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Searching for indicators of age, sex and population in European mouflon mandibles

Running title:

Mandibular telltales of mouflon early growth rate variations

Abstract

Mandibles from separate populations of free-living mouflons (*Ovis aries musimon*) from Southern Spain, submitted to different ecological conditions, were studied. Searching for ontogenetic shape variations we used geometric morphometrics tools and we explored the use of several mathematical models such as the von Bertalanffy curve for describing growth rates variations between populations and sexes. A strong allometry was detected with variations in shape mainly matching with molar and premolar eruption. Mandible shape did not vary significantly with sex nor was sexual size dimorphism detected in adults, whatever the population. By modeling growth we detected differences between populations in all parameters such as the maturity rate describing precocity, and the time it took to reach asymptotic size (varying from 9 up to 18 months). A longer period of growth did not result in a larger asymptotic size, but it led to smaller mandibles. Mouflons with relatively late teeth replacement, lower maturation rate and smaller adult size were those of the population submitted to extreme environmental conditions, like epizootic disease, droughts and ungulate overpopulations. We discuss how a delay in reaching mature size has probably an important subsequent impact on reproductive and life-history traits in this species. Being able to record the effects of density-dependent and density-independent factors, mandibles become a target of interest for ecological and management studies also on mouflons.

Keywords: Environmental constraints in Mediterranean ecosystems, Geometric morphometrics, mandibles, Mouflon, growth modeling, Von Bertalanffy model.

Introduction

The European mouflon (*Ovis aries musimon*) is a wild sheep spread into the Mediterranean islands of Corsica and Sardinia and is thought to be a wild remnant of the ancient domestic (Neolithic) sheep of Asian origin (Bruford and Townsend, 2006; Rezaei et al., 2010). From the 18th century the species was progressively introduced into many European countries. In Spain the first mouflon population was introduced in 1953 in the Sierras de Cazorla, Segura y las Villas Natural Park (Cazorla NP) (Arenzana et al., 1964). These animals originally came from the French National Reserve of Chambord, Luxemburg and Germany. Yet slowly and progressively other populations from mixed origins were released across different Spanish geographical areas, including the Sierra de Andújar Natural Park (Andújar NP) in the Sierra Morena Mountains Range, and even in the Teide National Park in the Canary Islands. Increasing concerns about its negative impact on native flora and environments, along with the economic interests of recreational hunting, are making the mouflon an interesting topic for applied research (Santiago-Moreno et al., 2001; Cassinello, 2017).

Interbreeding between wild and domestic sheep during the recent history of most of the European populations as well as environmental conditions, diet variability, and different management trends, could have made the mouflon a species with a high level of morphological variation. Physical features such as the shape of the horns, body weight, and even the tail length have been used to identify the "phenotypically true" European mouflon (Frisina and Frisina, 2013), while genes related to stature, such as height at withers, were found under selection in studies on their genotypic characterization (Barbato et al., 2017). However, very few studies have addressed the morphometric variations of the wild mouflon in their ecological context, studies with simultaneous size and shape analysis being very scarce. Some of them using craniofacial geometric morphometrics approaches detected differences among feral, wild and domestic *Ovis* skulls (Pares-Casanova and Sabaté 2013) and variations in both shape and size of mandibles from domestic and wild sheep (Yalçin et al., 2010; Parés-Casanova, 2013). These studies showed the mandibles as a useful skeletal piece for identifying different species of *Ovis*, but none of them deals with the wild European mouflon, nor with its mandibular development and growth rate variations in different environmental conditions.

Mandibular size has long been identified as the best indicator of body weight in ungulates (Suttie and Mitchell, 1983) and it has becoming an ecological indicator of the life history in deer species, being sensitive to the environment conditions and management to which a particular population has been subjected (De Crombrugghe et al., 1989; Bertouille and De Crombrugghe, 1995; Hewison et al., 1996). Moreover, it has been shown that adult mandibular size retrospectively reflects variations in population density during the year of birth (Azorit et al., 2003) and the availability of resources during the stages of youth and pregnancy (De Marinis et al., 2019). So in mouflons also mandibles could be useful structures for determining form and growth rate variations reflecting early life conditions.

In our study we evaluated the morphology of the mouflon mandible from two separate areas with different ecological contexts in order to obtain relevant information about variability in shape and size among ontogenetic stages, sexes and population sites. The study sample consisted then of mandibles from mouflons hunted in Andújar NP in 2007-2008, and mouflons sampled in Cazorla NP in 1996. The latter lived under the effect of epizootic disease conditions (León-Vizcaíno et al., 1999) plus a restriction of the availability of resources due to both drought and high densities of ungulates in previous periods (Escós and Alados, 1992; Peña-Gallardo et al., 2016). We used geometric morphometrics tools in a quantitative morphological analysis that evaluates both shape and size, providing in our case the centroid size (CS) as an integrating proxy for mandibular size. As modeling growth has demonstrated its utility for comparative purposes (Lewis et al., 2002), we explored the use of several mathematical models for describing growth and the age at which asymptotic growth is reached in each population by both sexes.

Searching for telltale indicators of age, sex and population, first we hypothesized allometric variations. We aimed to identify life periods in which the greatest variations in size and shape occur, describing morphological changes during ontogeny. We expected the main mandibular variations correlated to changes in diet to occur after weaning (around 3-5 months). Second, since the body mass of the adult males is usually greater than that of the females (Rodríguez-Luengo and Rodríguez-Piñero, 1989), we also hypothesized that the patterns of mandibular form could be affected by sexual dimorphism. Finally, we also expected to encounter differences in the size, shape and growth rate of mandible between populations. It has been shown that quality of diet is one of the most important factors in the growth rate in lambs (Khalifa et al., 2013). Hence, we hypothesized that both the parasitic load and the reduction of available resources, due to adverse climatic conditions together with an overabundance of wild and domestic ungulates, may have negatively affected early growth of the Cazorla NP mouflons.

Materials and Methods

Materials and areas studied

We used left hemimandibles collected from 178 mouflons hunted in Cazorla NP (n=79) during programs for population control implemented in 1996, and from Andújar NP (n=99) between 2007 and 2008 during both herd management culls and sport hunting. The Andújar NP covering 745 km^2 is a part of the vast Sierra Morena Range (38°17′23″N 4°01′43″O), and the Cazorla NP is located in the eastern area of the Baetic Mountain Range (38°05′00″N 2°45′00″O). More specifically, we focused on the Andalusian Game Reserve, which has an extension of 687 km^2 into the 2,140 km^2 of the Cazorla NP (see Fig.1). Differences in geology, ecology and management, with notable climatic variations, are distinctive features between these areas.

The Andújar NP reaches average altitudes of 500 m with a maximum height of 1,291 m. Plant communities are typical of siliceous soils and Mediterranean ecosystems with the *dehesas* (an old *Quercus* sp. forest with bushes partially removed) as the most typical and frequent ecosystem. Cattle is raised on some properties. However, the hunting of wild ungulates, including the mouflon, which was released in some sites between 1950 and 1970, is the main economic activity in this area. There are endangered species such as the Iberian lynx (*Lynx pardinus*) and a relict population of the Iberian wolf (*Canis lupus signatus*) as potential predators of the mouflons (Muñoz-Cobo et al., 2002).

In the case of the Cazorla NP these mountains reach heights of more than 2,100 m, the soil is limestone and the terrain is very steep and rugged, with Mediterranean vegetation and a greater abundance of *Pinus* sp. Latitude and altitude combine to create a markedly seasonal continental climate.

The typically Mediterranean climate in southern Spain is characterized by an almost total lack of rainfall and high temperatures during the summer, with recorded inter-annual periods of severe drought due to a strong lack of rainfall (i.e. during the periods 1992-1995 and 2008-2012) (Peña-Gallardo et al., 2016). In 1987 Cazorla NP hosted a large population of wild ruminant species including the mouflon (Escós and Alados, 1992). From 1987 to 1995 a first mange epizootic occurred in the Cazorla NP and it was extended to all ruminants in the Park, both wild and domestic ones (León-Vizcaíno et al., 1999). In 1996, as a measure of disease control, a large number of animals were hunted in population control programs, and some of them were collected for this study.

Age estimation

For under 3 year-old mouflons, age was determined through a combination of the incisors replacement and the eruption of molar teeth. The order of eruption of the permanent incisor teeth (I_{1-4}) is the most widely used age indicator in sheep and mouflons (Rieck, 1975). However, we also used the moment of eruption of the first, second and third lower molars (M_1, M_2 and M_3, respectively), as they do not have deciduous teeth or predecessor milk teeth and are less susceptible to delaying the time of eruption (Ochoa-Cordero and Díaz-Gómez, 2000). Similarly to sheep, in mouflons M_1 is present at 3 months and M_2 at 9 months after birth. I_1 comes out at 12-18 months and I_2 is present at 18-24 months. The third molar (M_3) and the premolar teeth begin to come out at 18 months, and the third cusp of M_3 and the third incisor (I_3) take between 24 and 30 months to emerge (Ochoa-Cordero and Díaz-Gómez, 2000). Tooth eruption and replacement are reliable criteria used to estimate age until 3 ½ years (Rieck, 1975). In over 3 year-old mouflons, in which all the permanent teeth have already sprung (including the I_4 which emerged at 30-36 months), we used the growth lines in the dental cement to achieve a more reliable age determination. For mouflons, cement growth lines have provided accurate age estimates that are even more precise than dental eruption patterns (Hess et al., 2011). We prepared undecalcified roots sections using petrographic methods (Azorit, 2011) in order to study rest lines in cementum. Similar methods of grinding by hand were reported as the simplest, quickest and most dependable methods for using cementum growth lines in *Ovis aries* age determination (Rudge, 1976).

