Horn growth pattern in Cantabrian chamois *Rupicapra pyrenaica parva*: Influence of sex, location and phaenology

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Sexual dimorphism in Cantabrian chamois *Rupicapra pyrenaica parva* (Cabrera, 1911) horn length was recorded annually for the first five years of life. The horns of males were larger than those of females, though horn growth rate in the first two years (ie horn length in the first two years divided by horn length in the first five years) was greater in females than males. Sexual dimorphism in horn length of Cantabrian chamois adults was found to be the highest of genus according to available data. Males and females with faster horn growth in the first two years of life reduced their horn growth rate in the third and fourth year. Chamois' horns from the Eastern Cantabrian Mountains were smaller than those from Western Cantabrian Mountains, although at five years of age these differences were not evident. Total horn length and jaw length showed significant positive correlation (females: $r_p^2 = 0.75$, males: $r_p^2 = 0.54$, $p < 0.05$ in both cases). This relationship suggests that horn growth dynamics may be used as an estimation of body-size dynamics. Horn growth / jaw length correlation was higher in females than in males. Horn growth was also positively correlated with annual precipitation in the previous year, but not with precipitation in the current year. Winter horn growth was observed in the younger age classes. Post-winter horn growth was recorded in 55% of the animals in March. The use of this information to age Cantabrian chamois is described.

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Introduction

Chamois of both sexes are characterized by hook-like horns derived from epidermal tissue. Horn growth is a continuous process throughout an animals life, although the growth rate can be affected by season, the rut in males, pregnancy, lactation in females, and disease (Niethammer 1957). These factors produce marks along the horn. Often, narrow boundaries represent winter marks, caused by a cessation of horn growth, as Couturier (1938) suggested, or a reduced rate of growth in that season (Schröder 1971, Koubek and Hrabě 1983a). Wide segments between two boundaries correspond to a fast horn growth rate. Throughout an

animals life, the horn growth rate diminishes and annual growth is constant after five years of age (Koubek and Hrabě 1983a).

Although the systematics of *Rupicapra* is still unclear (Nascetti *et al.* 1985, Miller and Hartl 1986, Masini and Lovari 1988), ten subspecies have been described, each from different mountain chains (Schröder 1985). Information about skull and horn morphometrics is available for most subspecies: *Rupicapra rupicapra rupicapra* (Couturier 1938, Hrabě and Koubek 1983, Koubek and Hrabě 1983a), *R. r. cartusiana* (Couturier 1938), *R. r. tatrica* (Hrabě and Koubek 1984, Koubek and Hrabě 1984), *R. r. carpatica* (Couturier 1938, Koubek *et al.* 1985, Hrabě *et al.* 1986), *R. r. asiatica* (Couturier 1938, Lovari and Scala 1984), *R. r. caucasica* (Couturier 1938, Koubek and Hrabě 1983b), *R. r. balcanica* (Couturier 1938, Massei *et al.* 1994), *R. r. pyrenaica, R. p. ornata* (Couturier 1938, Scala and Lovari 1984, Fernández-López and García-González 1986). For *R. p. parva* only Couturier's scant (1938) data and the study by Fernández-López and García--González (1986) are available, and these studies do not deal with horn growth dynamics.

The aim of this study is to analyse the pattern of horn growth and identify sexual and regional differences in the Cantabrian chamois. Relationships between horn size and jaw length, and the influence of annual rainfall on horn growth are described.

