Factors affecting horn growth
in male Spanish ibex (Capra pyrenaica)

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Summary. – Variability of annual growth rate of the horn in Spanish ibex (Capra pyrenaica Schinz, 1838) was studied in a sample of 47 male skulls from Sierra de Cazorla, Spain. Assuming that each horn segment represents horn growth in a calendar year, three hypotheses can be put forward to explain the possible factors that introduce variation in the annual horn growth: determination by previous horn growth, age dependent growth, and environmental factors showed by a Xericity Index (XI). The results suggest that all three factors are related to annual horn growth variation, among them age being the best predictor.

Résumé. – La variation de l'allongement annuel des cornes du bouquetin d'Espagne (Capra pyrenaica Schinz, 1838) a été étudiée sur 47 crânes de mâles adultes provenant de la Sierra de Cazorla. Si nous considérons que chaque segment sur la corne représente la croissance en une année, on peut présenter trois hypothèses pour expliquer les facteurs responsables de l'introduction de variations dans le développement des cornes : détermination préalable de la croissance, développement lié à l'âge, et facteurs de l'environnement déterminés par l'indice de sécheresse (XI). Selon les résultats, les trois facteurs ont une relation avec la variation de la croissance annuelle des cornes, bien que l'âge soit le meilleur indicateur.

INTRODUCTION

Horn growth in bovids continues throughout the animal's life. This feature has permitted the documentation of the relationships between size and quality of horns with characteristics such as individual rank or demography (Geist 1966, Nievergelt 1966), or with factors that directly affect horn growth, such as food supply (Hoefs 1974, Bunnell 1978), precipitation (Nievergelt 1966), or snow cover (Heimer and Smith 1975).

Horn growth has many biological implications. The horn growth and shape have been related to behaviour (Schaffer and Reed 1972, Kitchener 1985, Alvarez 1990). Annual horn growth in Caprinae has been used mainly for age determination (Caughey 1965, Gray and Simpson 1985, Fandos 1991). For the Spanish ibex horn size has been used to estimate the body mass of individuals (Fandos et al. 1989) and to confirm differences between populations (Fandos and Vigal 1988).

The goal of this study was to investigate the relationships between particular annual horn growth and general horn development, age, and environmental factors affecting food availability. I have formulated three hypotheses: annual growth is dependent on previous horn growth, variation in annual growth patterns depends on age, and variation in annual growth is indirectly related to the availability of food.

STUDY AREA AND METHODS

The study is based on Spanish ibexes shot in the Cazorla Mountains, Spain, between 1980-83. General characteristics of the study area have been described in previous studies (Martinez et al. 1985, Fandos 1991).

To estimate the differences in horn segments, I assumed that in Spanish ibex, as in another bovids, each segment of horn growth corresponded to one calendar year (Cou turier 1961, Hemming 1969), thus, the number of segments represents the absolute age in years of the individuals. Previous studies with captive Spanish ibex of known age (Fandos 1991), showed that both annual growth segments of the horn and cementum incremental lines in the teeth are valid absolute age criteria. Annual horn growth was measured as the distance between two complete grooves following the previous crest (± 3 mm). This measurement represents the relative length of annual horn growth (Bunnell 1978), and cumulative total horn growth with age follows Von Bertalanffy's exponential function model (Fandos and Vigal 1988, Fandos 1991). Thus, the relative position to the first segment on the horn of a particular segment is related with its age.

According to the first hypothesis, individuals showing little horn growth in early years also would show similar low growth patterns throughout their lives, after the development model proposed by Geist (1966) and Bunnell (1978). In the case of adult specimens with more than nine annual segments measured, correlation analysis was used to study the relationship between the lengths of the eighth and ninth segments and the lengths of the third and fourth segments.

The second hypothesis (annual growth patterns depending on age) was tested by variance analysis using the means of the length of each age class segment.