Mandible measurements and morphometric analyses

We performed a geometric morphometric (GM) study to investigate biological form (size and shape) in a fully quantitative approach. This method is implemented as a series of operations called the *Procrustes paradigm* (Adams et al., 2013). First, it is based on digitated landmarks as a set of homologous anatomical items located precisely from one specimen to another. Next, a Generalized Procrustes Analysis (GPA) consists of translating all landmarks configuration to a common location, rescaling all to unit centroid size (CS), and rotating all into an optimal least-squares alignment with an iteratively estimated mean reference form (average configuration called consensus). Then data are located in a Euclidean space where statistical methods are viable and multivariate statistical tools used to test biological hypotheses. Finally shape variation among superimposed configuration can be visualized in several ways, such as a thin-plate spline deformation grid or through a principal components analysis of warp scores. One of the more powerful aspects of the *Procrustes paradigm* is the combination of statistical analysis with visualizing shape changes graphically (Adams et al., 2013).

Landmark configuration coordinates

We performed a 2D geometric morphometric procedure where the geometry of the labial side of the left branch of the mandible was represented with both landmarks and semilandmarks as described below (see Fig. 2 and Tab. 1). Then we placed each jaw on a substrate (built with ground coffee support) that allowed the perfect horizontal leveling of each specimen lying on its lingual face. All digital pictures were taken with the same setting, camera model, resolution, objective and distance from the mandible. The hemimandibles were photographed using a digital camera mounted at a perpendicular angle to the sample. Pictures were taken always at a distance of 50 cm in order to minimize image distortion and parallax error. A total of 30 points were selected to capture mandible shape (see Fig. 2; Tab. 1). This approach includes a better characterization of the specific curved shape of the mandibular angle and it allowed us to cover most of the ratios used for classical morphometric characterization of ungulates jaws (Endo et al., 2000; Azorit et al., 2003). The points 1, 2, 5, 6, 13, 14, 15, 17, 18 and 20 were treated as landmarks (homologous points clearly defined on all mandibles), whereas the remaining ones (3-4, 7-12, 19, 21-30) were treated as semilandmarks (calculated in a standardized way on mandibular curved edges). Semilandmarks were placed using the program MAKEFAN8 from the Integrated Morphometrics Software 8 Package (IMP 8) (Sheets, 2014). All landmarks and semilandmarks were digitized using TPSDig2 (Rohlf, 2006). Semilandmarks were then allowed to relax by sliding (Zelditch et al., 2004) to the position which minimized the squared Procrustes distance between the form of the hemimandible of a given specimen and the consensus reference form from all specimens analyzed using the program SEMILAND8 (Sheets, 2014).

Generalized procrustes analysis

Procrustes coordinates and centroid sizes (CS) were generated by using COORDGEN8 (Sheets, 2014). Centroid size (CS) is computed as the square root of the sum of the squared distances of all landmarks from their centroid (Bookstein, 1997). CS is considered as the most explicit measure of size in geometric morphometrics and represents an integrative measure of the overall geometric size of each specimen (Zelditch et al., 2004). Partial warp scores (PWS) were derived from the landmarks used for capturing the shape of the hemimandibles upon Procrustes alignment and calculation of the mandibular consensus reference form. PWS and their principal components (PC, also known as relative warps) were computed using PCAGEN8, which is included in the IMP 8 suite (Sheets, 2014).

PWS were used as shape variables in our analyses since they capture the entire shape variability over the sample without loss of information. The use of partial warp scores was preferred over relative warps (i.e. those principal components of the partial warps scores accounting for most, but not all of the variation in shape), given the fact the observed differences in shape in our case are rather subtle and crucial shape information might be lost when reducing the number of shape variables in the study (Zelditch et al., 2004).

Allometry assessment: shape variations through the growth

Ontogenetic allometry, also called growth allometry or changes of shape versus size, deals with covariation among anatomical features during growth (Klingenberg and Zimmermann, 1992). In GM in the absence of allometry the centroid size is the only size measurement that is uncorrelated with shape variations (Zelditch et al., 2004). We then tested allometric growth by regressing PWS on Log(CS) using the program REGRESS8 (Sheets, 2014). This program builds a two components uniform regression model using the mean shape of the five specimens in the sample with the smallest values of CS as the reference form. The dependent variable (shape) is multivariate, but the predictor Log(CS) is univariate. Detailed statistics on the regression model are provided in Tables 1 to 3 of the Supplementary Material. REGRESS8 was also used to generate the deformation grids and vectors describing allometric growth. We tested the existence of allometry for both the Andújar NP and Cazorla NP populations separately. Furthermore, we tested statistically the differences between the growth vectors of both populations, and compared with the alternative model considering the growth pattern of the pooled 178 individuals. The absence of statistically significative differences in the angle between the respective growth vectors was tested using the tool VECCOMPARE8, a feature included within REGRESS8.

Assessment of shape variation due to locality and sex

Due to the strong allometry present in the populations studied we cannot perform a straightforward comparison of the variation in shape. Prior to that, the variation of shape with size (mainly due to age) must be removed. This was accomplished by standardizing all the shape coordinates to a common value of CS using the PWS versus Log(CS) regression model for all the individuals (178 specimens in the combined sample), once we checked that the differences in the growth vectors of the two populations under study were not statistically significant. The standard CS was the median CS value for the entire dataset. Standardization was carried out by means of the tool STANDARDIZE8 within the REGRESS8 software.

The standardized datasets was tested for differences in mandible mean shape due to sex (86 male individuals versus 92 female individuals) and locality (99 individuals from Andújar NP versus 79 individuals from Cazorla NP) using the program TWOGROUP8.

The program calculates the mean Procrustes distances between mandible shapes of two groups, defined in our case either by sex or population site. The statistical significance of the differences of the mean mandibular shape was assessed using resampling methods (bootstrapped Goodall's F-test, 400 bootstraps).

Recording size variation and sexual size dimorphism (SSD)

Mandibular size variations with age group, sex and population were assessed using both centroid sizes (CS) and mandibular length (L) which were taken to the nearest millimeter from the *processus angularis* to the anterior part of the dentary bone (Fig. 2). Variance analyses were used to search for size differences in L and CS between factors (sex and population) in each age group via post-hoc Tukey HSD comparisons.

In comparative studies of sexual size dimorphism (SSD), the methods used to quantify dimorphism are controversial (Smith, 1999). Sexual dimorphism in size was also studied for each population and age class through several indices using both L and CS values. Two indices were calculated as the ratio the mean size of males (M) to the mean size of females (F), and also on the logarithmic scale of this index which is equal to the differences between the logarithms of the males and female mean values, as:

$$\mathrm{SSD}_1 = \frac{M}{F} \quad ; \quad \mathrm{SSD}_2 = \ln\left(\frac{M}{F}\right) = lnM - lnF$$

A third index was also performed in a similar way to De Marinis et al., (2019) as:

$$\mathrm{SSD}_3 = \frac{M - F}{M} = 1 - \left(\frac{F}{M}\right)$$

The values of SSD_1 will be 1 in the absence of sexual dimorphism, whereas SSD_2 and SSD_3 values will be negative when females are larger than males, but values for males larger than females are compressed into a positive range from 0 to 1.00 (Smith, 1999).

Statistical models describing growth

Altogether, three *potential* models were used for modeling growth, using both mandibular length (L) and mandibular Centroid Size (CS) as a function of age. These models were: Von Bertalanffy, Gompertz and the Monod-type logistic growth model.

We fitted the three growth models to size-at-age data separated by sex (male or female) and population (Andújar NP or Cazorla NP).

The most common parameterization of the Von Bertalanffy (Bertalanffy, 1938) growth model is

$$L_t = L_\infty(1 - e^{-K(t-t_0)})$$

where L_∞ is the maximum length term, indicative of asymptotic growth, K describes how quickly L_∞ is reached and t_0 is interpreted as the age when an individual would have been of zero length assuming the equation to be valid at all ages (Quist et al., 2012). The Gompertz growth model (Gompertz, 1825) is a sigmoidal growth curve that assumes an exponential decrease of the growth rate with age. The most common parametrization of the Gompertz model is

$$L_t = L_\infty e^{(-b_0 b_1^t)}$$

with L_∞ representing the asymptote, b_0 a numeric parameter related to the value of the function when age is zero and b_1 a numeric parameter related to the scale of age. The third is the Monod-type logistic growth model (Monod, 1949), fashioned after the Michaelis–Menten model (Michaelis and Menten, 1913), this model takes the form

$$L_t = \frac{V_m \cdot t}{K_m + t}$$

where the asymptote is reached with a value of V_m, K_m is the t value such as $L_t = V_m/2$.