Study area and methods

The available material (142 females, 198 males and 6 unknown sex animals of Cantabrian chamois, *Rupicapra pyrenaica parva*) came from private hunting trophies, collections and animals shot between 1964 and 1994, a large percentage of which were collected in order to monitor the incidence of sarcoptic mange (131 individuals in 1994 in Asturias). Casualities due to natural causes provided some additional data. The samples were collected from throughout the whole area of distribution of this subspecies in the Cantabrian Mountains from Cantabria to western Asturias, including animals from the León region. Two study areas were established, Area 1: Eastern Cantabrian Mountains (Picos de Europa and Covadonga National Park), Area 2: Western Cantabrian Mountains (Aller, Caso, Riaño and Mampodre regions). The following data were recorded: length of each growth segment along frontal edge ± 0.1 mm of the left horn (right horn was used when the left was broken or worn); total horn length ± 1 mm (hereafter THL); jaw length ± 0.1 mm (from *processus angularis* to the exterior edge alveolus of I$_4$ tooth; age; date of death, and the starting date of post-winter horn growth. Individuals found dead were sexed using discriminant analysis with animals of known sex. The boundary between the 1st and 2nd annual growth increment is unclear in Cantabrian chamois. The growth increments of the first two years were therefore pooled (Koubek and Hrabě 1983a, Massei *et al.* 1994). Jaw length can be measured with accuracy and it has been used extensively as an indicator of body size in other ungulate species (Mitchell and Crisp 1981, Reimers 1983, Skogland 1989). Horn measurements were made by two different researchers, although differences due to this factor were not detected ($F_{70,1} = 0.972$, $p = 0.328$). Age was estimated using annual horn growth increments (Couturier 1938, Pflieger 1982, Bargagli and Lovari 1984, Schröder and Elsner-Schack 1985, Pérez-Barbería and Fernández-López, in press), taking the 1st of May as the putative birth date (Pérez-Barbería 1994a). From birth to 12 months of age, an animal was considered to be within the one-year old age class, and one year was added every birthday.

The terminology used for each horn annual growth increment is as follows: L_{1+2} – increment of the first two years, L_3 – increment of the third year, L_4 – increment of the fourth year; and $L5$ – increment of the fifth year. As horn growth continues throughout a chamois' life, the length of the first five segments (from now on, L_{1+5}) was taken as a reference length, against which the length of each increment was scaled (Koubek and Hrabě 1983a and Massei *et al.* 1994 consider the first 6 years). RL_{1+2} is the relative length of L_{1+2} with respect to L_{1+5} ($RL_{1+2} = L_{1+2} / L_{1+5}$), RL_3 is the same for L_3 ($RL_3 = L_3 / L_{1+5}$), and so on. Although RL_n is a measurement which includes two non--independent lengths (because L_{1+5} includes the other horn segments), the comparisons of RL_n between areas and sexes are valid because there was no variation due to these factors. In order to assess the formation date of the horn boundaries, individuals older than 2 years were used, because the boundaries from the first two years were unmarked.

Relationships between horn growth and rainfall were analyzed using L_3 and L_4. Although L_{1+2} showed the highest annual horn growth increment, L_{1+2} was not used as it contains the pooled increments of two different years. From these annual increments an annual horn growth index (GI) was calculated (Bunnell 1978). A set of nine years were selected, each containing at least 5 individuals. As Bunnell's index (1978) compared the annual increment of a given year with the mean of all years, the years which have a large number of individuals bias the value of the mean. In order to avoid this, the index was modified by replacing the arithmetic mean by a weighted mean.

Results

Horn growth pattern: differences between areas and sexes

L_{1+5} did not differ between areas ($F_{1,164} = 0.767$, $p = 0.382$), but it differed between sexes ($F_{1,164} = 367.32$, $p < 0.001$). Interaction between area and sex was not significant.

L_{1+2} showed sexual dimorphism, with larger horns in males than in females. This trend recurred in each annual increment (Table 1). In Area 2, L_{1+2} is larger than in Area 1, but this trend was reversed for L_3 (Table 1). L_4 and L_5 did not show significant differences between areas (Table 1).

RL_{1+2} was larger in Area 2 than in Area 1, but the trend was reversed for RL_3 and RL_4 (Table 2). RL_5 did not show differences between areas. RL_{1+2} was significantly larger in females than in males. The opposite was the case with RL_4. In RL_3 and RL_5, differences between sexes were not detected (Table 2). The percentages of each annual increment in relation to L_{1+5} varied for females between L_{1+2}: 71–75%, L_3: 31–41%, L_4: 7%, L_5: 3% and for males between L_{1+2}: 68–74%, L_3: 44–49%, L_4: 11–13%, L_5: 4%.

Animals, which showed fast horn growth throughout the first two years of life, had reduced growth during the third and fourth year. This was observed in both areas and for both sexes, except for L_4 and L_3 in females from Area 2 (correlation coefficients, L_3 versus L_{1+2}, Area 1: females, $r_P = -0.50$; males, $r_P = -0.59$; Area 2: males, $r_P = -0.49$; L_4 versus L_{1+2}, Area 1: females, $r_P = -0.40$; males, $r_P = -0.39$; Area 2: males, $r_P = -0.26$; $p < 0.05$ in all cases). Considering L_{1+2} versus L_3, the regression lines for females between areas did not differ in elevation and slope (ANCOVA; $F_{1,78} = 2.10$, $p < 0.05$; $F_{1,77} = 1.06$, $p < 0.05$; respectively. Snedecor and Cochran 1975). The regression lines for males differed in elevation between areas ($F_{1,121} = 9.35$, $p < 0.01$), but they did not differ in slope (Fig. 1).

