

Craniometric variability of the Iberian desman, *Galemys pyrenaicus* (Mammalia: Erinaceomorpha: Talpidae)

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Abstract. A craniometric study was conducted on a sample of 209 specimens of the Iberian desman, representing the main areas of the species' distribution range: Pyrenees, Iberian System, Cantabrian area, Atlantic area, and Central System. No age differences were found in the sample but, conversely to previous reports, results revealed a slight sexual dimorphism in size. Multivariate size and shape analyses performed on both sexes separately indicated that the Pyrenean sample is the one that differs most from the others. Skull of specimens from the Atlantic area was smaller than those from the Cantabrian area, Iberian System, and Central System, and very similar in size to the desmans from the Pyrenees. Nevertheless, in the canonical plots for size and shape both males and females from the Atlantic area clearly fall within the range of variation of non-Pyrenean desmans. Although our analyses showed that there is a general morphological skull differentiation between the two classic subspecies of the Iberian desman described in the literature, it is clear that further morphological and genetic studies are needed to clarify the infraspecific taxonomy of this species fully.

Key words: Iberian desman, morphometrics, skull, Iberian Peninsula

Introduction

The Iberian desman, *Galemys pyrenaicus*, is a member of the Talpidae family and is endemic to the mountain areas of the northern half of the Iberian Peninsula. The species was first described by E. Geoffroy Saint-Hilaire (1811), who assigned a specimen from the northern side of the Pyrenees to *Mygale pyrenaica*. The generic name *Galemys* was used for the first time by K u p (1829), though it was not generally used until M i l l e r ' s 1912 Catalogue. Meanwhile, G r a e l l s (1897) attributed desmans from the Sierra de Guadarrama (central Spain) to a new taxon, *Myogalea rufula*, on the basis of its more yellow shading on its back, legs and nails than the Pyrenean type specimen.

M i l l e r (1912) recognised one species of the Iberian desman, *Galemys pyrenaicus*, with two subspecies, *pyrenaicus* and *rufulus*. He maintained that it occurred in the Pyrenees and adjacent parts of southern France, and probably also in north-eastern Spain north of the Ebro river; its presence in Asturias was also suggested. According to M i l l e r (1912), the form *rufulus* was distributed in central Spain, south of the Ebro Valley. To distinguish the two subspecies, this author indicated the larger hindfoot, larger condylobasal length,

more massive skull, and slightly lighter fur colour of *rufulus*. This taxonomic pattern was followed by C a b r e r a (1914), who mentioned that *rufulus* was larger than *pyrenaicus*. The characters distinguishing *pyrenaicus* and *rufulus* indicated by C a b r e r a (1914) were also the hindfoot and condylobasal lengths. Nevertheless, he found no differences in fur colour between the two forms.

N i e t h a m m e r (1970) indicated that the body and skull sizes of the specimens from Burguete (western Pyrenees) were, in general terms, slightly smaller than those from other zones of northern (Sierra de Cameros in the Iberian System, and Cantabria) and central Spain (Guadarrama). He specified that these differences were most relevant in the condylobasal length and that the mean body weight recorded in his *rufulus* specimens was clearly higher than the values mentioned by R i c h a r d & V a l l e t t e V i a l l a r d (1969) for animals from the French Pyrenees. Nevertheless, N i e t h a m m e r (1970), like C a b r e r a (1914), found no differences in the fur colour of *pyrenaicus* and *rufulus*. Using a full sample of specimens from all geographic zones, he indicated that both sexes were very similar in their body and skull dimensions as well as in fur colour.

P a l m e i r i m & H o f f m a n n (1983) mentioned the two subspecies, although they pointed out that they had few morphological differences. They based themselves on N i e t h a m m e r ' s (1970) observations to state there was no size dimorphism between sexes.

In J u c k w e r ' s (1990) review of the species, the validity of *pyrenaicus* and *rufulus* was maintained on the basis of the size characteristics mentioned by M i l l e r (1912), C a b r e r a (1914), and N i e t h a m m e r (1970). J u c k w e r (1990) found no significant differences in body or skull size between males and females from the Sierra de Cameros. In a more detailed morphological analysis of these forms, G o n z á l e z - E s t e b a n e t a l. (1999) concluded that the identity of the two subspecies was doubtful since body and skull sizes of desmans from the western Pyrenees fell completely within the range observed in specimens from more western zones (Iberian System mountains, Cantabria, Asturias, León, and Galicia). Pooling specimens from different geographic zones in a common sample, these authors found no significant differences in body and skull sizes between sexes, corroborating N i e t h a m m e r ' s (1970) and J u c k w e r ' s (1990) findings. According to G o n z á l e z - E s t e b a n e t a l. (1999), fur colour varies geographically in such a way that specimens from Pyrenees, Basque Country, and Iberian System are noticeably darker than those from most western sites (Asturias, León, and Galicia). Nevertheless, they specified that these morphological patterns did not correspond to the classic differentiation between the subspecies *pyrenaicus* and *rufulus*.

We have been compiling craniometric data on the Iberian desman for several years. Preliminary analyses of these data suggested that several biometric relationships between geographic samples and sexes differed from certain results reported in the literature. Additionally, no information on skull shape variation in the distribution area of the species has ever been reported. With all this in mind, the aims of this paper are: i) to analyse the extent of sexual dimorphism in skull size of the Iberian desman at a local level; ii) to review geographic variation in skull size; and iii) to determine for the first time the intraspecific relationships in skull shape of *G. pyrenaicus* in most of its distribution area. It is worth remembering that the Iberian desman is included in Appendices II and IV of the Habitats and Species Directive (see B l a n c o & G o n z á l e z 1992) and has recently been listed as Endangered in the Atlas of the terrestrial Mammals of Spain (N o r e s e t a l. 2002). Therefore, information on the morphologic characteristics of the species throughout its geographic range could be of interest to conservation and management programmes aiming to preserve the full genetic variability of this endangered insectivore.

Material and Methods

The sample analysed consisted of 209 specimens kept in the scientific collections of the following institutions: the Natural History Museum (London, United Kingdom), Museo Nacional de Ciencias Naturales (Madrid, Spain), Estación Biológica de Doñana (Sevilla, Spain), Muséum National d'Histoire Naturelle (Paris, France), Laboratoire Souterrain (Moulis, France), and Instituto Pirenaico de Ecología (Jaca, Spain). The specimens were grouped into five geographic samples (Fig. 1, Appendix 1), following those established by González-Esteban et al. (1999): Pyrenees (P; 14 males, 13 females), Iberian System (IS; 8 males, 13 females), Central System (CS; 4 males, 6 females), Cantabrian area (C; 49 males, 40 females) and Atlantic area (A; 32 males, 30 females). Age-class determination was based on the wear of the canine and first premolars (class 0: no wear; class 1: worn at teeth tip; class 2: teeth half worn; class 3: teeth worn to root), known to be a useful age criterion (González-Esteban et al. 2002). Fourteen skull and dental measurements were taken (in mm) with a digital calliper to 0.01 mm (Fig. 2): condylobasal length (CBL), basal length (BL), palatal length (PL), skull case length (SCL), length of the upper dental series (UDS), rostral width (RW), interorbital width (IOW), zygomatic width (ZW), skull case width (SCW), occipital width (OW), skull case height (SCH), length of the mandible (ML), length of the lower dental series (LDS), and coronoid height (CH).

