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SEXUAL DIMORPHISM OF PYRENEAN CHAMOIS (*RUPICAPRA P. PYRENAICA*) BASED ON SKULL MORPHOMETRY

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ABSTRACT.– Sexual dimorphism in skull characteristics of Pyrenean chamois is studied in a sample of 85 adults (36 males and 49 females) by means of 26 quantitative variables. Skull variables were analised by multiple regression and principal component techniques. The Pyrenean chamois shows one of the smallest sexual skull dimorphisms of the Rupicapra *subspecies. Only length, thickness, and related variables of horns present significant differences between sexes. Nevertheless, horn height was statistically identical in both sexes. Ecological implications of skull variability and skull variables relationships are discussed. Several discriminant functions were developed by means of discriminant analysis. Those that better identified sexes include horn core diameters. We also developed other functions based on upper skull variables that could be used to identify incomplete specimens or archaeological remains.*

RÉSUMÉ.– Nous avons étudié les dimorphismes sexuels de l'isard en travaillant sur 26 mesures cranéométriques issues d'un échantillon de 85 crânes adultes (soit 36 mâles et 49 femelles). Les analyses ont porté sur la comparaison des moyennes, la régression multiple et l'analyse en composante principale. Il s'avère que l'isard pyrénéen présente un des plus bas dimorphisme cranéal du genre Rupicapra. *Seuls la longueur et l'épaisseur des cornes et leurs variables associées ont montré des différences significatives entre les sexes. Les implications écologiques de la variabilité entre les crânes et des relations entre les variables cranéométriques sont discutées. En utilisant l'analyse discriminante, nous arrivons à développer quelques fonctions nous permettant d'identifier le sexe des exemplaires complets ou incomplets. Les fonctions se basant sur l'épaisseur des cornes ont permis une meilleure classification.*

RESUMEN.– Se ha estudiado el dimorfismo sexual del sarrio a partir de 26 medidas craneométricas tomadas en una muestra de 85 cráneos adultos (36 machos *y 49 hembras). Hemos realizado un análisis de comparación de medias y análisis de regresión múltiple y de componentes principales. El sarrio presenta uno de los menores dimorfismos craneales del género* Rupicapra. *Solo la longitud y grosor de los cuernos y variables relacionadas con ellos, mostraron diferencias significativas entre sexos. Sin embargo, la altura de los cuernos no presentó diferencias significativas. Se discuten las implicaciones ecológicas de la variabilidad encontrada en los cráneos y de las relaciones entre variables craneométricas. Por medio de análisis discriminantes desarrollamos varias funciones que permiten la identificación sexual de ejemplares completos e incompletos. Las funciones que permiten una mejor clasificación se basan en las variables del grosor de los cuernos.*

Key-words: Pyrenean chamois, skull dimorphism, horn, discrimant functions.

1. Introduction

Sexual dimorphism is common and widely recognised in ungulates. Its origin appears to be closely linked to sexual selection but also has important ecological consequences (SLATKIN, 1984; JANIS, 1982; PÉREZ-BARBERÍA *et al.*, 2002). In present-day bovids it manifests itself in the dimensions of the horns, which tend to be bigger in males. However, sexual dimorphism in the *Rupicaprini* tribe, and especially in the *Rupicapra* genus, is not very evident (BUBENIK *et al.*, 1977). Thus, the Pyrenean chamois for example often does not present differences in body size due to sex (CRAMPE *et al.*, 1997; GARCÍA-GONZÁLEZ *et al.*, 2000) and sexual discrimination may not be easy for inexperienced people.

Sexual dimorphism in the *Rupicapra* genus has been studied in many of its subspecies (SALZMAN, 1977; HRABE & KOUBEK, 1982; KOUBEK & HRABE, 1983; LOVARI & SCALA, 1984; MASSEI *et al.*, 1994 a, b). *R. p. pyrenaica* has proved to be one of the subspecies with the smallest sexual dimorphism in skull characters, in contrast with *R. p. parva* (FERNÁNDEZ-LÓPEZ & GARCÍA-GONZÁLEZ, 1986; PÉREZ-BARBERÍA *et al.* 1996).