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Table 1. Horn measurements of Cantabrian chamois (Cantabrian Mountains, Spain). L_{1+2} – horn annual increments in the first two years, L_3 – horn annual increment in the third year, L_4 – horn annual increment in the fourth year, L_5 – horn annual increment in the fifth year, L_{1+5} – horn increment in the first five years, Area 1 – Eastern of Cantabrian Mts (Aller, Caso, Riaño and Mampodre), Area 2 – Western of Cantabrian Mts (Picos de Europa and Covadonga National Park). ANOVA was used to compare differences between areas and sexes, and interaction area × sex. ** – $p < 0.01$, *** – $p < 0.001$, ns – no significant differences.

| | Area 1 | | | | | | Area 2 | | | | | | Between areas | | Between sexes | | Inter-action |
| | Females | | | Males | | | Females | | | Males | | | | | | | |
	Mean	SD	n	Mean	SD	n	Mean	SD	n	Mean	SD	n	F	p	F	p	p
L_{1+2}	99.12	11.59	44	116.01	12.14	55	104.17	10.93	47	127.99	12.48	71	28.16	***	152.55	***	ns
L_3	28.39	7.81	46	36.14	6.59	54	24.43	7.52	37	29.56	6.59	72	31.66	***	41.37	***	ns
L_4	7.67	3.42	52	13.11	4.60	66	7.89	2.18	36	11.33	3.78	68	0.900	ns	81.09	***	**
L_5	3.31	1.20	48	4.64	1.70	63	3.66	1.35	34	4.28	1.26	50	0.001	ns	30.26	***	ns
L_{1+5}	138.93	9.49	41	170.56	9.95	49	39.39	11.87	31	172.81	11.90	44	0.767	ns	367.32	***	ns

Table 2. Annual increments in each year with respect to horn length in the first five years in Cantabrian chamois (Cantabrian Mountains, Spain). Symbols as in Table 1. ANOVA was used to compare differences between areas and sexes, and interaction area x sex. * – $p < 0.05$, ** – $p < 0.01$, *** – $p < 0.001$, ns – no significant differences.

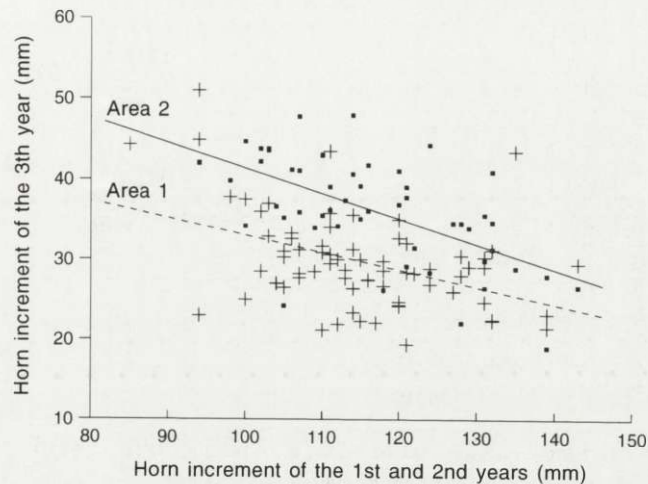| | Area 1 | | | | | | Area 2 | | | | | | Between areas | | Between sexes | | Inter-action |
| | Females | | | Males | | | Females | | | Males | | | | | | | |
	Mean	SD	n	Mean	SD	n	Mean	SD	n	Mean	SD	n	F	p	F	p	p
L_{1+2}/L_{1+5}	0.71	0.07	41	0.68	0.06	49	0.75	0.06	31	0.74	0.04	44	31.14	***	0.41	*	ns
L_3/L_{1+5}	0.20	0.05	41	0.21	0.04	49	0.17	0.05	31	0.17	0.03	44	32.00	***	0.25	ns	ns
L_4/L_{1+5}	0.06	0.03	41	0.08	0.03	49	0.06	0.01	31	0.06	0.02	44	9.12	**	16.96	***	*
L_5/L_{1+5}	0.02	0.01	41	0.03	0.01	49	0.03	0.01	31	0.02	0.01	44	0.15	ns	0.02	ns	ns

Fig. 1. Horn increment in the 3th year versus horn increment in the 1st and 2nd years pooled (mm), in males. Area 1 (dashed line and crosses): Eastern Cantabrian Mts; Area 2 (solid line and dots): Western Cantabrian Mts.