Data were tested for normality using Kolmogorov-Smirnov D-statistics, and for homogeneity of variances using Levene's test. First, to assess the effects of geographic origin, sex, and age on inter-sample variation, a three-factor analysis of variance (ANOVA) was

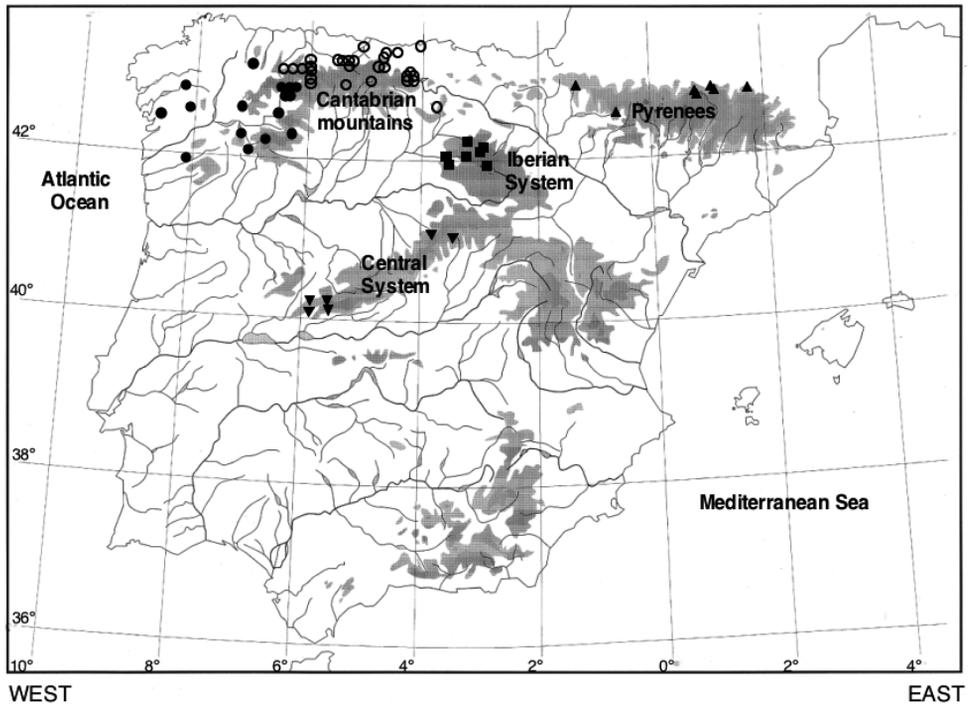


Fig. 1. Geographic origin of the samples studied. Points correspond to localities or groups of localities geographically very close. Symbols: ▲, Pyrenees; ○, Cantabrian area; ●, Atlantic area; ▼, Central System; ■, Iberian System.

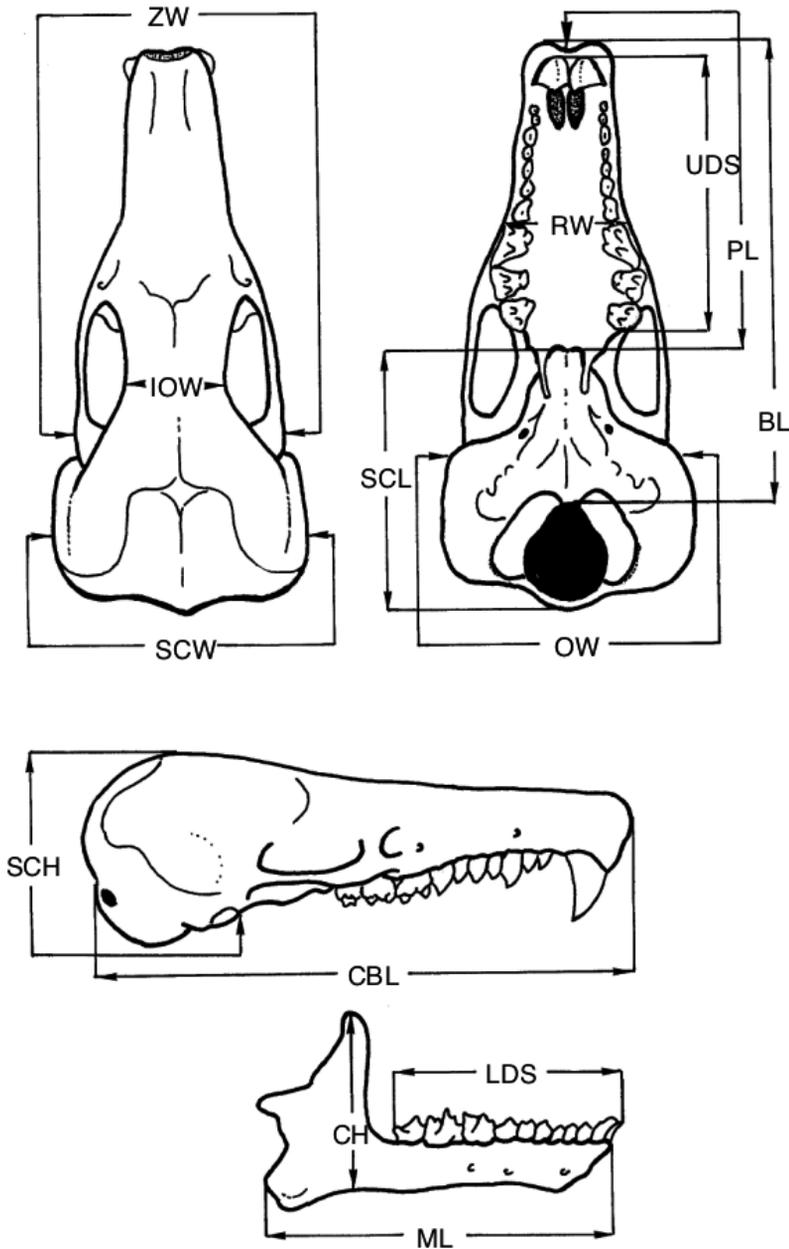


Fig. 2. Skull and mandible measurements of *Galemys pyrenaicus*. Explanations of abbreviations are given in Material and Methods.

performed on the whole data set. Sexual dimorphism within each sample was further analysed by Student-t tests. Because of sample sizes and missing values, canonical function analysis between sexes was conducted separately only for the Cantabrian and Atlantic area samples.