When only incomplete bone remains are available for examination, either contemporary samples or those from archaeological sites, sexual identification is often difficult. The use of discriminant functions based on skull characters can be helpful in these cases (WIIG, 1980; NUGENT, 1989). This study analyses the degree of sexual dimorphism present in *R. p. pyrenaica* from skull characteristics and develops various discriminant functions which enable the identification of sex in doubtful skulls.

2. Materials and methods

A total of 85 skulls (49 female and 36 male) were studied. This diverse sample came from the Spanish Central and Western Pyrenees (Viñamala, Los Circos, Benasque Hunting Reserves), including individuals found dead in the field, private donations, selective hunts and confiscation from poachers. Some skulls are incomplete causing some variation in sample size.

The determination of sex was carried out by observation of the genital organs in complete individuals or by measuring the thickness of the horns and horntip curvature on skulls (BUBENIK *et al.*, 1977). In the latter case, individuals were examined independently by 5 experts and the results were only included in the sample if there was unanimous agreement. The individuals used in the study were of a minimum age of 3 years, with three pairs of permanent incisors and complete dentition (FERNÁNDEZ-LÓPEZ & GARCÍA-GONZÁLEZ, 1986).

26 skull measurements were taken and are recorded in Table 1. The majority coincide with those defined in FERNÁNDEZ LÓPEZ & GARCÍA GONZÁLEZ (1986), and 5 new measurements were added: Anteroposterior Horncore (DLO), mean of maximum diameters at the base of each horncore; Transversal Horncore Diameter (DTO), mean of the minimum diameters at the base of each horncore; Trophy Height (HT), the minimum vertical distance between frontal suture and the middle point of an imaginary line which joins the horns at their maximum height, and the Width between Horn Tops (SC), the distance between the points of maximum height of each horn. These last two measurements are used in trophy-hunting scores. Finally, the Horizontal Mandible Length (LHM) was taken between the incisive alveolus and the external edge of the mandible angle (Figure 1).

A univariate test comparing the means between sexes, and various multivariate analyses were carried out. These last comprised: a multiple correlation followed by a cluster analysis to determine the relation between variables and the degree of redundance between them; a principal component analysis (PCA) to determine which variables explain a greater percentage of total variability of the sample, and a stepwise discriminant analysis to establish the equations which best discriminate between the two sexes. Statistica 5.1 software was used for the statistical analysis.

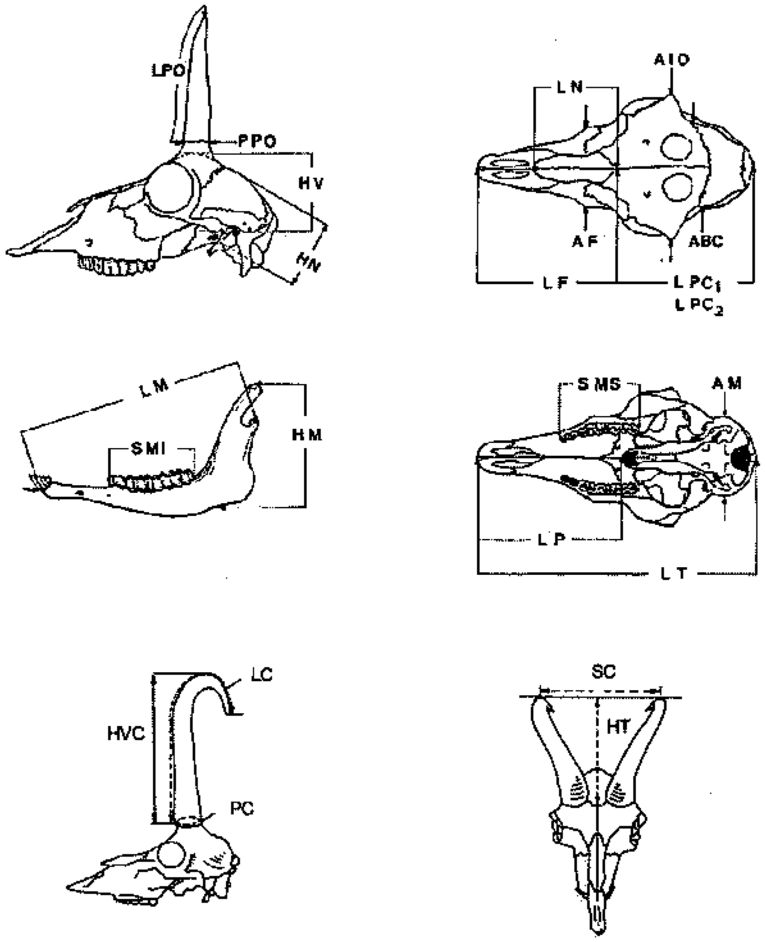

Figure 1. Schematic representation of the skull and horn measurements taken in Pyrenean chamois skulls.