To test the third hypothesis (annual horn growth reflecting food availability), horn growth was related to environmental parameters by one quality index « QI » (Table 1), similar to another one developed by Bunnell (1978), \( QI = GL_{ij} - GL_i \), where : \( GL_{ij} \) = the mean annual growth for age class \( i \) during year \( j \) and \( GL_i \) = the mean annual growth for age class \( i \) over all years.

This index compares the mean annual growth increment of each age class in a specific year with the mean annual growth increment over all years.

<table>
<thead>
<tr>
<th>Year</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>7</th>
<th>8</th>
<th>X</th>
</tr>
</thead>
<tbody>
<tr>
<td>1975</td>
<td>-0.33</td>
<td>0.09</td>
<td>0.35</td>
<td>-0.07</td>
<td>-0.15</td>
<td>-0.01</td>
<td>0.81</td>
<td>-0.43</td>
<td>0.03</td>
</tr>
<tr>
<td>1976</td>
<td>1.83</td>
<td>0.01</td>
<td>-0.11</td>
<td>0.20</td>
<td>1.99</td>
<td>0.62</td>
<td>0.04</td>
<td>0.25</td>
<td>0.60</td>
</tr>
<tr>
<td>1977</td>
<td>0.02</td>
<td>1.47</td>
<td>0.31</td>
<td>0.00</td>
<td>1.99</td>
<td>1.74</td>
<td>0.38</td>
<td>1.02</td>
<td>0.86</td>
</tr>
<tr>
<td>1978</td>
<td>-1.49</td>
<td>-0.92</td>
<td>0.70</td>
<td>0.56</td>
<td>-0.41</td>
<td>1.20</td>
<td>0.19</td>
<td>-0.11</td>
<td>-0.03</td>
</tr>
<tr>
<td>1979</td>
<td>-0.02</td>
<td>-1.03</td>
<td>-0.66</td>
<td>-0.28</td>
<td>-0.79</td>
<td>-0.69</td>
<td>0.32</td>
<td>-1.34</td>
<td>-0.56</td>
</tr>
<tr>
<td>1980</td>
<td>0.13</td>
<td>0.54</td>
<td>-2.10</td>
<td>-1.09</td>
<td>-1.07</td>
<td>-0.22</td>
<td>-1.07</td>
<td>0.64</td>
<td>0.53</td>
</tr>
</tbody>
</table>

\( QI = GL_{ij} - GL_i \) where \( GL_{ij} \) is the mean annual horn growth for age class \( i \) and year \( j \), and \( GL_i \) is the mean annual horn growth over all years; after Bunnell (1978)
Since environmental parameters are related to food availability, an annual Xericity Index « XI » was developed to estimate the intensity and duration of the annual dry period, typical of the Mediterranean climate:

\[ X_{I_y} = \sum [(3T_{my} - P_{my}) + (3T_{my} - P_{my})/2] \]

where \( X_{I_y} \) is the xericity index of the year \( y \); \( T_{my} \) is the temperature (in °C) of month \( m \) in the year \( y \), and \( P_{my} \) is the precipitation (in mm) of month \( m \) in the year \( y \). This index is formulated so that only dry months on which \( 3T > P \) will yield non-zero arguments to the sum. In our data set, dry months extended from June to September in most years.

I used climatic data recorded at three meteorological stations from 1975 to 1980 by the Spanish Meteorological Service (Vadillo, Nava de San Pedro and Cañada de las Fuentes) located in the Cazorla Mountains.

RESULTS

I measured 368 annual growth segments from 47 male Spanish ibex. The mean length (\( \bar{x} \pm SE \)) was 63.59 ± 16.50 mm (Table 2).

First Hypothesis. – The existence of a significant correlation between the length of the eighth – ninth segments and the length of the third – fourth supports the idea that specimens having slow growth rates when young continue to have slow growth rates as adults (third + fourth) = 79.34 ± 0.48 (eighth + ninth) (\( r = 0.77, n = 18, P = 0.016 \)).