We fitted data on both the mandibular length and the centroid sizes at the ages from 0.25 (3 months) to 15 years in males and from 0.25 up to 17 years in females. Choosing the best function to describe animal growth is an important task that must be based on objective criteria and tested before selecting the model (Topal et al., 2004; Malhado et al., 2009). We performed a goodness of fit test based in an adjusted R^2 and we also used the p-value for the Shapiro-Wilk (S-W), testing the normality for the residuals as a criteria. Then we compared the three candidate growth models using Akaike's Information Criterion corrected for small sample size (AICc). The model with the smallest AICc value (AICc,min) was selected as the "best" among the models tested. The AICc differences Δ AICc,i=AICc,i - AICc,min were computed over all candidate models. Models with Δ AICc,i < 2 have substantial support, while there is considerably less support for models with 4 < Δ AICc,i < 7, and models with Δ AICc,i > 10 have essentially no support and might be omitted. We also calculated AICc weights (AICcWt,i) for each model (Burnham and Anderson, 2002). We performed a goodness of fit test based on an adjusted R^2. Once the best function had been selected multiple range tests were used to determine whether the growth coefficients obtained from the models were significantly different for each sex and population. The calculations were performed in R version 3.5.2 (R Core Team, 2018) using several packages such as "ggplot2" (Wickham, 2016), "AICcmodavg" (Mazerolle, 2019), "FlexParamCurve" (Oswald et al., 2012) and "nlstools" (Baty et al., 2015).

Results

Allometry assessment: shape variations through the growth

A multivariate regression of all shape variables (partial warp scores) on log-transformed CS was statistically significant for both populations, meaning that specimens pass through significant ontogenetic changes in their mandible shape (see Supplemental information Tab. S1-S3). Indicating a strong allometric growth, the variation in size explained a large and significant amount of the variance of shape data based upon summed squared Procrustes distances: 49 % for the Andújar NP population (F = 93.58, p < 0.001), and 67.6 % the Cazorla NP population (F = 160.7, p < 0.001). The results indicate that there are no significative differences in the angle between the respective growth vectors: The angle between the growth vector for individuals from Andújar NP and the common model was 6.76º, whereas in the case of individuals from Cazorla NP it was 5.23º. Since the found 95% range of differences in angles was -2.73º to 8.50º, i.e. an interval which contains 0º, the corresponding differences are not statistically significant. Then, the morphological patterns in individuals from the Andújar NP and Cazorla NP are essentially identical in shape ontogenetic variations.

As can be observed in the graphical results (Fig. 3), these general allometric trends correspond almost exclusively to a great modification in the mandibular horizontal ramus over the tooth row. Results showed that landmarks 13-17 have a high implication in the variance especially landmarks 13 and 15, which are related to the first molars and premolars respectively (see Fig. 3). The main shape variations were due to the eruption of permanent molar teeth (M_2) which occurs at 9 months, and to the eruption of the permanent premolar teeth and the third molar (M_3), whose eruption usually starts from 18 months old. Also at the level of landmarks 24, 27 and 29 we detected a simultaneous and consistent backward displacement of the angular process (see Fig. 3), which represents an extension into the area of associated masticatory muscles insertion. Significant shape variations were then detected up to about 18 month of age, but there was an almost total lack of shape variation in adulthood, especially after three years old at which age all the permanent teeth have already sprung.

Assessment of shape variation due to locality and sex

The results from the principal component analysis (PCA) of the PWS, standardized data, are showed in Fig. 4. PC1 and PC2 were statistically significant, and represent 41.6% and 18.8% respectively of the overall variance in shape data once variation in size was removed. Prior to standardization, the variation in size in the total dataset was highly significant ($F = 218.673$, $p < 0.001$), and explained 55.4 % of the variance of shape data based upon summed squared Procrustes distances. As can be seen in Fig. 4, PC1 represents the main source of shape variability in the dataset, this consisting of modification in the mandibular horizontal ramus over the tooth-row due to the replacement of premolars and eruption of permanent molar teeth, and also the variation in the thickness from the exterior of the last dental alveoli to the mandibular angle. PC2 represents a displacement occurring towards the angular process, decreasing their convexity at the time of a more caudal and horizontal position of the coronoid and the articular process, as well as the ventral margin of the mandibular sigmoid notch.

Mean mandible shape did not vary significantly with sex (Procrustes distance between means: 0.0062, bootstrapped F-test: $F = 0.96$, $p = 0.365$), suggesting the absence of sexual dimorphism at this level. However, when comparing the standardized mandible shapes of individuals from the Andújar NP (99 specimens) and Cazorla NP (79 specimens), we did find slight but statistically significant differences between the two sites (Procrustes distance between means: 0.0212, bootstrapped F-test: $F = 28.09$, $p = 0.0025$). The differences in mean mandible shapes between the populations from the Andújar NP and Cazorla NP are shown in Fig. 5. We detected differences in the position of landmarks 14 and 15 on the anterior alveolar margin of the first molar and the first premolar respectively (Fig. 2 and 3), representing a variation in the eruption time between populations of permanent premolars. In addition, a more pronounced concavity of the caudal edge of the mandibular ramus was also found for Cazorla NP mouflons (reference point 29-30).

Variations in size and differential growth rates

The number of males and female mouflons from each location grouped by age class are shown in Tab. 2. The chance of including mouflons from culling and population control programs in both areas allowed us to obtain a valuable collection of mandibles of a wide age range, from young lambs of less than 3 months, mouflons of 5-9 months and up to ewes and rams more than 15 years old.

Variations of the mandibular size, both the centroid size (CS) and the mandibular length (L), according to populations and sex for each age class are shown in Tab. 3. Differences were detected in size ($P < 0.05$) between populations, with the mouflons from Cazorla NP generally being the smallest. Males from Andújar NP recorded the largest mandiblular sizes while the Cazorla NP females recorded the smallest ones.

Sexual size dimorphism (SSD) results were similar through all the three indices performed. Those calculated as the ratio of males/females on a logarithmic scale (SSD_2 in methods section) are shown in Tab. 4. We detected slight sexual dimorphism in size at 3 months of age, with females unexpectedly larger than males in both populations (average SSD = -0.094, -0.0051 in Andújar NP and Cazorla NP, respectively using CS), but SSD was not detected in older animals (all values below 0.05, see Tab. 4).

For growth model selection, the results of the goodness-of-fit test and Akaike´s Information Criterion are shown in Tab. 5. There were no significant differences among the mathematical models except for the Monod-type Logistic model in the Andújar NP males (AICc = 18.43, AICcWt = 0.00, Tab. 5). We decided to discard the Monod model because the p-value for the Shapiro-Wilk (S-W) test showed a lack of normality for the residuals in the same cases (Tab. 5). There were no significant differences between the Von Bertalanffy and Gompertz models so we used the Von Bertalanffy model for simplicity. The centroid size was always highly correlated with the mandible length, and the modeling of the growth curve results was the same using either of them. Fig. 6 shows the Von Bertalanffy growth curves fitted with values of the mandibles centroid size (considered as an integrative value) and the age in years, while the parameter estimates of growth are shown in Tab. 6.

The growth rate coefficient (K) is also called the maturity or precocity rate and represents the speed with which the animal approaches asymptotic size at maturity. We detected the fastest growth during the pre-weaning period in males and females from the Andújar NP, with higher K values and a great precocity in reaching the asymptotic size at an earlier age than the Cazorla NP mouflons (see Fig. 6 and Tab. 6). The coefficient representing the time necessary to reach mature size (t_{max}) is related to the inflection point in the growth curve. This moment appears after the post-weaning state in the mouflons from Andújar, which showed the lowest values (at 0.865 years in males and 0.933 in females). The mouflons from Cazorla took more time to reach the mature size, over 12-18 months (1.05 and 1.56 years in males and females respectively, in Tab. 6). We detected a great differential growth-rate index among populations and sexes with the initial mandibular size at the origin (CS_0) being higher in females than in males both from Cazorla NP and Andújar NP, but ultimately the asymtotic size (CS_∞) or adult size, which estimates the size at maturity, was higher in males and females from Andújar NP than from Cazorla for both sexes ($P< 0.05$).

Discussion

Ontogeny and shape variations

Geometric morphometric methods provide powerful tools, allowing us to describe allometry also as a way to relate structural and functional growth trajectories in the mouflon mandibles. In this research we detected strong allometry, similarly as described in *Ovis aries*, where most of the differences in shape were found to be explained by changes in expanding molar length, as M_2 and M_3 erupt rostro-nuchally with age (Parés-Casanova, 2013).