3. Results

Table 1 summarizes the basic statistics and the results of the analysis of comparison between sexes.

Significant differences are only apparent in variables related to horns (excluding those referring to height), in two widths of the upper skull (AIO y ABC) and in two skull heights: the vertical (HV) and the neurocraneal (HN). The remaining variables show no significant relationship between sexes.

Table 1. Number of individuals (N), mean values (in millimetres), standard deviation (SD), and results of t-Student test between males and females for each skull variable. Significance level: * p< 0.05; ** p<0.01; *** p<0.001.

	Sex	*N*	*Mean*	*SD*	*p (t-Student)*	
LT – Total length of skull	M	15	198.5	7.8	0.457	
	F	27	196.9	5.9		
LF – Facial length	M	28	112.6	5.5	0.762	
	F	41	112.2	5.1		
LN – Nasal length	M	25	64.8	6.7	0.820	
	F	34	64.4	5.0		
LPC1 – Frontal + postfrontal length (straight)	M	16	100.8	5.9	0.745	
	F	27	100.3	4.2		
LPC2 – Frontal + postfrontal length	M	13	130.5	7.0	0.789	
(along sagital curvature)	F	22	131.0	5.6		
LP – Palatal length	M	31	102.7	4.0	0.934	
	F	41	102.7	4.4		
SMS – Maxillary tooth row length	M	35	54.2	2.4	0.273	
	F	45	53.6	2.5		
AIO – Interorbital width	M	33	104.2	3.4	0.031	*
	F	45	102.4	3.7		
AF – Facial width	M	33	60.8	2.6	0.273	
	F	47	60.1	2.9		
AM – Mastoid width	M	17	56.5	2.8	0.260	
	F	29	55.7	2.3		
ABC – Brain case width	M	36	63.4	2.6	0.024	*
	F	44	62.3	1.8		
HN – Neurocranium height	M	16	58.6	1.7	0.013	*
	F	23	57.1	1.8		
HV – Maximum vertical height	M	29	60.7	2.7	< 0.001	***
	F	31	58.0	2.7		
LPO – Maximum horn core length	M	34	94.6	6.9	< 0.001	***
	F	45	75.4	8.0		
PPO – Horn core basal circumference	M	34	59.3	4.0	< 0.001	***
	F	45	46.3	3.9		
DLO - Anteroposterior horn core diameter	M	29	19.5	1.5	< 0.001	***
	F	36	15.4	1.3		
DTO – Transverse horn core diameter	M	28	17.2	1.3	< 0.001	***
	F	36	13.3	1.4		
LC – Maximum horn length	M	34	205.5	17.0	< 0.001	***
	F	45	175.2	15.9		
HVC – Top-base horn length	M	34	138.6	15.0	0.101	
	F	45	132.4	17.1		
PC – Horn basal circumference	M	35	68.7	3.7	< 0.001	***
	F	45	54.2	3.9		
HT – Trophy height	M	24	141.2	15.3	0.108	
	F	32	131.0	27.7		
SC – Width between horn tops	M	24	101.5	18.9	0.004	**
	F	30	82.5	26.2		
LM – Maximum mandible length	M	12	156.6	7.7	0.898	
	F	24	156.9	5.2		
LHM – Horizontal mandible length	M	9	147.4	9.0	0.824	
	F	20	147.9	5.0		
SMI – Mandible tooth row length	M	12	57.2	2.0	0.401	
	F	24	56.6	2.1		
HM – Maximum mandible height	M	12	81.9	5.4	0.650	
	F	23	82.6	3.3		

Table 2. Factor loadings of the skull variables in the three first factors of a principal components analysis that account for the 61% of explained variance. Sex has been converted into a quantitative variable assigning the value of 1 to the males and 2 to the females. Factors > 0.7 are marked in bold.