Morphometric variation between geographic samples was evaluated for each sex by one-way ANOVA and pairwise comparisons of character means were performed by Scheffé's

method. For each sex, phenetic relationships between geographic samples were determined by cluster analyses, using the Euclidean distance matrix derived from standardised character means and an unweighted pair-group (UPGMA; Sneath & Sokal 1973). To assess geographic variation patterns and population affinities, a multiple-group principal-component analysis (MGPCA) was run on the skull characters of all samples. Component scores were then subjected to a canonical variate analysis (CVA), first using all factors and then excluding the first factor to remove the effect of size (Thorpe 1988). For all sequential tests, P values were corrected by the Bonferroni adjustment (Rice 1989), as modified by Chandler (1995). Statistical analyses were performed with SPSS 11.0, except cluster analyses which were computed by NTSYSpc (version 2.01d).

Results

Three-way ANOVA showed differences between samples in 10 and five out of 14 variables due to geographic origin and sex, respectively, after the Bonferroni adjustment (Table 1). In contrast, no age differences were found (Table 1). In general, males were larger than females, although the extent of sexual dimorphism varied depending on the geographic sample (Appendix 2). Specifically, males showed significantly higher mean values than females in six variables in the Cantabrian area, three in the Iberian System, three in the Central System, and two in the Atlantic area. Canonical function analyses between sexes performed separately for the Cantabrian and Atlantic areas provided for each one a significant discriminant function (Cantabrian area: Wilk's lambda = 0.656; $\chi^2 = 28.672$, d. f. = 14, $p < 0.012$; Atlantic area: Wilk's lambda = 0.461; $\chi^2 = 26.34$, d. f. = 14, $p < 0.023$), which classified correctly 79.2 and 86% of cases, respectively. On the basis of these results, in subsequent comparative analyses between geographic samples, specimens from all age-classes were pooled, but sexes were treated separately.

One-way ANOVA showed significant geographic differences in nine and seven out of 14 variables for males and females, respectively (Table 2). Comparisons between

Table 1. Results of three-factor analysis of variance, according to geographic location, sex, and age. Significant p-values after the Bonferroni adjustment: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

| Variable | n | Geographic sample | | Sex | | Age | |
|----------|-----|-------------------|-----------|-------|-----------|------|---------|
| | | F | p-value | F | p-value | F | p-value |
| CBL | 176 | 7.88 | 0.000 *** | 8.45 | 0.004 * | 0.30 | 0.829 |
| BL | 174 | 8.51 | 0.000 *** | 8.80 | 0.000 *** | 0.01 | 0.999 |
| PL | 186 | 8.03 | 0.000 *** | 3.73 | 0.055 | 0.31 | 0.815 |
| SCL | 169 | 3.64 | 0.008 * | 6.36 | 0.013 | 1.18 | 0.320 |
| UDS | 193 | 6.34 | 0.000 *** | 3.62 | 0.059 | 1.41 | 0.242 |
| RW | 196 | 4.79 | 0.001 *** | 1.44 | 0.232 | 1.72 | 0.165 |
| IOW | 188 | 5.59 | 0.000 *** | 3.61 | 0.059 | 0.83 | 0.480 |
| ZW | 166 | 1.31 | 0.269 | 4.35 | 0.039 | 1.70 | 0.171 |
| SCW | 172 | 1.78 | 0.137 | 2.44 | 0.120 | 0.48 | 0.696 |
| OW | 173 | 2.62 | 0.037 | 6.83 | 0.010 * | 0.26 | 0.852 |
| SCH | 172 | 0.56 | 0.694 | 1.53 | 0.218 | 0.83 | 0.477 |
| ML | 197 | 16.63 | 0.000 *** | 4.66 | 0.032 | 0.51 | 0.675 |
| LDS | 197 | 4.25 | 0.003 * | 7.38 | 0.007 * | 2.29 | 0.080 |
| CH | 198 | 7.33 | 0.000 *** | 10.90 | 0.001 *** | 1.40 | 0.244 |

Table 2. Results of one-way ANOVA between samples of *G. pyrenaicus*. P: Pyrenees; IS: Iberian System; CS: Central System; C: Cantabrian area; A: Atlantic area. Levels of significance: * p<0.05, ** p<0.01, *** p<0.001 (p-values corrected by the Bonferroni adjustment).

| Variable | Males | | | | Females | | | |
|----------|-------|-------|-----|-------------|---------|------|-----|-------------|
| | n | F | p | < mean < | n | F | p | < mean < |
| CBL | 94 | 10.89 | *** | P-A-C-IS-CS | 87 | 3.93 | * | P-A-CS-C-IS |
| BL | 93 | 11.46 | *** | P-A-C-CS-IS | 86 | 4.82 | ** | P-A-C-CS-IS |
| PL | 98 | 8.79 | *** | P-A-C-IS-CS | 93 | 4.88 | *** | P-A-CS-IS-C |
| SCL | 96 | 3.35 | | A-P-C-IS-CS | 78 | 1.65 | | A-C-IS-CS-P |
| UDS | 101 | 6.65 | *** | P-A-C-IS-CS | 96 | 3.75 | * | P-A-IS-CS-C |
| RW | 103 | 3.21 | | A-C-P-IS-CS | 98 | 3.10 | | A-C-IS-CS-P |
| IOW | 101 | 8.16 | *** | A-IS-C-CS-P | 92 | 3.87 | * | A-IS-C-CS-P |
| ZW | 91 | 2.47 | | P-A-C-IS-CS | 80 | 2.11 | | IS-A-P-C-CS |
| SCW | 95 | 3.77 | * | P-A-C-IS-CS | 81 | 0.99 | | P-CS-A-IS-C |
| OW | 94 | 3.47 | | P-A-C-IS-CS | 84 | 1.52 | | A-P-C-CS-IS |
| SCH | 96 | 0.56 | | A-P-IS-C-CS | 80 | 0.44 | | A-CS-P-IS-C |
| ML | 103 | 19.04 | *** | P-A-C-IS-CS | 100 | 8.80 | *** | P-A-IS-C-CS |
| LDS | 101 | 5.13 | *** | A-P-C-IS-CS | 99 | 2.36 | | P-A-CS-C-IS |
| CH | 105 | 11.02 | *** | P-A-C-CS-IS | 99 | 4.19 | * | P-CS-A-IS-C |

pairs of samples revealed that, in both sexes, the Pyrenean specimens showed the highest morphometric differentiation, while samples from Cantabrian area, Iberian System, and Central System did not differ significantly from each other (Table 3).