In our mouflons a strong allometry was detected with variations in shape mainly matching not only with molar but also with the premolar eruptions. As the space occupied by the premolar teeth in the dentary bone decreased (forward displacement of landmarks 13-14 because of the eruption of the permanent premolar teeth which are relatively smaller than deciduous), we also observed the angular process increasing (landmarks 25-29, Fig. 3-5) in a similar way to that described by Cardini and O'Higgins (2005). These morphological changes during ontogeny led in adulthood to a lower ratio of the premolar/molar row lengths than in young mandibles and deeper mandibles due to a consistent backward displacement of the angular process (see Fig. 3), which represents an extension in the area of associated masticatory muscles insertion.

The variation in the mandibular morphology of mammals has always been understood as a specialization for different diets, with the larger shape modifications occurring in the areas directly involved in the mechanics of mastication (Cardini and O'Higgins, 2005). After controlling for phylogenetic effects, some studies on ungulates mandible design interpreted the correlation between function and morphology as driven by adaptation. This is the case for several mandibular traits such as the coronoid process (Perez-Barbería and Gordon 1999) and hypsodonty index (Raia et al., 2009) that were more correlated to dietary habits than to phylogeny in grazing selenodont artiodactyls like the mouflons. Therefore, we could expect consistent mandibular shape variations concentrated not only in the angular process but also in the coronoid process correlating with dietary changes, such as those occurring after weaning, with the transition from breastfeeding to a harder diet. However the main allometric shape variations occurred very quickly, not as we had thought during the weaning period, but later and until the teeth finished erupting. Very little percentage of variance was explained by the slight elongation of the coronoid process in our study. As already mentioned, the main allometric changes were concentrated almost exclusively in a great modification in the mandibular horizontal ramus over the tooth-row due to the eruption of the molariform teeth.

Interestingly we found small but significant differences between populations. Mouflons from Cazorla NP showed a slower mandibular angular process and less consistent backward displacement of the angular process and a less pronounced convexity of the caudal edge of the mandibular ramus. We observed a less forward displacement of molariform teeth along with a difference in the position of the 14 and 15 landmarks. This matched with the presence of deciduous premolar teeth which occupied a relatively larger space in the mandible tooth-row than subsequent permanent premolar teeth (Fig. 3 and Fig 5). This shape variation, interpreted as a delay in the eruption time in Cazorla NP mouflons, was similar to those recorded in island Soay sheep, with teeth erupting at an older age and tending to grow more slowly than improved mainland sheep breeds (Geiger et al., 2018).

Early growth rate and mature size variations

By modeling growth we detected differences between populations in all parameters (Tab. 6) with the involvement of mandibular shape, variations in mature size and possible life-history implications. We detected significant differences in the maturity rate (K) with a high precocity in reaching asymptotic adult size in the Andújar NP, while in the Cazorla NP the mouflons took more time, both males and females, over 12-18 months (1.05 and 1.56 years in males and females respectively, as can be seen in Tab. 6). However, a longer period of growth did not result in a larger asymptotic size, conversely it led to smaller mandibles. Adult size (CS_∞), which estimates the size at maturity, was lower in specimens from the Cazorla NP than those from the Andújar NP independently of sex ($P< 0.05$).

We found that the final asymptotic size in our populations was a consequence of a great differential growth-rate index among populations and sexes (Tab. 6). The asymptotic size seems to have been influenced more by the speed with which the mouflons approach the adult stage (K) than by their initial size, which is greater in females from both populations. Although the females´ initial size was greater, (CS_0 being higher in females than in males both from Cazorla NP and Andújar NP, see Tab. 6), the differential in growth rate led to an ultimately lesser asymptotic mandibular size.

Although, similarly to De Marinis et al. (2019) using the same SSD, we detected that females were larger than males at the age of 3 months, sexual size dimorphism was not detected in adults whatever the population. Being the differences in pre-maturational growth, age at maturity, or both considered as the primary determinants of sexual dimorphism in adult body size (Shine, 1990), the reduced growth in females may also explain the lack of SSD in the adult stages, in a similar way to that found in other *Ovis* species (LeBlanc et al., 2001; Van Vuren and Bakker, 2009).

Van Vuren and Bakker, (2009) compared the growth and mature mass of sheep living wild with those born in the same ecosystem but raised on farm nutrition with a balanced diet. They found that feral sheep were smaller and that rams attained greater mass in farm conditions but ewes did not, suggesting phenotypic plasticity in ram body mass leading to an increase of SSD under favorable environmental conditions. SSD decreasing in ungulates during unfavorable environmental conditions was also noted in bighorn sheep (LeBlanc et al., 2001). It seems that the females are more sensitive to adverse environmental conditions and invest more in reproduction than in their own growth, which subsequently influences the maturation age and reproductive success.

A delay in reaching mature size probably has an important impact on reproductive and life-history traits in this species. Usually mouflons approach the adult stage very quickly, and essentially reach adult size in their first year of life. Sexual maturity is closely linked to physical maturity, which occurs after the onset of fertility at puberty (Lincoln, 1998). Mouflons from Andújar reach adult size at an early age, after the post-weaning stage (at 0.865 years in males and 0.933 in females, Tab. 6). However the mouflons from the Cazorla NP prolonged the period of growth until many months after the theoretical puberty period of 9 months of age (1.05 and 1.56 years in males and females respectively, Tab. 6). Mouflons under 4 months are in the breastfeeding period, while the mouflons of 5-9 months are between the post-weaning and puberty state, which starts at 8-9 months in Mediterranean ecosystems, although depending on a body weight threshold (Santiago-Moreno et al., 2001). Body size represents a real threshold for lambs in the attainment of sexual maturity, with the occurrence of the first ovulation in female mouflon lambs delayed below 24 kg of body mass (Santiago-Moreno et al., 2001). Thus, a delay in reaching optimal size and weight may lead to a larger delay of more than one year in females' sexual maturity, with consequences for the population life history. A further ripple effect may also be expected because of subsequent delayed birth periods.

Differential maturity rates and mandible size have also been explained by differential birth size, parturition type and genetic group. Malhado et al., 2009 noted that lambs from single births present a better performance in their early development than animals from double parturition, which can be partly explained by the lack of competition for maternal milk in lambs from single parturition when compared to twins. In addition, suckling time after the first 2 weeks was positively related to both the maternal body mass and the offsprings´ early growth (Birgesson and Ekvall, 1997).

In deer it was found that together with the maternal condition, both climate and population density during early growth were decisive in the configuration of body architecture (Høye and Forchhammer, 2006). The differences observed in mandibular size and growth rates also have an environmental explanation related ultimately to diet quality, which is one of the most important factors affecting the growth rate of lambs (Khalifa et al., 2013). Unfavorable early conditions retard growth, and this is not fully compensated for later in life (De Crombrugghe et al., 1989; Bertouille and De Crombrugghe, 1995: Hewison et al., 1996). A parallel negative effect of deer abundance on growth was also observed, revealing a strong influence of climatic conditions experienced in the year of birth in southern Spain (Azorit et al., 2003). Recently, ecological conditions experienced by offspring during pregnancy and early postnatal life have also been shown to be important in determining mandible size in roe deer (De Marinis et al., 2019). In addition these authors found that temporal changes in the length of the anterior section of the mandible are a particularly suitable index of growth constraints.

In our study mouflons with relatively late teeth replacement, lower maturation rate and smaller adult size were those of the population submitted to extreme environmental conditions. The Andújar NP mouflons that were collected during 2007-2008 and did not live through the drought conditions might have had a growth near their potential, contrary to the mouflons of the Cazorla NP that were sampled in 1996, when they lived under the effect of epizootic diseases plus a low availability of resources due to drought and large densities of ungulates. According to Lewis et al., (2002), real growth may well depart from potential growth due to unfavorable environmental conditions and health problems.

Our findings show that in wild ungulate populations the mandibles record unfavorable environmental conditions during the early growth of individuals. The variations in mandibular measurements reflect the changes in the ecological context and hence the variation in animal and populations performance. Very useful information can be obtained about the environment and the management to which the mouflons have been subjected by measuring the morphometric and the growth rates of the mandibles. By enabling researchers to record the effects of density-dependent and density-independent factors, mandibles become a target of interest for ecological and management studies of the mouflon.

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Table 1. Landmarks of the mouflon mandible viewed from the left labial surface and description of areas covered by selected semilandmarks points for capturing the shape of jaws for the geometric morphometric analysis.

Table 2. Number and age of males and female mouflons from the Sierra de Andújar Natural Park (Andújar NP) and the Sierras de Cazorla, Segura y las Villas Natural Park (Cazorla NP) in Jaén, Spain.

Table 3. Variations in age, sex and population of the mandibular size of mouflons from the Sierra de Andújar Natural Park (Andújar NP) and the Sierras de Cazorla, Segura y las Villas Natural Park (Cazorla NP) in Jaén, Spain. CS is the morphometric geometric centroid size; L is the length of the jaw in cm.

Table 4. Mandibular Sexual dimorphism in size (SSD) of mouflon (Ovis aries musimon) from the Sierra de Andújar Natural Park (Andújar NP) and the Sierras de Cazorla, Segura y las Villas Natural Park (Cazorla NP) in Jaén, Spain. The SSD indices were calculated through the logarithm of mean size of males / mean size of females ratio, using both mandibular length (L) and centroid sizes (CS) in each age group.