Second Hypothesis. – There were differences (\( F = 40.07, d.f. = 11-356, P < 0.001 \)) in the length of annual growth segments among age classes (Fig. 1). Peaks in annual growth occur in the first year of life (\( \bar{x} = 84.56 \pm 11.85 \) mm; \( n = 44 \)). Lowest annual growth occurs during old age.

Fig. 1. – Mean and standard error (bars) of annual growth increment length in each age class in mm, of male Spanish ibex from Cazorla, 1971-1983. Below : Sample size.
TABLE 2. – Mean length (\( \bar{X} \pm SE \)) (mm) of annual horn growth segments of Spanish ibex in Cazorla Mountains, Spain, 1975-1980.

<table>
<thead>
<tr>
<th>Year</th>
<th>( \bar{X} \pm SE ) n</th>
<th>( \bar{X} \pm SE ) n</th>
<th>( \bar{X} \pm SE ) n</th>
<th>( \bar{X} \pm SE ) n</th>
<th>( \bar{X} \pm SE ) n</th>
<th>( \bar{X} \pm SE ) n</th>
<th>( \bar{X} \pm SE ) n</th>
<th>( \bar{X} \pm SE ) n</th>
</tr>
</thead>
<tbody>
<tr>
<td>1975</td>
<td>79.0 ± 8.35</td>
<td>4</td>
<td>67.2 ± 4.50</td>
<td>11</td>
<td>64.0 ± 5.49</td>
<td>4</td>
<td>64.2 ± 7.49</td>
<td>4</td>
</tr>
<tr>
<td>1976</td>
<td>86.5 ± 1.50</td>
<td>2</td>
<td>66.0 ± 4.63</td>
<td>6</td>
<td>58.8 ± 3.36</td>
<td>11</td>
<td>67.6 ± 6.10</td>
<td>4</td>
</tr>
<tr>
<td>1977</td>
<td>84.8 ± 4.27</td>
<td>6</td>
<td>70.0 ± 2.00</td>
<td>2</td>
<td>63.5 ± 4.51</td>
<td>6</td>
<td>65.3 ± 3.66</td>
<td>11</td>
</tr>
<tr>
<td>1978</td>
<td>82.3 ± 0.88</td>
<td>3</td>
<td>60.5 ± 2.37</td>
<td>6</td>
<td>71.5 ± 11.5</td>
<td>2</td>
<td>70.2 ± 3.51</td>
<td>6</td>
</tr>
<tr>
<td>1979</td>
<td>84.3 ± 8.37</td>
<td>3</td>
<td>61.7 ± 2.33</td>
<td>3</td>
<td>53.0 ± 4.42</td>
<td>6</td>
<td>61.5 ± 9.50</td>
<td>2</td>
</tr>
<tr>
<td>1980</td>
<td>85.5 ± 4.50</td>
<td>2</td>
<td>68.5 ± 3.50</td>
<td>2</td>
<td>53.6 ± 1.76</td>
<td>3</td>
<td>54.6 ± 4.37</td>
<td>5</td>
</tr>
</tbody>
</table>

Third Hypothesis. – Annual growth rate differed among years (Table 3). The growth rates of annual horn growth represented by the annual mean of QI showed a significant negative regression with the XI for year 1975 to 1980 [QI + 1]100 = 394.02 - 5.97XI; \( R^2 = 0.796; P < 0.05 \) (Fig. 2). However, the mean length of the first annual growth segment did not show significant differences among years (\( F = 0.24, d.f. = 1-4, P = 0.90 \)).

TABLE 3. – Analysis of variance table for means of annual horn growth segments Spanish ibex from Cazorla Mountains among 1975 and 1980.