Formation date of horn boundaries and winter horn growth

In March, 54.8% of the sample ($n = 31$) was found to have indications of post-winter growth, and this proportion remained in April (50.0%, $n = 20$). In May, all horns observed had formed the last boundary ($n = 9$).

In two-year-old animals, shot between March and April, winter growth could be detected. At this age, epidermal tissue deposited throughout the winter months appears more bulkiness than epidermal tissue deposited in other months. This mark was not visible in two-year-old animals shot in June. The horn growth in the second winter of the animal's life represented 14% (mean = 17.36, SD = 2.80, $n = 15$) of the total increment in the first two years, both sexes pooled.

Relationships between horn size and annual rainfall

GI of L_3 and L_4 showed the same trend for the set of years considered ($r_S = 0.825$, $p < 0.05$, Spearman rank correlation coefficient). GI of L_3 in the current year were positively correlated with annual precipitation, in mm, in the previous year ($IG_n = 0.0004 \times rainfall_{n-1} - 5.51$, $r^2 = 0.63$, $n = 9$, $p < 0.05$, IG_n: horn growth index in the current year, $rainfall_{n-1}$: annual precipitation (in mm) in the previous year, Fig. 2), but not with precipitation in the current year.

Relationships between jaw length and horn size

There was a significant correlation between jaw length and total horn length in both males and females (Females: $r_P^2 = 0.75$, Males: $r_P^2 = 0.54$, $p < 0.05$ in all cases). Female correlations were higher than male ($p < 0.001$, Correlation coefficients comparison, Zar 1984).
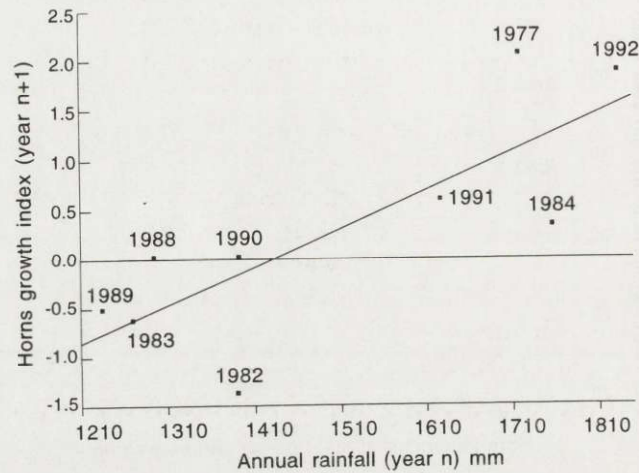
Fig. 2. Relationships between annual rainfall (mm) in year *n* and horn growth index in year n+1. The year is shown next to each point.

Discussion

Horns obtained from hunted animals for analysis may not be truly representative of the whole population, as individuals to be killed are selected by the hunters (Hrabě and Koubek 1983, Hrabě *et al.* 1986). However, this source of information is useful when comparisons between horn growth patterns are made with respect to age and horn size.

THL and jaw-length were related in both sexes, which suggests that horn growth patterns can be used to estimate body-size growth patterns when only horn measurements are available. This would increase the value of the results from the study of hunting trophies. Fandos *et al.* (1989) also found good correlations between body weight and horn length in Cantabrian chamois. In our sample, the correlation coefficients of THL against jaw length were higher in females than in males. However, Fandos *et al.* (1989) found r^2 values for females lower than for males in the correlation of live weight against THL, body length and chest girth. This was possibly due to the higher energetic cost of reproduction. Body weight is, however, directly sensitive to changes in energetic demand, while jaw-length and the size of other bones are less affected.

Sexual dimorphism in horn length was evident at all ages, with males having longer horns than females (Table 1). However, this difference did not persist in all segments in the analysis of length relative to L_{1+5} (Table 2). Females had a higher relative horn growth rate than males during the first two years of life. This difference was reversed by the fourth year. However, males from other subspecies (*R. r. rupicapra* – Koubek and Hrabě 1983a, *R. r. tatrica* – Koubek and Hrabě 1984, *R. r. carpatica* – Hrabě *et al.* 1986) have been shown to have higher annual

relative horn growth than females up to 3–4 years of age, with this difference
reversed in older ages. In our population these differences in sexual dimorphism
in relation to age may be due to differences in maturing date between sexes.
However, we need additional information to test this hypothesis.