Table 5. Results of goodness-of-fit test using adjusted R^2 (Adj. R^2), the p-value for the Shapiro-Wilkes (S-W) test for the residuals and model selection procedure using Akaike´s Information Criterion corrected for small size (AIC*c*). The Von Bertalanffy (VB), Gompertz (G), and Monod-type Logistic (ML) growth models were tested on males and females of mouflon (*Ovis aries musimon*) belonging to two populations from southern Spain: Sierra de Andújar Natural Park (Andújar NP) and Sierra de Cazorla Segura y las Villas Natural Park (Cazorla NP).

Table 6. Parameter estimates from fitting the Von Bertalanffy growth model for males and females of mouflon (*Ovis aries musimon*) from the Sierra de Andújar Natural Park (Andújar NP) and the Sierras de Cazorla, Segura y las Villas Natural Park (Cazorla NP) in Jaén, Spain. CS_∞ is the asymptotic length, K is the growth constant, t_0 is the theoretical age when CS_0 equals zero in the graphic model, CS_0 is the initial length at the origin and t_{max} is the predictor of a maximum age.

Figure 1. Location in the province of Jaén (Spain) of the mouflons populations sampled: the Sierra de Andújar Natural Park (Andújar NP) with 745 km2 in the Sierra Morena mountains (38°17′23″N 4°01′43″O), and the Andalusian Game Reserve, which has an extension of 687 km2 in the 2,140 km2 of the Sierras de Cazorla, Segura and las Villas Natural Park (Cazorla NP) in the eastern side of the Betic mountain range (38°05′00″N 2°45′00″O).

Figure 2. Points used to capture jaw shape in the morphometric analysis on the buccal side of the left hemimandible. The numbers represent landmarks and semilandmarks as described in Table 1. L is the length of mandibular bone.

Figure 3. Shape changes associated with allometric growth for the populations from Andújar NP (A) and Cazorla NP (B). Both ontogenetic trajectories are essentially identical, and were determined by multivariant regression of PWS (calculated using the consensus shape of the five smallest individuals for each of the populations) on Log(CS).

Figure 4. 2D scatter plot of the two main principal components of PWS of standardized shape coordinates showing the corresponding deformation grids and vectors. PC1 represents 41.6 % variance in shape, and PC2 18.8 %. The symbols indicate the population of origin for each individual: Andújar NP (●) and Cazorla NP (○).

Figure 5. Differences in mean mandible shape between the populations from Andújar NP (red line) and Cazorla NP (blue dashed line). The differences were determined by comparison of shape coordinates standardized to a common value of CS, namely the median CS value for the entire dataset.

Figure 6. Von Bertalanffy's growth curve of male and female mouflons hunted in two populations: in the Sierra de Ándújar Natural Park (Andújar NP) and the Sierras de Cazorla, Segura y las Villas Natural Park (Cazorla NP) in Jaén, Spain, during 2007-8 and 1996, respectively. The symbols indicate the population for each individual: Andújar NP (●) and Cazorla NP (○). The growth models were fitted by using values of centroid size of the mandibles (from a morphometric geometrics study), and the age (estimaded by the eruption and by rest lines in dental cementum).

Supplemental Information

Results of Regressing PARTIAL WARP SCORES on Log (CENTROID SIZE) for the indicated datasets using REGRESS8 (Sheets, 2014). Listing starts at highest numbered PWx, then PWy Last two rows are uniform terms, higher warp numbers are higher in bending energy or spatial localization of deformation. Data is the regression slope and intercept, the correlation coefficient r and Z-score is equal to 0.5*ln(1+r/1- r)/(n-3)^0.5 which is based on the regression coefficient r, assuming normally distributed residuals.

Table S1. Results of Regressing PARTIAL WARP SCORES on Log (CENTROID SIZE) for mandibular shape data of individuals from Andújar NP (99 specimens).

Table S2. Results of Regressing PARTIAL WARP SCORES on Log (CENTROID SIZE) for mandibular shape data of individuals from Cazorla NP (79 specimens).

Table S3. Results of Regressing PARTIAL WARP SCORES on Log (CENTROID SIZE) for mandibular shape data of all individuals in the sample (178 specimens).

Table 1. Landmarks of the mouflon mandible viewed from the left labial surface and description of areas covered by selected semilandmarks points for capturing the shape of jaws for the geometric morphometric analysis.

Landmarks	**Names and Description**
1	Tip of de condilar process
2	Ventral margin of the mandibular sigmoid notch
5	Ventrocaudal margin of the coronoid process
6	Tip of the coronoid process
13	Posterior alveolar margin of M_1
14	Anterior alveolar margin of M_1
15	Anterior alveolar margin of the first premolar
17	Dorsal margin of the fourth incisor tooth
18	Ventral margin of the first incisor tooth
20	Posterior margin of the mandibular symphysis
Semilandmarks	**Description Traits**
3 to 4	Concavity of the posterior border of the coronoid apophysis
7 to 12	Convexity of the anterior edge of the coronoid process which continues until the molar alveolus
16	In the mandibular diastema at the level of the Semilandmark 21
19	Rostro-vental margin of the horizontal ramus of the mandible at the level of the posterior alveolar margin of fourth incisor
19 to 29	Convexity of the ventral margin of the horizontal ramus of the mandible from the anterior alveolar margin of the premolar level to the posterior margin of the angular process
29 to 30	Concavity of the caudal edge of the mandible ramus

Table 2. Number and age of males and females mouflons from the Sierra de Andújar Natural Park (Andújar NP) and the Sierras de Cazorla, Segura y las Villas Natural Park (Cazorla NP) in Jaén, Spain.

	Sex	**Age in months**		**Age in years**					
		2-4	**5-9**	**1**	**2**	**3-5**	**6-9**	**10-17**	**Total**
Andújar NP	Males	3	7	10	11	22	8	2	63
	Females	4	6	6	3	8	7	2	36
Cazorla NP	Males	6	2	3	3	2	5	2	23
	Females	13	5	5	4	12	10	7	56
Total		26	20	24	21	44	30	13	178

Table 3. Variations in age, sex and population of the mandibular size of mouflons from the Sierra de Andújar Natural Park (Andújar NP) and the Sierras de Cazorla, Segura y las Villas Natural Park (Cazorla NP) in Jaén, Spain. CS is the morphometric geometric centroid size; L is the length of the jaw in cm.

Age (years)	**Sierra de Andújar Natural Park**						**Sierras de Cazorla, Segura y las Villas Natural Park**						**p-values**	
	Males			**Females**			**Males**			**Females**				
	n	L	CS	n	L	CS	n	L	CS	n	L	CS	L	CS
0.25	3	12.90±0.4	**254.4±7.1** ^{a}	4	13.19±0.3	**279.9±7.2** ^{b}	6	13.06±0.2	270.8±5.2^{ab}	13	13.45±0.1	**283.7±2.6** ^{b}	0.198	0.015
0.75	7	15.10±0.2	**323.4±4.6**	6	15.02±0.2	320.4±5.9	2	14.40±0.3	303.8±9.0	5	14.39±0.2	**299.6±4.2**	0.227	0.044
1	10	**15.95±0.2**	**348.9±3.9**	6	15.43±0.2	334.9±5.9	3	15.88±0.3	334.1±7.4	5	**14.97±0.2**	**318.4±4.2**	0.009	0.001
2	11	**16.27±0.2**	**350.9±3.7**	3	16.16±0.3	348.8±8.4	3	16.01±0.3	331.7±7.4	4	**15.58±0.2**	**327.7±4.7**	0.028	0.008
3-5	22	**16.48±0.2**	**353.0±2.6**	8	16.06±0.2	343.6±5.1	2	16.21±0.3	353.1±9.0	12	**15.84±0.1**	**336.5±2.7**	0.006	0.003
6-9	8	**16.68±0.2**	**356.7±4.3**	7	16.57±0.2	353.4±5.5	5	16.32±0.2	340.7±5.7	10	**16.07±0.1**	**340.0±3.0**	0.045	0.002
10-17	2	16.60±0.4	354.9±8.7	2	16.77±0.4	352.3±10.2	2	16.58±0.3	344.9±9.0	7	16.04±0.2	343.3±3.6	0.126	0.595

Bold values indicate statistically significant differences at 5% between factors (sex and population) and the values for L and CS, via post-hoc Tukey HSD comparisons. a, b are used indicating statistically significant differences when more than two differences exist.

Table 4. Mandibular Sexual dimorphism in size (SSD) of mouflon (Ovis aries musimon) from the Sierra de Andújar Natural Park (Andújar NP) and the Sierras de Cazorla, Segura y las Villas Natural Park (Cazorla NP) in Jaén, Spain. The SSD indices were calculated through the logarithm of mean size of males / mean size of females ratio, using both mandibular length (L) and centroid sizes (CS) in each age group.