	Factor 1	Factor 2	Factor 3
SEX	0.036	**-0.893**	0.089
LT	**0.894**	0.098	0.047
LF	0.664	0.027	-0.187
LN	0.418	0.037	-0.272
LPC1	0.682	0.093	0.242
LPC2	0.654	0.022	0.285
LP	0.636	-0.005	-0.151
SMS	0.108	0.187	**-0.764**
AIO	**0.704**	0.259	0.104
AF	0.617	0.186	0.053
AM	**0.738**	0.170	-0.038
ABC	0.597	0.269	-0.117
HN	0.587	0.306	-0.135
HV	0.529	0.405	0.054
LPO	0.115	**0.893**	-0.028
PPO	0.109	**0.929**	-0.007
DLO	0.068	**0.910**	0.142
DTO	0.048	**0.908**	0.131
LC	0.210	**0.780**	0.406
HVC	0.406	0.351	0.567
PC	0.067	**0.941**	-0.103
HT	0.339	0.320	0.539
SC	0.052	0.420	0.642
LM	**0.892**	0.033	0.066
LHM	**0.872**	0.014	0.069
SMI	0.040	0.074	-0.572
HM	0.572	-0.056	-0.292
Expl.Var.	7.375	6.530	2.575
Prp.Totl.	0.273	0.242	0.095

Table 2 shows the factor loadings of the skull variables studied for the first three factors of the analysis of principal components. These three factors explain 61% of the total variance and the analysis was carried out with varimax rotation and missing values substituted by means.

Factor 1 is a component related to the maximum length and width of the skulls and other highly correlated variables (Figure 2). This would seem to indicate that the first source of variation in the sample studied was the global skull size regardless of sex. Factor 2 separates the sex variable on the negative side from the variables related to horns on the positive side, which would seem to indicate that the main source of variation due to sex is found in horn dimensions. Factor 3 divides, on the one hand, some variables related to mastication (SMS, SMI y HM), and on the other, variables related to the shape of the horns (SC, HVC y HT). Although this is hard to interpret, it may bear some relation to morphological adaptations derived from different feeding strategies (see Discussion).

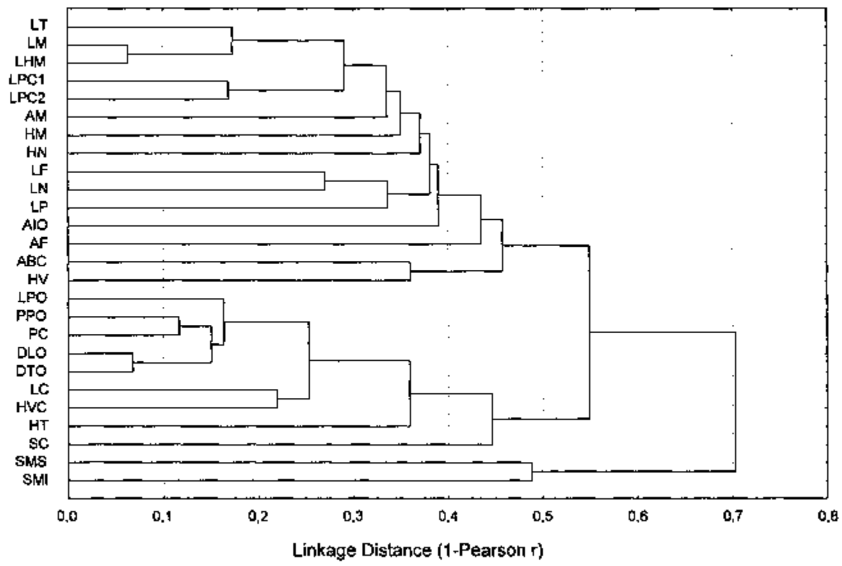

Figure 2. Results of the cluster analysis showing the relationships between skull variables.

Both the analysis of principal components and the cluster analysis (Figure 2) demonstrate the existence of highly associated groups of variables which were found to be redundant in the analyses. So for example, all the horn variables are usually correlated, although the maximum distance (SC) and the height of the horns (HT) are less so. The longitudinal dimensions are usually inter-related, as are those of width. The dimensions related to facial length (LF, LN y LP) also form an inter-related group.