Cluster analyses for size provided identical results for males and females (Fig. 3). In both distance phenograms two main clusters appeared, the smaller specimens from the Pyrenees and Atlantic area, and then the large-sized desmans from the other samples. In MGPCA, the first eigenvector explained 66.8% and 68.0% of total variation in males and females, respectively. Homogeneity in sign and magnitude of its coefficients led us to consider this component as a multivariate expression of skull size. Canonical variate analyses on scores of all factors provided four significant canonical functions in both sexes (males: Wilk's lambda = 0.15, $\chi^2 = 143.47$, d. f. = 56, p < 0.001; females: Wilk's lambda = 0.23, $\chi^2 = 87.09$, d. f. = 56, p < 0.005), which correctly classified 80.2% and 68.6% of the specimens,

Table 3. Comparisons between pairs of samples in *G. pyrenaicus*. P: Pyrenees; IS: Iberian System; CS: Central System; C: Cantabrian area; A: Atlantic area. Levels of significance revealed by Scheffé's method: * p<0.05, p<0.01, *** p<0.001. Pair-wise comparisons no significant are not shown.

| Variable | Males | | | | | | | Females | | | | |
|----------|-------|-----|-----|------|-----|-----|------|---------|-----|-----|------|-----|
| | P-A | P-C | P-I | P-SC | A-C | A-I | A-SC | P-A | P-C | P-I | P-SC | A-C |
| CBL | | *** | *** | * | ** | * | | | * | | | |
| BL | | * | *** | | ** | *** | | | * | * | | |
| PL | | ** | ** | * | * | * | * | | * | | | * |
| UDS | | ** | * | | | | | | | | | |
| IOW | *** | | | | ** | | | ** | | | | |
| ML | * | *** | *** | *** | *** | * | ** | | *** | * | ** | * |
| LDS | | | | | | * | | | | | | |
| CH | * | *** | *** | * | | * | | | * | | | |

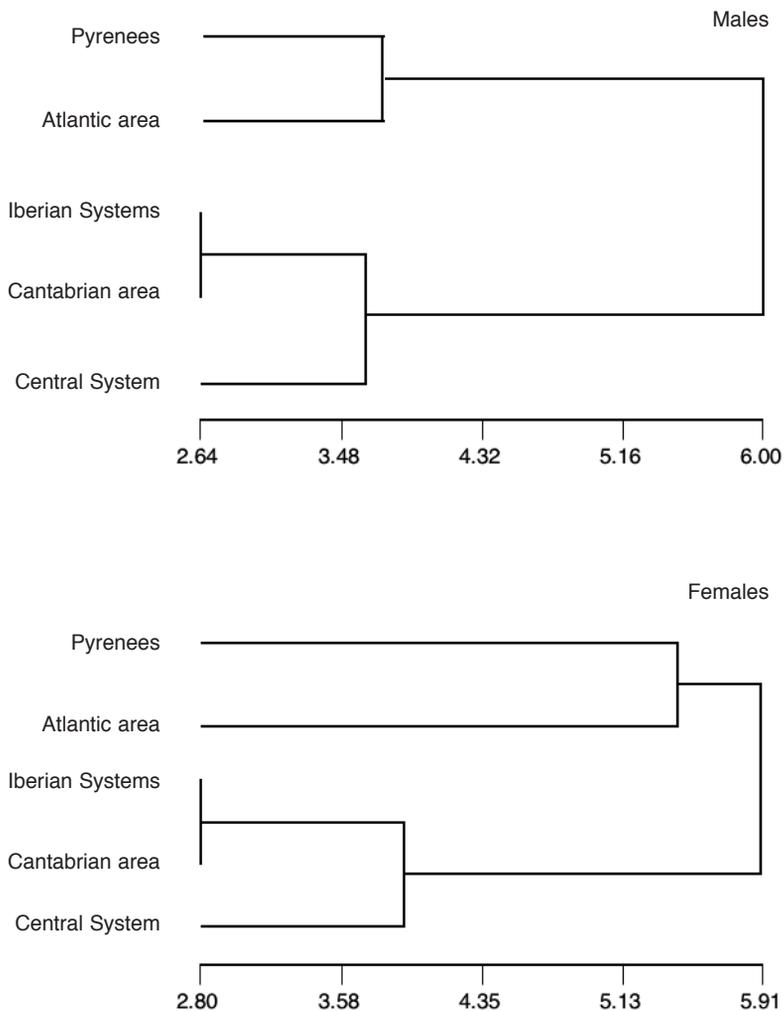


Fig. 3. Distance phenograms showing relationships between samples of *G. pyrenaicus*, for each sex. Cophenetic correlation coefficient was 0.71 for males and 0.93 for females.

respectively. The first two canonical axes accounted for 56.3% and 29% of the total variation in males and 51.3% and 31.1% in females. Projection of individual scores onto these axes (Fig. 4) revealed that in both sexes the first canonical function correlated negatively with size, with Pyrenean specimens showing, in general terms, the highest scores. The other samples were not clearly separated on this axis. A great overlap of all samples appeared on the second canonical axis, which correlated positively with RW and IOW in males, and positively with IOW and negatively with CH in females.

Canonical analysis excluding the first factor (size) also furnished four significant discriminant functions (males: Wilk's lambda = 0.27, $\chi^2 = 99.776$, d. f. = 52, $p < 0.001$; females: Wilk's lambda = 0.28, $\chi^2 = 75.743$, d. f. = 52, $p < 0.017$), which classified correctly 75.6% and 68.6% of males and females, respectively. The first two canonical axes accounted for 65.5% and 18.1% of total variation in males and 54.9% and 26.2% in females. Projection

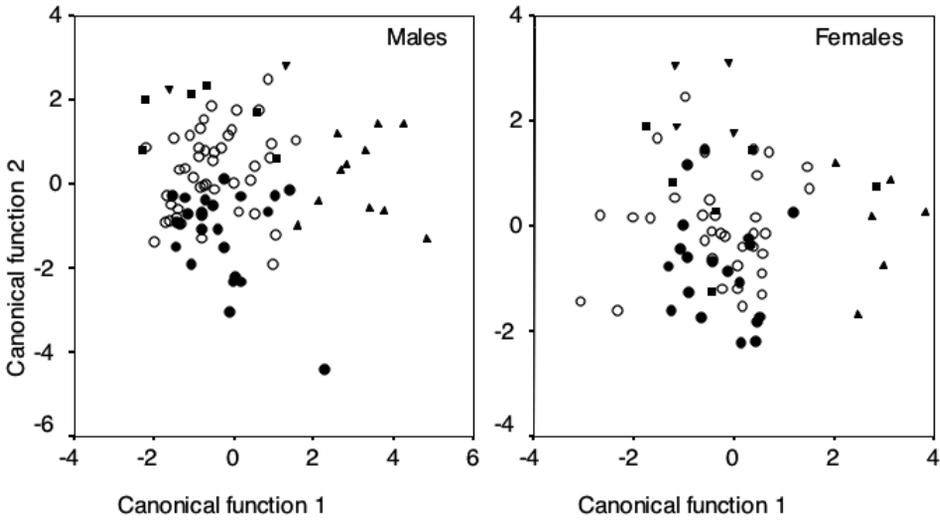


Fig. 4. Projection of the individual scores onto the two canonical axes for size. Symbols: ▲, Pyrenees; ○, Cantabrian area; ●, Atlantic area; ▼, Central System; ■, Iberian System.

of individual scores onto these axes (Fig. 5) showed that, even when adjusted for size, in both sexes the Pyrenean specimens were the most clearly separated from those corresponding to other samples, showing in general higher scores on the first canonical axis; in both males and females, this axis mainly correlated positively with IOW. Discrimination of samples in the second canonical function was very low in both sexes. In the two canonical variate analyses, 90.9% of Pyrenean males and 100% of Pyrenean females were classified correctly.

