by means of a flexible ruler. The remaining segments (L3, L4, L5, L6) were measured by means of an electronic calliper. Fig. 1 shows the horn growth pattern and the measures taken. Measures were taken only up to L6 because horn growth reduces to a few millimetres per year after 5½ years of age (Fig. 2a). As animals were shot between mid-September and mid-November, when the horns were likely to be still growing (Couturier, 1938), to avoid biases we only measured the length of the completed segments (i.e. L2 and L3 in animals of at least 3½ years of age, L2, L3 and L4 in animals of at least 4½ years of age, L2, L3, L4 and L5 in animals of at least 5½ years of age and L2, L3, L4, L5 and L6 in animals of at least 6½ years of age, see Fig. 1). Because not all shot animals had reached 6½ years of age, sample size varied from a maximum of  $N = 194$  individuals (101 males, 93 females) for L2 and L3 to a minimum of  $N = 117$  (49 males, 68 females) for L6. Total

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