	SSD Andújar NP			**SSD Cazorla NP**		
Age (years)	n	L	CS	n	L	CS
0.25	7	-0.020	-0.094	19	-0.031	-0.051
0.75	13	0.010	0.010	7	0	0.010
1	16	0.030	0.039	8	0.058	0.049
2	14	0.010	0.010	7	0.030	0.010
3-5	30	0.030	0.030	14	0.020	0.049
6-9	15	0.010	0.010	15	0.020	0
10-17	4	-0.010	0.010	9	0.030	0

Values of SSD near to 0 indicate absence of sexual size dimorphism. Negative values indicate females larger than males. For males larger than females SSD are compressed in a positive range into 0 to 1.00.

$SSD = \ln\left(\frac{M}{F}\right)$

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Table 5. Results of goodness-of-fit test using adjusted R^2 (Adj. R^2), the p-value for the Shapiro-Wilkes (S-W) test for the residuals and model selection procedure using Akaike´s Information Criterion corrected for small size (AIC*c*). The Von Bertalanffy (VB), Gompertz (G), and Monod-type Logistic (ML) growth models were tested on males and females of mouflon (*Ovis aries musimon*) belonging to two populations from southern Spain: Sierra de Andújar Natural Park (Andújar NP) and Sierra de Cazorla Segura y las Villas Natural Park (Cazorla NP).

Sex	**Populations**	**Model**	**k**	**AIC*c***	**ΔAIC*c***	**Wt**	**Adj.R^2**	**S-W**
Male	Andújar NP	VB	4	494.56	0.36	0.45	0.755	0.947
		G	4	494.20	0.00	0.54	0.756	0.945
		ML	3	504.25	10.04	0.00	0.708	0.610
	Cazorla NP	VB	4	191.17	2.37	0.19	0.832	0.100
		G	4	191.17	2.36	0.19	0.832	0.105
		ML	3	188.81	0.00	0.62	0.836	0.276
Female	Andújar NP	VB	4	307.53	2.10	0.20	0.687	0.107
		G	4	307.45	2.02	0.21	0.688	0.113
		ML	3	305.43	0.00	0.58	0.692	0.133
	Cazorla NP	VB	4	416.75	0.00	0.51	0.855	0.248
		G	4	416.84	0.09	0.49	0.855	0.280
		ML	3	431.43	14.68	0.00	0.807	0.028

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Table 6. Parameter estimates from fitting the Von Bertalanffy growth model for males and females of mouflon (*Ovis aries musimon*) from the Sierra de Andújar Natural Park (Andújar NP) and the Sierras de Cazorla, Segura y las Villas Natural Park (Cazorla NP) in Jaén, Spain. CS_∞ is the asymptotic length, K is the growth constant, t_0 is the theoretical age when CS_0 equals zero in the graphic model, CS_0 is the initial length at the origin and t_{max} is the predictor of a maximum age.

Population	**Sex**	$\mathbf{CS_\infty}$	**K**	$\boldsymbol{t_0}$	$\boldsymbol{t_{max}}$	$\mathbf{CS_0}$
Andújar NP	Males	353.93±1.95 $^{\mathbf{a}}$	2.827±0.40 $^{\mathbf{a}}$	-0.195±0.07	0.865	149.95
	Females	349.23±3.30 $^{\mathbf{a}}$	2.034±0.43 $^{\mathbf{b}}$	-0.540±0.18	0.933	232.84
Cazorla NP	Males	342.97±4.13 $^{\mathbf{b}}$	1.800±0.48 $^{\mathbf{c}}$	-0.615± 0.23	1.050	229.45
	Females	340.42±1.98 $^{\mathbf{b}}$	0.919±0.15 $^{\mathbf{d}}$	-1.699±0.33	1.561	268.96

a, b, c and d: Different letters indicate statistically significant differences (Tukey post-hoc test, $p < 0.05$) between positions (sex and population) for the parameters CS_∞ and K, respectively.

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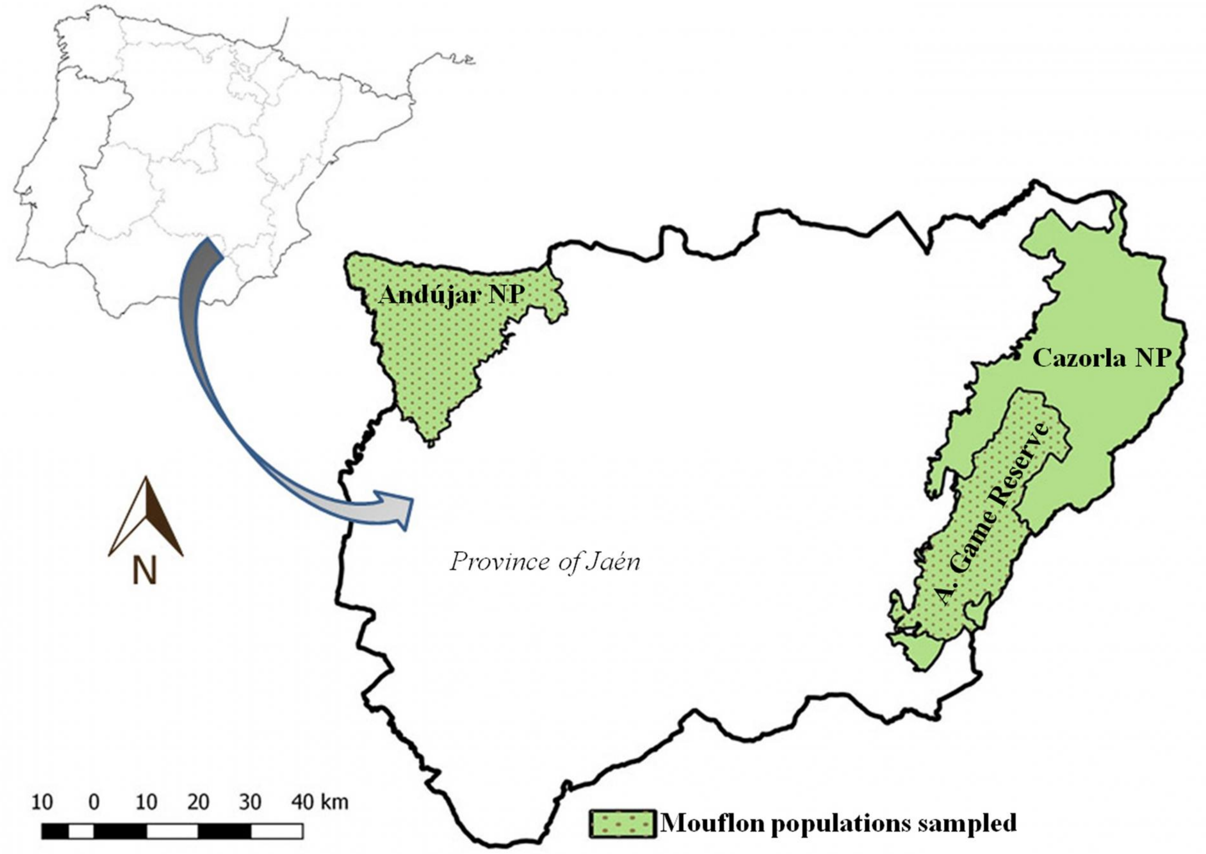