In order to avoid an excessive number of missing values, some variables which were redundant with other variables and contained few data were eliminated during the second stage of analysis. The variables were: LT, LPC1, LPC2, AM, HN, PPO, HT, SC and the 4 mandible measurements. The repetition of the PCA with reduced variables essentially gives the same result, although the variance explained increases to 69% and the axis which relates sex and horn dimensions occupies first place (Factor 1).

Discriminant Analysis

With the selected variables, a discriminant analysis was carried out following the Forward stepwise procedure with a value of F to enter equal to 1. The cases with missing values have been removed. The objective of this first analysis is the elaboration of a model which optimizes the number of cases which are correctly classified, even if that means including a large number of variables or in other words, when whole skulls are available and maximum precision is sought in the classification process. The model obtained selects 8 variables with a Wilks' Lambda value = 0.06 ($F = 60.1$; $P < 0.001$). It shows 100% effectiveness in the correct determination of sex over a total of 44 cases. The centroid value for males is -4.3979 and for females, 3.1414 ($D^2 = 60.2$). The discriminant function is:

x = -1.04447 DLO + 0.33024 DTO - 0.18953 PC + 0.18346 HV - 0.17474 ABC + 0.15842 SMS + 0.12975 HVC - 0.08611 LC + 14.48396

Occasionally, only incomplete or fragmented skulls are available, for example, in the case of excavations or deterioration for other reasons. For use in these cases, we have obtained another model based on the dimensions of the upper part of the skull, which normally remains intact for longer. To this end we took the AIO, ABC, HV, SMS, DLO, DTO variable and carried out a Forward stepwise analysis with the same conditions as in the previous model. The model obtained selected 3 variables with Wilks' Lambda value = 0.18 ($F = 49.4$; $P < 0.001$). Over a total of 61 cases, it shows 95.1% efficiency in the correct determination of sex. The centroid value for males is equal to 2.149 and for females, -2.051. The discriminant function is:

x = 0.98458 DLO - 0.13153 AIO + 0.11365 ABC - 10.63651

With the same objectives and only one variable, a third model was obtained which aimed to determine very damaged specimens or specimens with broken horncores. The Anteroposterior Horncore Diameter (DLO) is the variable which allowed us to determine 65 individuals with a 93.85% success rate with a Wilks' Lambda value = 0.3 ($F = 149.1$; $P < 0.001$). The model consists of two classification functions. In order to test an unknown case, its value is calculated in the two equations and classified in the group with the highest value:

Males: x = 10.4288 DLO - 102.7355; Females: x = 8.2031 DLO - 63.6556

In order to identify the sex only from horn sheaths, a fourth model has been obtained. It is based on three horn measurements which can even be obtained from loose sheaths: LC, PC y HVC. The discriminant function provides 100% accuracy over 74 individuals, with centroid values of – 2.7973 and 2.1615 for males and females (Wilk's Lambda = 0.14; F = 153.1; P < 0.001):

x = - 0.184 PC - 0.0932 LC + 0.089 HVC + 16,671

If horns are incomplete, the following equations based solely on Horn Basal Circumference (PC) can be used. This model provided 98.7 % reliability in a sample 79 individuals (Wilk's Lambda = 0.21; F = 288.3; P < 0.001). As with DLO the highest value obtained classifies the sample into its corresponding group.

Males: x = 4.7641 PC - 164.5337 Females: x = 3.7516 PC - 102.11

4. Discussion

The sample of *R. p. pyrenaica* studied shows little sexual dimorphism. The differences are only evident in horn dimensions as shown in the univariant (Table 1) and multivariant (Table 2) analyses. The best measurements for defining sexual dimorphism in Pyrenean chamois skulls are those of length and diameter of the horns and horncores. These are of greater dimensions in males than in females. It is interesting to note that measurements such as Top-base Horn Length (HVC) or Trophy Height (HT), often used in trophy-hunting scores, have no real significance with regard to sexual dimorphism.