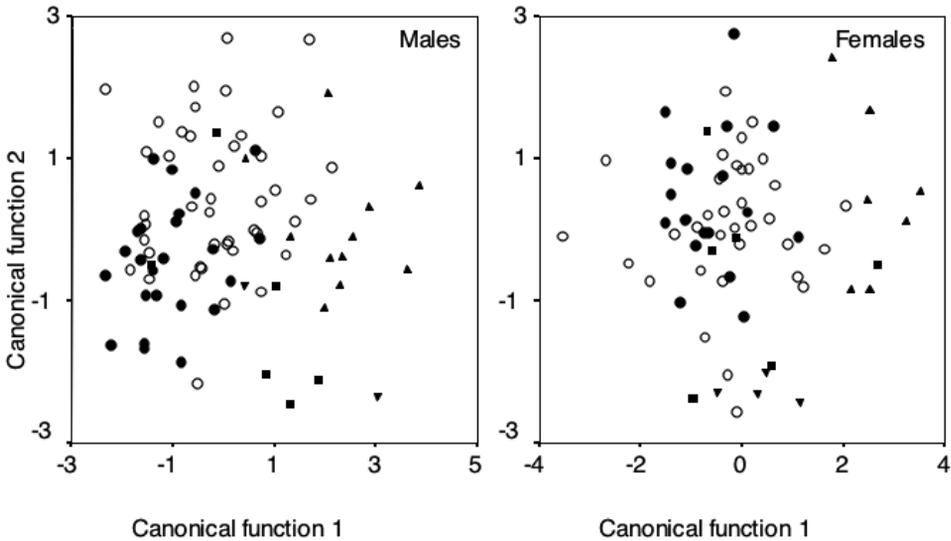


Fig. 5. Projection of individual scores onto the two canonical axes for shape. Symbols: ▲, Pyrenees; ○, Cantabrian area; ●, Atlantic area; ▼, Central System; ■, Iberian System.

Discussion

Age and sex variation

The lack of sexual dimorphism in body and skull sizes of the Iberian desman has been reported in several studies (Niethammer 1970, Juckwer 1990, González-Esteban et al. 1999). Nevertheless, it should be emphasised that this assessment was based on the analysis of animals coming from a specific location (Sierra de Cameros; Juckwer 1990) or on general observations based on pooling of specimens from different geographic zones (Niethammer 1970, González-Esteban et al. 1999). Our results showed that, in all geographic samples, skull size is in general slightly larger in males than in females. Statistical analyses revealed that, although in all samples mean values of many parameters did not differ significantly between sexes, sexual monomorphism in skull size seems not to be the rule in the species. In fact, the degree of differentiation between males and females depended on the geographic sample analysed. Thus, although males and females from the Pyrenees were very similar in all cranial variables, several significant differences between sexes were recorded in desmans from other areas. Specifically, in the Cantabrian area sample differences occurred in 43% of the parameters considered; as for the other variables, mean values were always higher (but not significant) in males. In the remaining samples (Iberian System, Central System, and Atlantic area), differences attained statistical significance only in a few characters.

Available data concerning the biology of the species do not allow us to explain the causes of the slight sexual dimorphism in skull size or of the different patterns we found throughout its distribution area. Information on the social organization, spatial distribution, and activity patterns of the species (Stoñe 1985, 1987a,b) indicated that paired adults defend their shared territory from neighbouring desmans by patrolling, surveillance, and scent-marking, and that in such pairs males cover more territory than females. Likewise, the home ranges of neighbouring males overlap to a small extent, but the territory of a male and that of a neighbouring female do not overlap (Stoñe 1987a). Paired males appear to invest more time defending the borders of their shared home range than do females, which spend most of their time within the centre of the range. Though females also participate in territorial defence, their activities are concentrated in this central region. Despite some degree of territorial overlap between neighbouring desmans, their mutual avoidance, achieved through a system of temporal range utilization, means that there are few agonistic encounters (Stoñe 1987a,b). Therefore, the slight sexual dimorphism in skull size detected could be related, at least in part, to these patterns of social ecology.

As for the geographic differences in the extent of dimorphism here reported, we tentatively suggest that the effect of different sample sizes underlies these results. Thus, whereas most significant differences and/or a higher degree of sexual differentiation occurred in the larger samples from the Cantabrian and Atlantic areas, differences between males and females were mostly undetectable in the other samples. In consequence, we would expect that, if more specimens were added to these latter samples, sexual differences would attain statistical significance in more skull variables. Therefore, we conclude that in the Iberian desman the skull is on average slightly larger in males than in females, but these differences attain statistical significance only when a larger sample size of a specific population is examined. This is probably the reason why sexual dimorphism in skull size has been ruled out in analyses based on small size samples or in multivariate analyses based on a whole sample composed of subsamples with heterogeneous composition of sexes (e.g.

Niehammer 1970, Juckwer 1990, González-Esteban et al. 1999). To test the latter question, we performed an additional multivariate analysis of variance (MANOVA) on our whole sample, taking age, sex, and geographic origin as factors. Unlike the results here obtained by univariate analyses, MANOVA did not show overall significant difference in skull size between sexes (Hotelling's $T^2 = 0.201$; $F = 1.782$; $p = 0.121$). In the light of our results, we recommend treating males and females separately when comparative analyses of skull morphology between geographic samples are undertaken.

We found no significant differences in skull dimensions between the four age classes established in *G. pyrenaicus*. This is consistent with the results by González-Esteban et al. (1999) and supports the idea that, as occurs in other Erinaceomorpha species (see Foreman 1994), when young animals leave the nest they have already reached adult skull size.