Sexual dimorphism in horn length of adult Cantabrian chamois is the highest
of all subspecies according to available data. The ratio THL males / THL females
for *R. r. rupicapra, R. r. tatrica, R. r. carpatica, R. r. asiatica, R. r. pyrenaica,*
varies between 1.07 and 1.20 (mean = 1.14) versus 1.23 in *R. pyrenaica parva* in
this study, and the same value (1.23) was obtained when it was calculated using
data from Fernández-López and García-González (1986).

The animals which showed rapid growth in the first two years of life had a
reduced growth rate in the third and fourth year. These results are consistent
with Bunnell (1978) and Massei *et al.* (1994) for rams of Dall sheep *Ovis dalli* and
Bulgarian chamois *R. r. balcanica*, respectively, and Koubek and Hrabě (1983) in
R. r. rupicapra from the Jeseníky Mountains (Czechoslovakia) and the Usov
collection (Alps) of horn samples. In the present data, the total length of the first
five segments did not differ between the two areas. This indicates that by five
years of age differential annual growth during the previous years is compensated.
Since the first two-year increments were pooled, it is not possible to establish if
horn growth rate is faster during the first or the second year of life or both. In
other studies, horn growth during the first year in relation to L_{1+5} was between
28.2% and 30.50% in females, and 31.80–38.60% in males. During the second year
the proportions varied between 32.70–33.70% and 35.50–40.4% in females and
males respectively (Koubek and Hrabě 1983a, 1984, Hrabě *et al.* 1986). These
values indicate that a similar proportion of total horn growth occurs during the
first and second years, and the large accumulated percentage in the L_{1+2} cathegory
may be due to the growth in the first or second year (or both). In the first year,
the variation might be due to differences in birth date or genetic differences.
Genetic differences between both areas have not been found (Pérez-Barbería
1994b). At one year of age, early birth date animals had bigger horns than late
birth animals. In the present data, the horn length at two years of age differed
between areas. If birth date were the cause of the horn growth differences, it would
therefore be expected that modes of birth date would also differ between areas.
However, differences in birth date, due to geographical or environmental factors,
are not expected because both areas are adjacent. The slower growth rate in the
third year in relation to the growth in the two first years was similar between
areas in males and females, but the regression line intercept of males from Area
2 was higher than males from Area 1. If horn increments are proportional to
body-size increments, then this suggests a different optimum size in young animals
(< 3 years) in both areas. However, since these differences did not persist at five
years of age, this would indicate that small body-size is only advantageous in
young animals from Area 1. Information is not available on competition either
within young age classes or between young animals and adults or livestock in both

areas, which might help to explain this result. Another possibility may be that energetic investment in horn growth is of less importance than energetic investment of other body structures, and resource limitation in Area 1 influences horn growth in young age classes. Area 1 had a higher chamois density (19.9 animals/km^2) than Area 2 (6.5 animals/km^2) (J. M. Fernández-López, pers. comm.), this suggests the possibility of higher intra-specific competition in Area 1.

L3 and L4 growth indices for the years covered by the data were similar, suggesting that climatic conditions affect horn growth. There was a positive correlation between horn growth and precipitation in the previous year, although none was evident in relation to the present year's precipitation. Fandos (1991) found the same relationships in *Capra pyrenaica*. This seems to indicate the existence of a lag between this climatic parameter and horn growth (as Fandos pointed out). It is possible that the rainfall in the previous year determines the body condition at which the animals go into winter. Animals reaching spring in relatively good condition, may have an enhanced horn growth rate. However, if horn growth rate is affected in this way, it could reasonably be expected that winter weather conditions are also a contributory factor.

In March, half the sample showed post-winter horn growth. This indicates that when horn growth segments are used for aging, it is necessary to make the following correction: in the horns that show signs of recent post-winter growth, this portion should not be counted until the putative birth date (1st May, Pérez-Barbería 1994a).

Schröder (1971) and Koubek and Hrabĕ (1983a) pointed out that horns continue growth throughout the winter, and growth does not stop as Couturier (1938) commented. In this study, the horns of young animals (2 years old), where growth rate is high, grew during winter. During the second winter of the animals life, growth of 14% in relation to horn length during the first two years was recorded.

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