As well as the horns, the Interorbital Width (AIO), the Brain Case Width (ABC), the Neurocranium Height (HN) and the Maximum Vertical Height (V) also showed significant differences between the sexes (Tabla 1). The differences found in the dimensions related to the neurocranium could indicate a greater cranial capacity in males. However, they could also be due to them having larger horns, which would provoke a thickening of the skull wall beneath the horn core (SCHAFFER & REED, 1972; GARCÍA-GONZÁLEZ, 1981). The greater development of the frontal sinus in males, due to their larger horns, could also be responsible for the differences found in Interorbital Width (AIO) and Maximum Vertical Height (HV) of the skull. Thus the differences between sexes appear to be solely linked to horn size and related variables.

According to the principal component analysis, the primary source of variation (F1) of the sample studied with all the cranial measurements was apparently the size of the individual, regardless of sex. The most significant variables of F1 axis include the maximum lengths and breadths of the skull, as well as the antero-posterior jaw lengths (Table 2). These variables are highly correlated to body weight (JANIS, 1990) and this would be an allometric factor linked to body size. This result may be a consequence of the heterogeneous origin of the study sample.

The second source of variation (F2) seems to be due to sex and horn variables related to it, as has been discussed above. The third factor of variation (F3) relates some variables linked to mastication function with the shape of the horns, also regardless of sex. Various studies have pointed out relationships between the dimensions of the chewing apparatus (mandible and molar row) and the feeding habits and habitat preferences in artiodactils, both at an interspecific (JANIS, 1990; SPENCER, 1995, SICURO & OLIVEIRA, 2002) and an intraspecific level (NUGENT & FRAMPTON, 1994; ARAGÓN *et al.*, 1998). Species or populations with short mandibles seem to prefer concentrate foods and/or dense habitats. An inverse relationship between the length of the molar row and the mandible height on the one hand, and the maximum horn distance and horn height on the other (Table 2) was found. These relationships could support the hypothesis that the phenotypes with a diet based on dicotiledons and/or forest-dwellers, possess better trophies than grazing phenotypes and/or those from open habitats (as is thinking by some wardens). An individual study of the feeding and habitat preferences of the Pyrenean chamois and its trophy scores would allow us to clarify this assumption.

Sexual dimorphism in cranial dimensions has been studied in various subspecies of the *Rupicapra* genus. PÉREZ-BARBERÍA *et al.* (1996) indicate that *R. p. parva* presents the greatest sexual dimorphism of all the subspecies studied up to the present day. The authors refer principally to horn length as a reflection of body size (FANDOS *et al.*, 1989). The *R. r. caucasica* and *R. r. balcanica* subspecies also present a marked sexual dimorphism with regard to skull and horn dimensions (KOUBEK & HRABE, 1983; MASSEI *et al.*, 1994 a, b), while in *R. r. asiatica* these sexual differences seem smaller (LOVARI & SCALA, 1984). In the *R. r. rupicapra* the information available appears to indicate that the degree of sexual dimorphism depends on the stable or pioneering character of the population. Thus the introduced populations in the Swiss Jura (SALZMAN, 1977) or in the Jesensky Mountains (Czech Republic) (HRABE & KOUBEK, 1982) presented greater sexual differences in skull measurements, when compared with other, more stable populations of the same subspecies. The same is true of populations introduced in New Zealand (NIETHAMMER, 1971). Furthermore the decrease of sexual dimorphism with an increase in density has been observed in other ungulates (VINCENT *et al.*, 1995).

It is difficult to establish if the scarce sexual dimorphism in *R. p. pyrenaica* is due to ecological factors (stable character of the populations) or genetic factors. The characteristics of the sample studied, which represents a broad variety of individuals in geographic and temporal terms, seem to suggest that there are genetic differences typical of this subspecies.

The species of ungulates with polygynous reproductive systems and from open habitats tend to present a greater sexual dimorphism (JARMAN, 1974; PÉREZ-BARBERÍA *et al.*, 2002). In this sense *R. p. pyrenaica* and other populations of the nominate subspecies (*R. r. rupicapra*) could represent an exception to this tendency. However, comparative morphological studies of Pyrenean populations in contrasting habitats and densities would help to clarify this subject.

The five discriminant functions presented offer a high percentage of accuracy in the determination of sex in the sample studied. Depending on the state of skulls, one or more functions can be used for their classification. The validity of the equations should be tested with new individuals of known sex.

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