Geographic variation

Our one-way ANOVA, after the Bonferroni adjustment, revealed that the skull size of *G. pyrenaicus* varies significantly over its distribution area. In general terms, desmans (both males and females) from the Pyrenees were smallest and those from the Cantabrian area, Iberian System, and Central System were largest. Likewise, canonical analyses showed an important distinction in both size and shape between the Pyrenean animals and the specimens traditionally assigned to *rufulus*. Specifically, excluding factor size, Pyrenean animals are characterised by their robust interorbital region and, additionally, males show a wider rostrum and females a shorter coronoid process. Although slightly larger, animals from the Atlantic area were very similar in size to the specimens from the Pyrenees. The relatively small size of the desmans from the Atlantic area was also reported by González-Esteban et al. (1999). Specifically, these authors found that animals from the western Pyrenees had an average size that was intermediate between desmans from westernmost Spain (Galicia and western Leon) and those from the Cantabrian region (Cantabria, Asturias, and northern Leon) and the Iberian System. Based on this and on their findings on geographic variability in the fur colour of the species, these authors argued against a subspecies differentiation founded on body and skull sizes. Thus, González-Esteban et al. (1999) suggested that the morphological variability of the species is related to several local factors, such as low population densities, the territorial behaviour of the species, and the partial or total isolation of populations. Although the effect of these factors at a local level cannot be discarded, our results do not discredit so radically the existence of morphometric differentiation between *pyrenaicus* and *rufulus*. Thus, excepting the animals from the Atlantic area, desmans from the Pyrenees are clearly smaller in size than those from the other areas considered here. In fact, the specimens assigned to *rufulus* lead one to think that a geographic cline in skull size exists as follows: smaller desmans in the west (Galicia), larger ones in the mountains of central Spain (Central System), and intermediate ones in the Cantabrian region and Iberian System. Specifically, animals from Galicia were significantly smaller in many skull variables than those from the other samples attributed to *rufulus*. Although these results and the relatively high overlap in skull dimensions between Pyrenean and Galician animals seem at first to contradict the taxonomic identity of *pyrenaicus* and *rufulus*, our analyses of skull size and shape by MGPCA and CVA revealed a substantial distinction between these forms, both in males and in females. In particular, in the corresponding canonical plots for size and shape, component scores of males and females from the Atlantic area fall within the range

of variation of the other samples of *rufulus*, and appeared separate to a large degree from Pyrenean desmans. It is worth mentioning that the relatively low mean values recorded in the sample from the Atlantic area were mainly due to the very small skull size of the specimens coming from a specific locality. Saa de Incio (for example, CBL: males, mean = 33.50, sd = 1.07, range = 32.3-34.5, n = 5; females, mean = 32.45, sd = 0.83, range = 31.4-33.3, n = 4. ML: males, mean = 21.26, sd = 0.73, range = 20.3-22.0, n = 5; females, mean = 20.67, sd = 0.54, range = 19.9-21.1, n = 4). Therefore, the similarity in size of certain skull measurements between Pyrenean and some Galician desmans may be due to the action of local factors. We conclude from these arguments that there is an overall morphological skull differentiation between the subspecies of the Iberian desman described in the literature. Differences observed between the Pyrenean population of *Galemys* and those from other Iberian regions could be explained by their geographical isolation, caused by changes that occurred during the last glacial event (Würm). Specifically, climate and vegetation changes in that period resulted in two, well-differentiated faunal groups, observed from 24000 to 12000 BP (Baryshnikov & Markova 1992): “Mammoth tundra-steppe assemblage”, and “Mediterranean mountain open woodlands assemblage”. In the Iberian Peninsula, the border between the two ran along the base of the southern slopes of the Pyrenees. Pleistocene remains of *G. pyrenaicus* are scarce, but they indicate the occurrence of a Pyrenean population in Würm times (Arribas 2004) living in cold tundra, in contrast to the other Iberian populations, which lived in temperate Mediterranean scrub. A similar process may have occurred in other mammal species with Pyrenean populations taxonomically different from those in the rest of the Iberian Peninsula, such as *Microtus arvalis meridianus*, *Chionomys nivalis aquitanicus*, *Clethrionomys glareolus vasconiae*, *Arvicola terrestris monticola*, or *Capra pyrenaica pyrenaica* (see e.g. Palomo & Gisbert 2002). It is clear that in the case of the Iberian desman results from other sources may help to establish the taxonomic identity of the two subspecies classically recognised for this insectivore.

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Appendix 1.

Specimens analysed in this study. For each specimen the following information is presented: country, province, locality, geographic coordinates, and sex (m: male; f: female).

Pyrenees.- France. Ariège: Ax-les-Thermes, 42°43'N, 1°50' E (1 m, 1 f); Moulis, 42°48'N, 1°05'E (6 m, 5 f); Saint-Girons, 42°59'N, 1°08'E (1 m); central Pyrenees, unknown locality (4 m, 5 f). Spain. Huesca: Jaca, 42°34'N, 0°33'W (1 f); Lleida: Bosost, 42°46'N, 0°41'E (1 m); Viella, 42°41'N, 0°47'E (1 m). Navarra: Burguete, 42°59'N, 1°20'W (1 f).

Iberian System (Spain).- Burgos: Barbadillo de Herreros, 42°09'N, 3°10'W (3 m, 4 f); Cubillo del Campo, 42°10'N, 3°36'W (1 m); Fresneda de la Sierra, 42°19'N, 3°08'W (2 f); Silos, 41°58'N, 3°25'W (2 m, 3 f); Logroño: Monte San Lorenzo, Sierra de la Demanda, 42°15'N, 2°58'W (1 m, 1 f); Tobía, 42°18'N, 2°50'W (1 m, 1 f); Soria: Quintanarejo de Vinuesa, 41°59'N, 2°37'W (1 f).

Central System (Spain).- Ávila: Hoyos del Espino, 40°20'N; 5°10'W (1 m, 1 f); Navacepeda de Tormes, 40°21'N, 5°14'W (1 f). Cáceres: río Ambroz, 40°16'N, 5°49'W (1 m). Guadalajara: Cantalojas, 41°14'N, 3°18'W (1 m, 2 f). Salamanca: Bejar, 40°24'N, 5°45'W (1 f). Segovia: Villa de Fuentidueñas, 41°26'N, 3°59'W (1 m, 1 f).

