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Skulls Symmetry of “White Rasquera” Goat

Pere M. Parés-Casanova

Department of Animal Production, University of Lleida, Lleida 25198, Catalunya, Spain

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Abstract: Three common categories of bilateral asymmetry have been described: directional asymmetry, antisymmetry, and FA (fluctuating asymmetry). FA is the most subtle of the three types of asymmetry, and differs from the patterns of the others in that paired structures tend to be symmetric in size. The analysis of FA allows to estimate the influence of stress factors on animal development and enables evaluation of resistance to stress. The aim of this work was to estimate the symmetry of skulls of a contemporary pure goat breed, as there is currently no study of FA as an estimate of individual quality for domestic goats. For this purpose, 11 landmarks were digitized in two dimensions from the crania of 24 adult goats (12 males and 12 females) belonging to the “White Rasquera” breed. The skulls showed nearly perfect bilateral symmetry. The low detected values of FA in skulls revealed a weak influence of developmental stress on this goat contemporary population and its strong ability to compensate stress.

Key words: Craniometry, fluctuating asymmetry, geometric morphometrics, morphological variation, Procrustes superimposition, shape analysis.

1. Introduction

Bilateral symmetry is a pervasive feature of the body plans of most animals, although radial symmetry and other types of symmetry exist as well. Symmetry implies that an organ or part of an organ is repeated in a different orientation or position and, therefore, that the spatial arrangement is strongly patterned and partly redundant. The structure inherent in morphological data from symmetric parts can be used for studies in a variety of biological contexts. An extensive body of work has used FA (fluctuating asymmetry), small differences between corresponding parts on the left and right body sides, to measure the imprecision of developmental systems in response to various stresses and, more contentiously, as an indicator of individual condition [1, 2].

The method of geometric morphometrics combines the powerful and flexible tools of multivariate statistics with explicit consideration of the spatial relations of parts, and therefore makes it possible to investigate morphological variation with direct reference to the anatomical context of the structure under study [3-5]. Previous studies have adapted these methods for the study of left-right asymmetry [6-8].

The topic of symmetry is relevant even for morphometric studies that do not focus directly on asymmetry, because nearly perfect bilateral symmetry of morphological structures can lead to statistical problems if it is not taken into account explicitly [9]. Therefore, the issue of symmetry is of concern for all morphometric studies of bilaterally symmetric structures.

1.1 Object Symmetry

Bilateral symmetry manifests itself in two ways, which can be distinguished as matching symmetry and object symmetry. With matching symmetry, a structure of interest is present in two separate copies as mirror images of one another, one located on either body side. With object symmetry, the structure is symmetric in itself and therefore has an internal line or plane of symmetry, so that its left and right halves are mirror images of each other.

Many parts of biological interest, such as the

Corresponding author: Pere M. Parés-Casanova, DVM, research field: biometry. E-mail: peremiquelp@prodan.udl.cat.

vertebrate skull, have an internal plane of symmetry and thus are bilaterally symmetric in themselves. These structures are instances of object symmetry. In addition to the shapes of parts on the left and right sides, studies of object symmetry also analyse variations of structural features in the median plane and the way the two halves of the body are connected. Real organisms rarely are perfectly symmetric however, and small asymmetries also affect those structural features that lie in the midsagittal plane of the idealized body plan. In other words, the surface containing the median landmarks, sutures, and similar midline structures can bulge locally to the left or right to some extent. Therefore, studies of variation in symmetric structures need to take into account variation in both the median plane and the paired structures on either side of it.

Even if symmetry or asymmetry is not the primary focus of a study, however, the symmetry in morphological structures is still a concern. It can cause statistical problems, for instance ill-conditioned covariance matrices, if all the landmark configurations are very nearly symmetric [9]. If there is exact symmetry, then the positions of the paired landmarks on one body side can be determined from the corresponding landmarks on the other side and those on the median plane. Algebraically, this is a linear dependence among the landmarks and, therefore, the covariance matrix of landmark positions will be singular, which causes difficulties for all statistical procedures that use the inverse or determinant of the dispersion matrix (e.g., canonical variate analysis). Even if symmetry is not perfect, there can still be difficulties because of ill-conditioned covariance matrices. This problem can be circumvented however, by taking the symmetry of the forms into account explicitly and adjusting the analysis accordingly.

1.2 Types of Asymmetries

Three common categories of bilateral asymmetry have been described: DA (directional asymmetry), AS (antisymmetry), and fluctuating asymmetry. These categories are characterized by the properties of a frequency distribution of right minus left values obtained from a sample of individuals collected from a population. Although individual organisms will exhibit deviations from perfect symmetry, their deviations are not described as being either DA, AS or FA, as these terms technically describe population-level patterns of variation [10]. FA is the most subtle of the three types of asymmetry, and differs from the patterns of both DA and AS in that paired structures tend to be symmetric in size. Furthermore, the deviations from perfect symmetry in a sample of individuals follow a normal distribution [10]. These departures from symmetry are assumed to lack a genetic basis, which is supported by empirical tests that have failed to detect any significant heritability of FA. The lack of a heritable basis for observed morphological variation has made FA the most studied of the three types of asymmetry, with many researchers interested in studying the origins and meanings of fluctuating asymmetry. Analysis of FA reveals the influence of stress factors on animal development and the ability of the organism to defend itself against stress. Most studies investigating FA in ungulates have focused on antler or horn asymmetry. FA in some species can be considered an indicator of genetic stress and, indirectly, of male reproductive success.