<table>
<thead>
<tr>
<th>Source</th>
<th>Sum Squares</th>
<th>d.f.</th>
<th>Mean Squares</th>
<th>E</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Annual horn growth segment</td>
<td>6908.6</td>
<td>7</td>
<td>986.9</td>
<td>9.55</td>
<td>0.0000</td>
</tr>
<tr>
<td>Year</td>
<td>1730.6</td>
<td>5</td>
<td>346.1</td>
<td>3.35</td>
<td>0.0065</td>
</tr>
<tr>
<td>Interaction</td>
<td>3413.0</td>
<td>35</td>
<td>97.5</td>
<td>0.94</td>
<td>0.5648</td>
</tr>
<tr>
<td>Error</td>
<td>18508.2</td>
<td>179</td>
<td>103.4</td>
<td>103.4</td>
<td>103.4</td>
</tr>
</tbody>
</table>

\( y = -5.976x + 394.025, \text{ R-squared: .796} \)

Fig. 2. – Relationship between Quality Index transformed (QI + 1)100 and Xericy Index XI in male Spanish ibex from Cazorla Range, 1975-1980.
I used two different tests to check whether the first annual growth segment wears off throughout the life of the individual, because this wearing might introduce an unknown bias to the data set. This possibility was rejected since neither the relationship between the length of the first segment and age \( R^2 = 0.32, \text{d.f.} = 1-43; F = 0.14, P = 0.71 \), nor an analysis of variance of the length of the first segment among age classes \( F = 1.04, \text{d.f.} = 12-32, P = 0.43 \) were significant.

**DISCUSSION**

Age changes in the growth pattern of the horn in the Spanish ibex differ from other members of Caprinae, such as the Dall's sheep (*Ovis dalli*) (Bunnell 1978) or the Barbary sheep (*Ammotragus lervia*) (Schaller 1977, Gray and Simpson 1985). In the Spanish ibex, the highest rate of growth occurs in the first growing period, as found in other species of the genus *Capra* (Schaller 1977) and in the mouflon (*Ovis gmelini musimon*) (Pfeffer 1967). In other species of the genus *Ovis* (Rieck 1963, Bunnell 1978, Hoefs 1982) and in the chamois (*Rupicapra rupicapra*) (Koubek and Hrabe 1983), the highest rate of growth occurs in the second or third growing period.

In the Bovidae family, the length and cross-section breadth of horns are one of the most variable morphological features throughout individual's life. In the Spanish ibex, this variability appears to be associated with individual potentiality, as shown by Geist (1966) in *Ovis*, and with age, as shown by Caughley (1965) in *Hemitragus jemlahicus*. This study indicates that environmental factors also affect horn growth in the Spanish ibex. Similar results were obtained by Bunnell (1978) in *Ovis*.

The decrease in growth rate after six years (Alvarez 1990) and mainly after eight years of age (Fig. 1) coincides with the age at which males begin to play an active role in the reproductive activities such as dominance fights, maintenance of females harems, and copulation (Alvarez 1990, Fandos 1991).

Wear of the horn tip is not so important in the Spanish ibex as in other members of Caprinae, especially when compared with the genus *Ovis* (Shackleton and Hutton 1971, Bunnell 1978, Petocz and Shank 1983), because of differences in horn morphology between the genus *Ovis* and *Capra* (Mloszewski 1982) and its distinct use in fights (Schaffer 1968, Geist 1971, Schaffer and Reed 1972, Alvarez 1990). In the genus *Ovis*, horns begin to develop a spiral at an early age, with horn tips diverging and coinciding with the greatest horn breadth. For this reason, in male sheep horn wear begins much earlier than in male ibex, caused mainly by the course of fights. On the contrary, there is little rubbing and wearing of the horn in *Capra pyrenaica* because horn tips converge and are directed upward, making rubbing more difficult.

Horn tip length (as first year horn growth) is not influenced by interannual variations in the availability of resources. Nourishment of young during the first six months of life depends on the mother's milk (Fandos 1991). The potential effect of low availability of resources in a particular year is, therefore, buffered by the mother's endurance.

In a little proportion, there are other larger variations in the pattern of length of annual growth segments in males that may be related to consequences of specific events that have occurred during the individual's life such as diseases, lesions, or natural catastrophes like fire or flood.
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