Figure 1

Figure 2

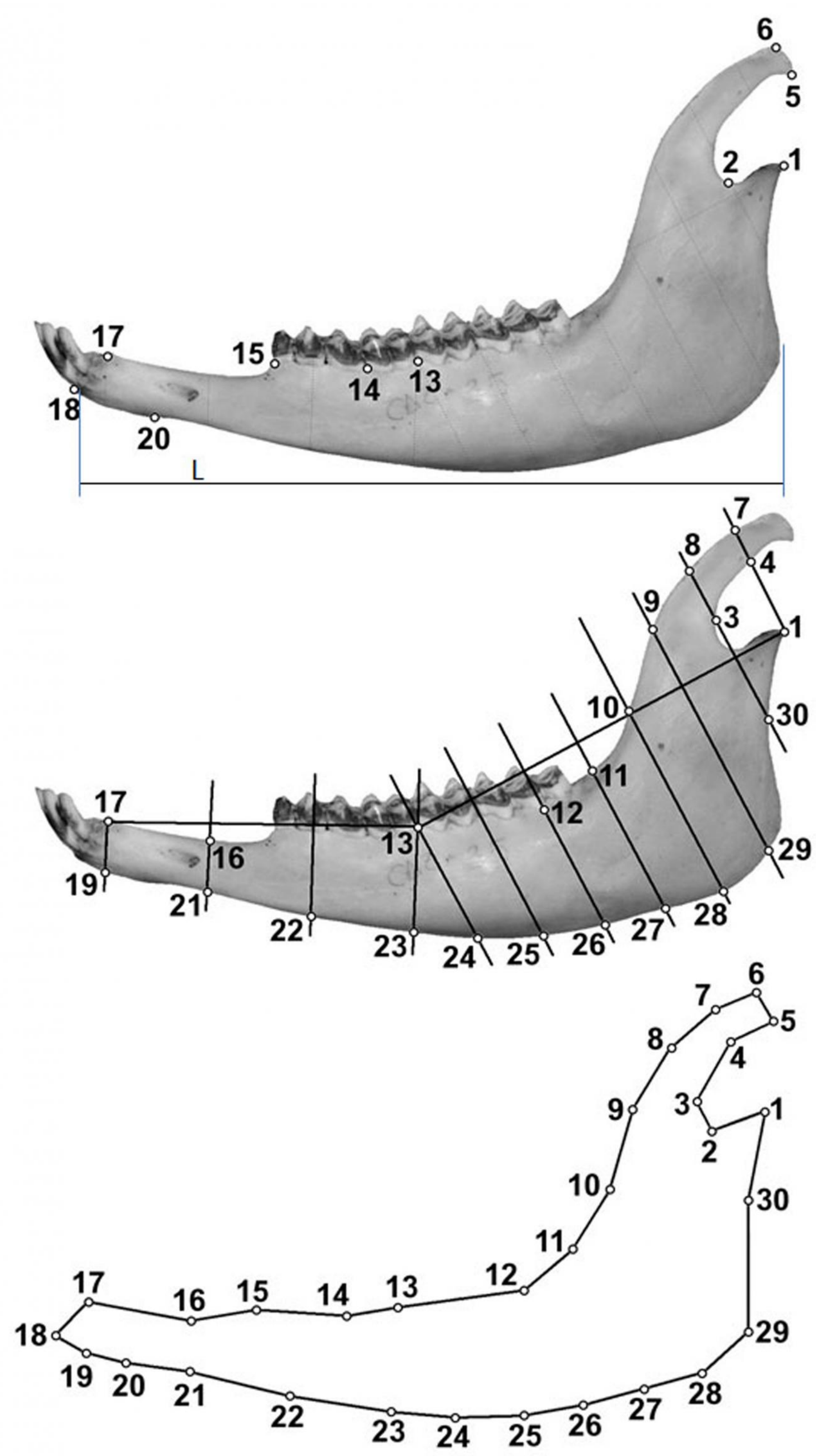

Figure 2

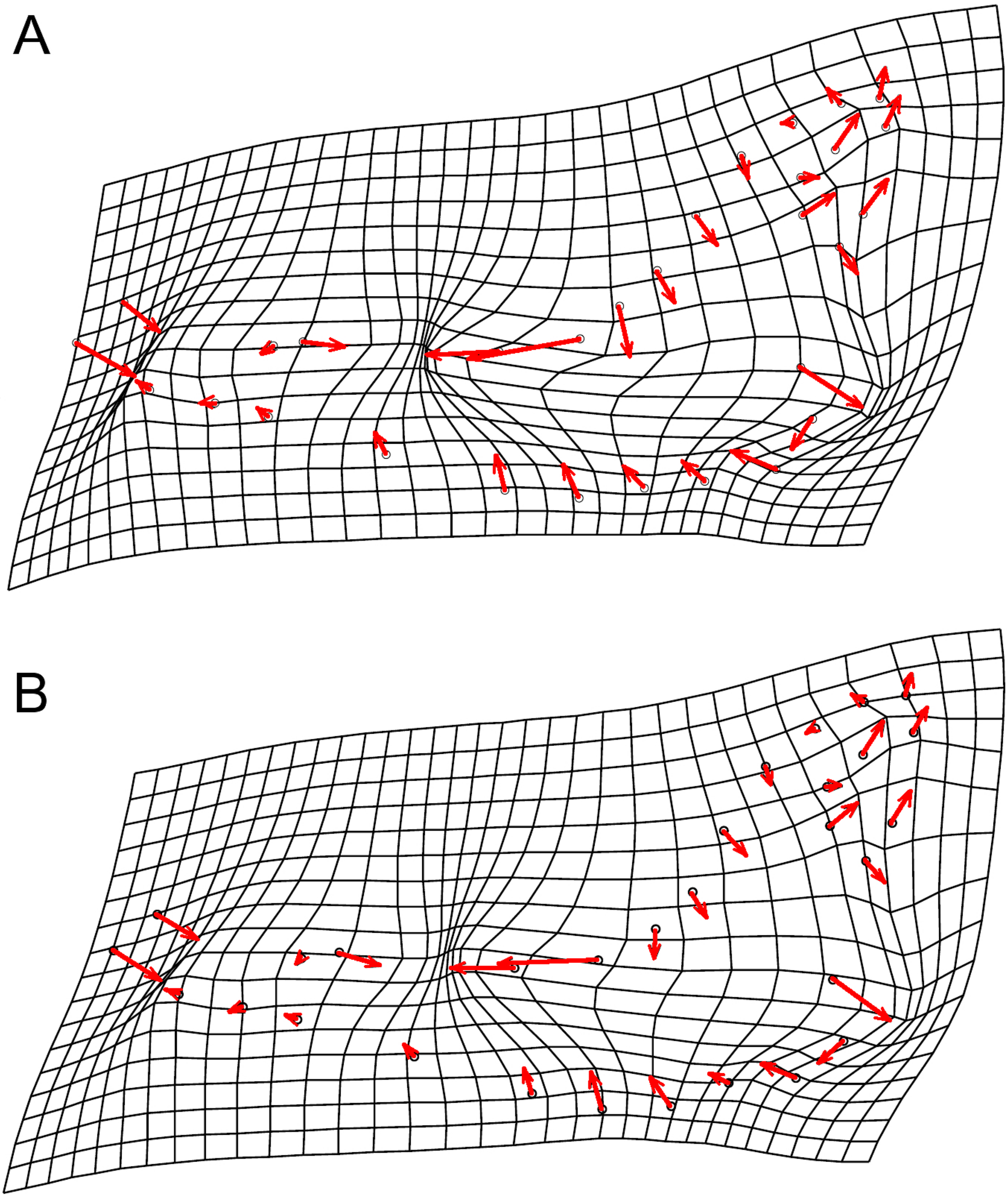

Figure 3

Figure 4

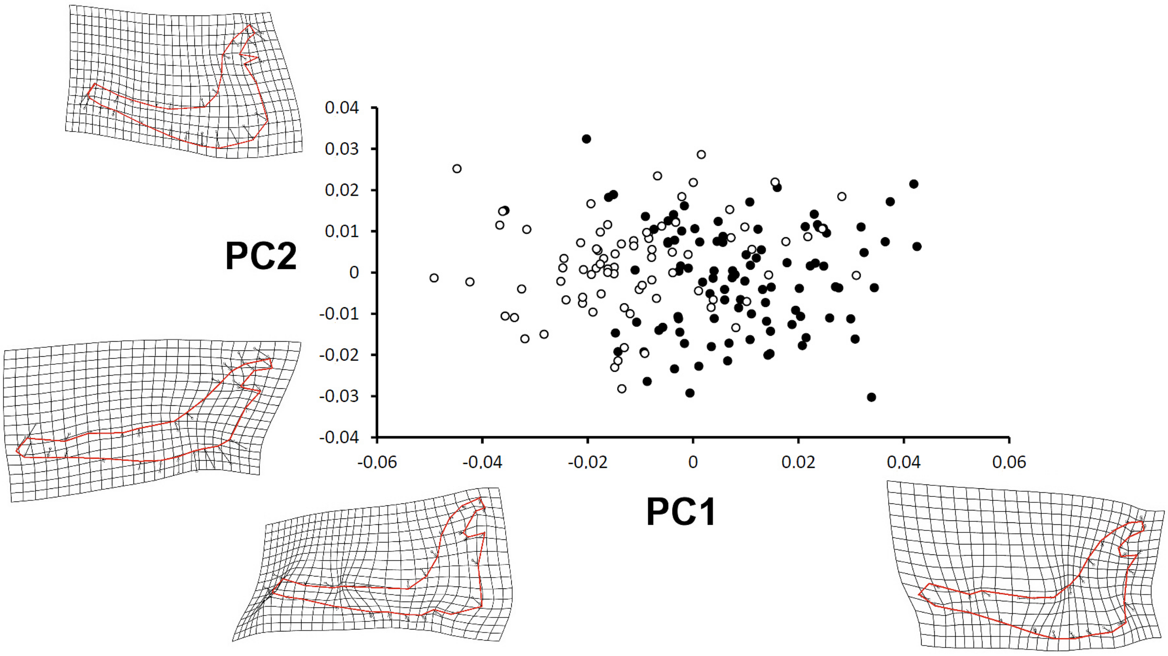

Figure 4

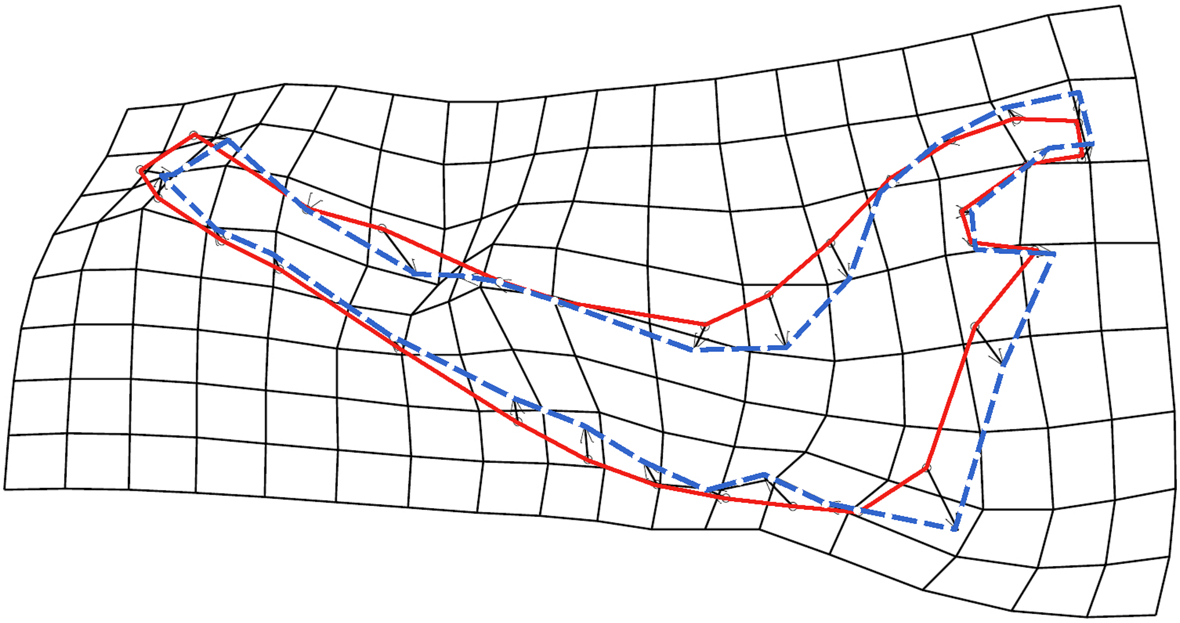

Figure 5

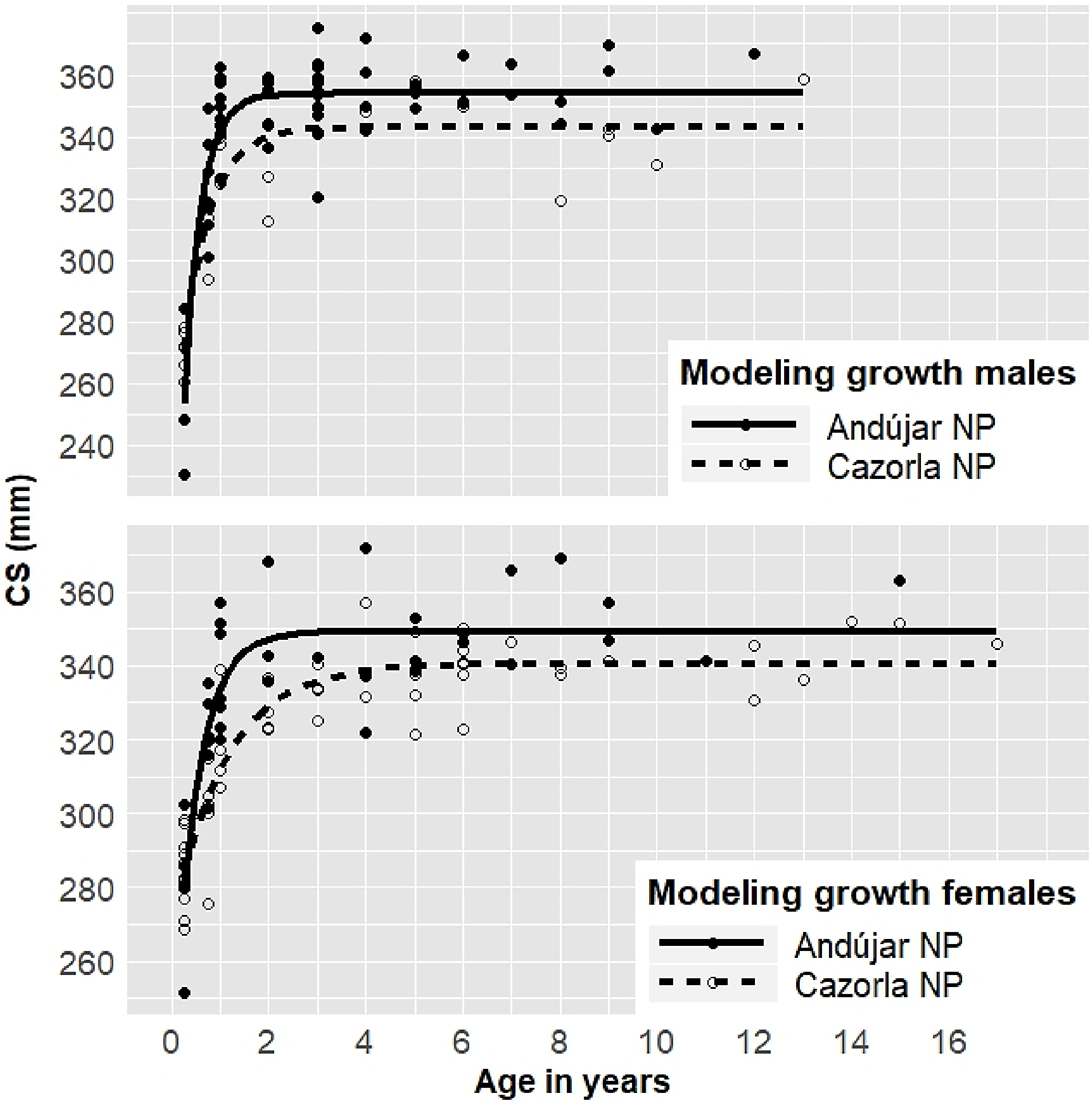
CS (mm)
360
340
320
300
280
260
240
Modeling growth males
Andújar NP
Cazorla NP
360
340
320
300
280
260
Modeling growth females
Andújar NP
Cazorla NP
0
2
4
6
8
10
12
14
16
Age in years

Figure 6

Manuscript body

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Tables

Table 1 - Download source file (16.24 kB)
Table 1. Landmarks of the mouflon mandible viewed from the left labial surface and description of areas covered by selected semilandmarks points for capturing the shape of jaws for the geometric morphometric analysis.

Table 2 - Download source file (16.62 kB)
Table 2. Number and age of males and female mouflons from the Sierra de Andújar Natural Park (Andújar NP) and the Sierras de Cazorla, Segura y las Villas Natural Park (Cazorla NP) in Jaén, Spain.

Table 3 - Download source file (25.51 kB)
Table 3. Variations in age, sex and population of the mandibular size of mouflons from the Sierra de Andújar Natural Park (Andújar NP) and the Sierras de Cazorla, Segura y las Villas Natural Park (Cazorla NP) in Jaén, Spain. CS is the morphometric geometric centroid size; L is the length of the jaw in cm.

Table 4 - Download source file (18.67 kB)
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Table 5 - Download source file (20.33 kB)
Table 5. Results of goodness-of-fit test using adjusted R2 (Adj. R2), the p-value for the Shapiro-Wilkes (S-W) test for the residuals and model selection procedure using Akaike´s Information Criterion corrected for small size (AICc). The Von Bertalanffy (VB), Gompertz (G), and Monod-type Logistic (ML) growth models were tested on males and females of mouflon (Ovis aries musimon) belonging to two populations from southern Spain: Sierra de Andújar Natural Park (Andújar NP) and Sierra de Cazorla Segura y las Villas Natural Park (Cazorla NP).