Cantabrian area.- Asturias: Bezanes, Soto de Caso, 43°09'N, 5°17'W (3 f); Caleao, 43°09'N, 5°24'W (4 m, 4 f); Coto de Reres, 43°10'N, 5°10'W (1 m); Muniellos, 43°02'N, 6°38'W (3 m, 1 f); Pola Somiedo, 43°05'N, 6°15'W (4 m, 3 f); Puente piedra de Caso, 43°11'N, 5°23'W (1 m); río Villar, Arriendas, 43°23'N, 5°11'W (2 m, 1 f); Tarna, 43°06'N, 5°13'W (2 m, 2 f); Valle de Lago, Somiedo, 43°04'N, 6°10'W (4 m); unknown locality (1m, 1 f). Burgos: Covanera, 42°43'N, 3°47'W (1 f); León: Candemuella, 42°59'N, 6°00'W (4 m, 5 f); Genestosa, 43°00'N, 6°00'W (1 m, 2 f); Manzaneda de Torío, 42°45'N, 5°30'W (1 f); Oseja de Sajambre, 43°08'N, 5°02'W (1 f); Pajares, 43°02'N, 5°47'W (1 f); Pozo Rebezo, Torrestío, 43°03'N, 6°03'W (3 m, 1 f); Puente Orugo, San Emiliano, 42°57'N, 6°00'W (2 m, 2 f); río Grande, Besande, 42°54'N, 4°53'W (2 m, 3 f). Santander: Barreda Pesagüero, 43°22'N, 4°02'W (1m, 1 f); Carmona, Puentenansa, 43°15'N, 4°24'W (1 f); Izara, 42°59'N, 4°11'W (1 m, 1 f); Matamorosa, 42°59'N, 4°08'W (1 m); río Deva, La Hermida, 43°15'N, 4°37'W (1 m); río Hajar, Peñalabra, 43°02'N, 5°37'W (1 m); Reinosa, 43°01'N, 4°09'W (1 f); Suano, 42°59'N, 4°13'W (1 f); Turieno-Camaleño, 43°08'N, 4°39'W (3 m, 3 f). Palencia: río Carrion, Triollo, 42°55'N, 4°40'W (5 m, 1 f); Vidrieros, 42°56'N, 4°39'W (1m, 1f). Atlantic area.- A Coruña: Susana, 42°49'N, 8°29'W (1 m). León: Castrocontrigo, 42°11'N, 6°11'W (1 m); Corbón del Sil, 42°49'N, 6°30'W (2 m, 1 f); Matarrosa del Sil, 42°45'N, 6°31' (4 m, 4 f); Paramo del Sil, 42°49'N, 6°27'W (2 m, 2 f); río Cua, Peranzanes, 42°52'N, 6°40'W (3 m, 1f); río Boeza, San Miguel de las Dueñas, 42°35'N, 6°30'W (1 m, 1f); Valle de Fornela, 42°53'N, 6°43'W (1f); unknown locality (1m, 1 f). Lugo: Pobra de Burón Fonsagrada, 43°08'N, 7°05'W (1 f); San Pedro de Incio, 42°38'N, 7°21'W (3 m, 1 f); Saa de Incio, 42°38'N, 7°21'W (5 m, 4 f); Trascastro de Incio, 42°38'N, 7°19'W (5 m, 8 f). Orense: río Pacín, Casal Entrimo, 41°57'N, 8°06'W (1 m); río Ribera, Pequeña Camba, 42°07'N, 7°19'W (1f); Soutiprede, Puebla de Trives, 42°20'N, 7°15'W (3 m). Pontevedra: Caldas de Reis, 42°36'N, 8°38'W (1 f); río Deza, Lalin, 42°38'N, 8°07'W (1 f). Zamora: Quintana de Sanabria, 42°04'N, 6°41'W (1 m, 2 f).

Appendix 2.

Cranial measurements (mm) and extent of sexual dimorphism within samples in *G. pyrenaicus*. P: Pyrenees; IS: Iberian System; CS: Central System; C: Cantabrian area; A: Atlantic area. Levels of significance revealed by Student's t-test: * p<0.05, ** p<0.01, *** p<0.001.

| Variable | | Males | | | | Females | | | | P |
|----------|----|-------|-------|------|-----------|---------|-------|------|-----------|----|
| | | n | mean | sd | range | n | mean | Sd | range | |
| CBL | P | 12 | 33.79 | 0.55 | 32.5-34.5 | 12 | 33.52 | 0.96 | 31.7-35.5 | |
| | IS | 7 | 35.21 | 0.41 | 34.7-35.7 | 9 | 34.57 | 0.88 | 33.5-36.1 | |
| | CS | 2 | 35.45 | 0.49 | 35.1-35.8 | 5 | 34.40 | 1.28 | 32.5-35.8 | |
| | C | 46 | 34.87 | 0.60 | 33.5-36.5 | 37 | 34.52 | 0.70 | 32.6-35.9 | ** |
| | A | 28 | 34.26 | 0.80 | 32.3-35.5 | 25 | 33.99 | 0.95 | 31.4-35.8 | |
| BL | P | 12 | 28.62 | 0.61 | 27.2-29.5 | 11 | 28.08 | 0.76 | 26.4-29.1 | |
| | IS | 7 | 29.99 | 0.53 | 29.0-30.5 | 9 | 29.32 | 0.82 | 28.4-30.8 | |
| | CS | 2 | 29.90 | 0.28 | 29.7-30.1 | 6 | 29.05 | 1.10 | 27.3-30.3 | |
| | C | 46 | 29.31 | 0.50 | 28.1-30.7 | 36 | 29.01 | 0.63 | 27.5-30.2 | ** |
| | A | 27 | 28.67 | 0.76 | 27.0-30.3 | 25 | 28.52 | 0.91 | 26.1-29.9 | |
| PL | P | 13 | 17.85 | 0.72 | 15.9-19.0 | 13 | 17.86 | 0.43 | 16.9-18.6 | |
| | IS | 7 | 18.84 | 0.32 | 18.2-19.2 | 11 | 18.40 | 0.44 | 17.7-18.9 | * |
| | CS | 3 | 19.13 | 0.42 | 18.8-19.6 | 6 | 18.37 | 0.79 | 16.9-19.2 | |
| | C | 47 | 18.50 | 0.44 | 17.4-19.4 | 38 | 18.48 | 0.52 | 17.3-19.5 | |
| | A | 29 | 18.07 | 0.63 | 16.4-18.9 | 26 | 18.00 | 0.61 | 16.5-19.0 | |
| SCL | P | 13 | 16.88 | 0.40 | 16.0-17.8 | 10 | 16.88 | 0.35 | 16.3-17.4 | |
| | IS | 7 | 17.13 | 0.62 | 16.5-18.0 | 7 | 16.71 | 0.47 | 16.0-17.2 | |
| | CS | 3 | 17.37 | 0.25 | 17.1-17.6 | 5 | 16.78 | 0.33 | 16.3-17.2 | * |
| | C | 46 | 16.89 | 0.36 | 15.8-17.5 | 35 | 16.71 | 0.38 | 15.7-17.4 | * |
| | A | 28 | 16.69 | 0.42 | 15.7-17.4 | 22 | 16.50 | 0.51 | 15.6-17.5 | |
| UDS | P | 13 | 16.42 | 0.56 | 14.9-17.0 | 13 | 16.41 | 0.64 | 15.0-17.3 | |
| | IS | 7 | 17.14 | 0.48 | 16.5-17.8 | 13 | 16.81 | 0.41 | 16.0-17.7 | |
| | CS | 4 | 17.17 | 0.15 | 17.0-17.3 | 6 | 16.85 | 0.72 | 15.5-17.6 | |
| | C | 48 | 16.94 | 0.39 | 15.9-17.8 | 38 | 16.87 | 0.38 | 15.9-17.4 | |
| | A | 30 | 16.65 | 0.42 | 15.9-17.4 | 27 | 16.49 | 0.55 | 15.2-17.5 | |