Table 6 - Download source file (22.43 kB)
Table 6. Parameter estimates from fitting the Von Bertalanffy growth model for males and females of mouflon (Ovis aries musimon) from the Sierra de Andújar Natural Park (Andújar NP) and the Sierras de Cazorla, Segura y las Villas Natural Park (Cazorla NP) in Jaén, Spain. CS□ is the asymptotic length, K is the growth constant, t0 is the theoretical age when CS0 equals zero in the graphic model, CS0 is the initial length at the origin and tmax is the predictor of a maximum age.

Figures

Figure 1 - Download source file (3.37 MB)
Figure 1

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Figure 2

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Figure 4

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Figure 5

Figure 6 - Download source file (176.21 kB)
Figure 6

Supplementary Online Material

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Supplemental Information

Results of Regressing PARTIAL WARP SCORES on Log (CENTROID SIZE) for the indicated datasets using REGRESS8 (Sheets, 2014). Listing starts at highest numbered PWx, then PWy Last two rows are uniform terms, higher warp numbers are higher in bending energy or spatial localization of deformation. Data is the regression slope and intercept, the correlation coefficient r and Z-score is equal to 0.5*ln(1+r/1- r)/(n-3)^0.5 which is based on the regression coefficient r, assuming normally distributed residuals.

Table S1. Results of Regressing PARTIAL WARP SCORES on Log (CENTROID SIZE) for mandibular shape data of individuals from Andújar NP (99 specimens).

Table S2. Results of Regressing PARTIAL WARP SCORES on Log (CENTROID SIZE) for mandibular shape data of individuals from Cazorla NP (79 specimens).

Table S3. Results of Regressing PARTIAL WARP SCORES on Log (CENTROID SIZE) for mandibular shape data of all individuals in the sample (178 specimens).