Appendix 2. continued.

| Variable | | Males | | | | Females | | | | p |
|----------|----|-------|-------|------|-----------|---------|-------|------|-----------|-----|
| | | n | mean | sd | range | n | mean | sd | range | |
| RW | P | 14 | 5.40 | 0.37 | 4.8-6.0 | 13 | 5.50 | 0.43 | 4.9-6.2 | |
| | IS | 8 | 5.50 | 0.20 | 5.3-5.8 | 13 | 5.42 | 0.23 | 5.1-5.9 | |
| | CS | 3 | 5.57 | 0.29 | 5.4-5.9 | 6 | 5.42 | 0.25 | 5.0-5.7 | |
| | C | 49 | 5.40 | 0.22 | 4.8-5.8 | 39 | 5.38 | 0.27 | 4.7-5.9 | |
| IOW | A | 30 | 5.24 | 0.24 | 4.7-5.6 | 28 | 5.21 | 0.25 | 4.7-5.6 | |
| | P | 14 | 6.57 | 0.07 | 6.5-6.7 | 12 | 6.48 | 0.18 | 6.1-6.7 | |
| | IS | 7 | 6.39 | 0.13 | 6.2-6.5 | 11 | 6.30 | 0.13 | 6.1-6.5 | |
| | CS | 3 | 6.47 | 0.12 | 6.4-6.6 | 6 | 6.33 | 0.10 | 6.2-6.5 | *** |
| ZW | C | 47 | 6.46 | 0.19 | 6.0-6.7 | 38 | 6.31 | 0.22 | 5.6-6.8 | |
| | A | 31 | 6.28 | 0.19 | 6.0-6.7 | 26 | 6.18 | 0.28 | 5.6-6.8 | |
| | P | 12 | 13.12 | 0.33 | 12.4-13.5 | 10 | 13.12 | 0.27 | 12.6-13.5 | |
| | IS | 7 | 13.44 | 0.26 | 13.1-13.9 | 8 | 12.89 | 0.43 | 12.0-13.4 | * |
| SCW | CS | 2 | 13.55 | 0.07 | 13.5-13.6 | 5 | 13.36 | 0.51 | 13.0-14.1 | |
| | C | 45 | 13.29 | 0.30 | 12.6-14.0 | 36 | 13.14 | 0.35 | 12.4-13.7 | * |
| | A | 26 | 13.17 | 0.30 | 12.5-13.6 | 22 | 12.97 | 0.37 | 12.2-13.8 | * |
| | P | 13 | 16.02 | 0.30 | 15.4-16.4 | 12 | 16.12 | 0.33 | 15.6-16.6 | |
| OW | IS | 6 | 16.73 | 0.45 | 16.1-17.4 | 6 | 16.28 | 0.47 | 15.8-17.1 | |
| | CS | 3 | 16.73 | 0.21 | 16.5-16.9 | 5 | 16.14 | 0.61 | 15.6-17.1 | |
| | C | 45 | 16.50 | 0.45 | 15.6-17.5 | 35 | 16.36 | 0.50 | 15.0-17.2 | |
| | A | 29 | 16.29 | 0.64 | 15.1-17.6 | 24 | 16.15 | 0.51 | 15.4-17.3 | |
| SCH | P | 12 | 14.89 | 0.38 | 14.1-15.4 | 12 | 14.88 | 0.29 | 14.4-15.2 | |
| | IS | 7 | 15.26 | 0.46 | 14.4-15.7 | 7 | 15.14 | 0.34 | 14.8-15.6 | |
| | CS | 3 | 15.63 | 0.45 | 15.2-16.1 | 6 | 14.97 | 0.70 | 14.1-16.1 | |
| | C | 44 | 15.20 | 0.38 | 14.4-16.0 | 36 | 14.95 | 0.37 | 14.2-15.8 | ** |
| ML | A | 29 | 14.98 | 0.46 | 14.1-15.9 | 24 | 14.75 | 0.46 | 13.9-15.7 | |
| | P | 13 | 10.68 | 0.29 | 10.1-11.1 | 11 | 10.63 | 0.48 | 9.6-11.2 | |
| | IS | 6 | 10.72 | 0.41 | 10.0-11.1 | 7 | 10.63 | 0.39 | 10.0-11.2 | |
| | CS | 3 | 10.93 | 0.40 | 10.5-11.3 | 5 | 10.60 | 0.40 | 10.1-11.1 | |
| LDS | C | 46 | 10.73 | 0.32 | 10.2-11.4 | 35 | 10.71 | 0.35 | 9.8-11.4 | |
| | A | 29 | 10.64 | 0.44 | 10.1-12.1 | 23 | 10.57 | 0.41 | 9.7-11.4 | |
| | P | 14 | 21.13 | 0.75 | 19.1-22.0 | 13 | 21.10 | 0.65 | 19.6-22.3 | |
| | IS | 8 | 22.39 | 0.47 | 21.7-23.3 | 13 | 21.95 | 0.63 | 21.1-22.7 | |
| CH | CS | 4 | 22.70 | 0.27 | 22.5-23.1 | 5 | 22.28 | 0.49 | 21.6-22.8 | |
| | C | 47 | 22.25 | 0.41 | 21.0-23.0 | 40 | 22.08 | 0.52 | 20.7-23.1 | |
| | A | 31 | 21.70 | 0.53 | 20.1-22.3 | 30 | 21.62 | 0.63 | 19.9-22.7 | |
| | P | 14 | 14.09 | 0.44 | 13.4-14.7 | 12 | 13.97 | 0.68 | 12.5-15.0 | |
| CH | IS | 7 | 14.56 | 0.42 | 13.9-15.1 | 13 | 14.28 | 0.46 | 13.4-15.4 | |
| | CS | 4 | 14.65 | 0.34 | 14.3-15.1 | 6 | 14.10 | 0.57 | 13.0-14.7 | |
| | C | 47 | 14.28 | 0.32 | 13.5-15.1 | 40 | 14.23 | 0.29 | 13.6-14.8 | |
| | A | 30 | 14.08 | 0.33 | 13.3-14.6 | 29 | 13.98 | 0.36 | 12.8-14.5 | |
| CH | P | 14 | 10.16 | 0.48 | 9.1-10.7 | 12 | 10.18 | 0.38 | 9.4-10.7 | |
| | IS | 8 | 11.00 | 0.32 | 10.5-11.5 | 13 | 10.51 | 0.33 | 9.9-10.9 | ** |
| | CS | 4 | 10.90 | 0.24 | 10.6-11.1 | 6 | 10.27 | 0.48 | 9.7-10.9 | * |
| | C | 48 | 10.78 | 0.30 | 9.8-11.4 | 40 | 10.60 | 0.37 | 9.8-11.5 | * |
| | A | 32 | 10.54 | 0.40 | 9.5-11.2 | 29 | 10.33 | 0.37 | 9.3-11.0 | * |