2. Material and Methods

2.1 Specimens and Data Collection

Twenty-four contemporary skelotonized skulls from adult pure-bred animals (a balanced sample of 12 adult males and 12 adult females, with all teeth erupted) belonging to the “Cabra Blanca de Rasquera” (White Rasquera) were sampled from a private local collection. Care was taken to avoid specimens lacking important parts.

The White Rasquera goat breed is a racial grouping located in the southern part of Catalonia (NE Spain).

This breed shows a strong sexual dimorphism, as well as remarkable morphostructural variability within genders. It has great rusticity and is perfectly adapted to local orographic and weather conditions.

2.2 Morphological Characterization

Skulls were photographed dorsally and on each picture 11 craniofacial landmarks were digitized. The DP (dorsal plane) of each skull was photographed using a standard procedure with a tripod-mounted digital camera. Skulls were photographed once each with the same procedure. The DP is an interesting structure in domestic breed studies as although anatomical landmarks are not numerous, it is the view from which lineal measurements are normally obtained in order to establish cephalic indexes for ethnological classification.

Morphometric analysis must be based on unambiguous and repeatable anatomical landmarks. The chosen landmarks represented different points on the neurocranium and viscerocranium (Fig. 1) and were chosen because of their ease of location on fixed bony points, and moreover to ensure that they were not “masked” by the large horns that characterize this breed. Eleven landmarks were collected for each individual: (1) akrokranion, (2) and (3) ectorbitales, (4) and (5) nuchal points to the facial tuberosities, (6) and (7) facial tuberosities, (8) and (9) premaxillas (widest part), (10) nasion, and (11) prosthion. In addition to being highly reproducible, these landmarks encompass elements of the entire cranium. Two additional landmarks spaced 40 mm apart also were included for scaling.

Shape variables were obtained as linear combinations of the original landmark coordinates after standardizing size and removing artifactual variation due to different positions of the specimens in the process of data collection (generalized Procrustes analysis [11]. Size information was retained as CS (centroid size). The TPS (thin plate spline) algorithm [3] was used to compute the deformation grid with the least bending energy between the reference and target landmark configurations.

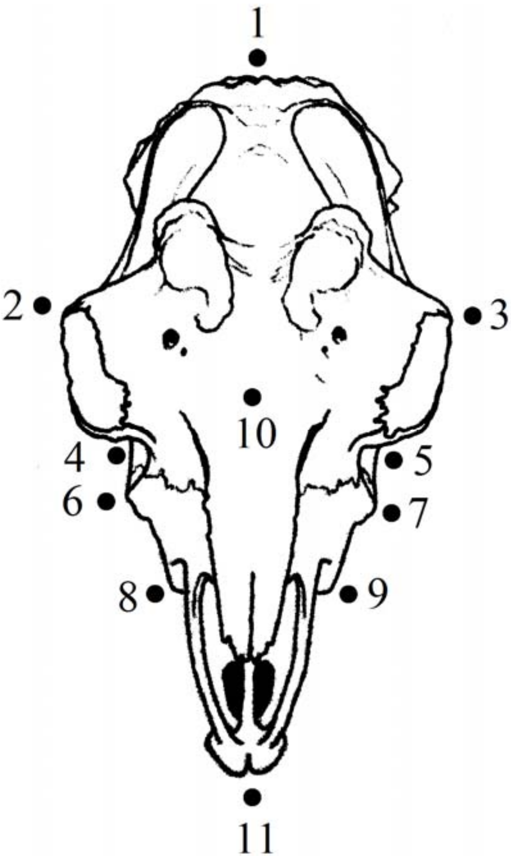


Fig. 1 Used landmarks (numbers correspond to definitions in text). Two additional landmarks spaced 40 mm apart also were included for scaling.

Landmarks were digitized twice using tpsDig 2.04 (F.J. Rohlf, life.bio.sunysb.edu/ee/rohlf/software.html). Landmark positions were converted to scaled x and y coordinates using CoordGen6f (H.D. Sheets, www2.canisius.edu/sheets). The matrices of Procrustes distances from each repetition was high (Mantel test $r = 0.688$).

2.3 Individual Levels of FA

Individual levels of FA were obtained using the “Symmetry and Asymmetry in Geometric Data” (SAGE) program, version 1.0. This software analysed the x- and y-coordinates, using a configuration protocol that divided both sides of the skull by considering the mid-sagittal plain as the axis of symmetry. Our configuration protocol considered 13 paired landmarks to estimate FA level (e.g., 2-28, 3-27; Fig. 1).

A two-way, mixed model ANOVA with two replicates was used. The main effect was “sides”, which had two levels (left and right). The block effect was “individuals”, each skull a random sample from the population. The “sides by individuals interaction” was a mixed effect. Finally, an error term representing measurement error (replications within “sides by individuals”) was included. The result is thus a nonrandomized observational design that incorporates blocking. Shape asymmetry data were analysed using a Procrustes factorial ANOVA with 1,000 permutations.

2.4 Ethics Statement

No specific permits were required for this study as it did not involve either slaughtering any animal nor endangered or protected organic parts.

3. Results

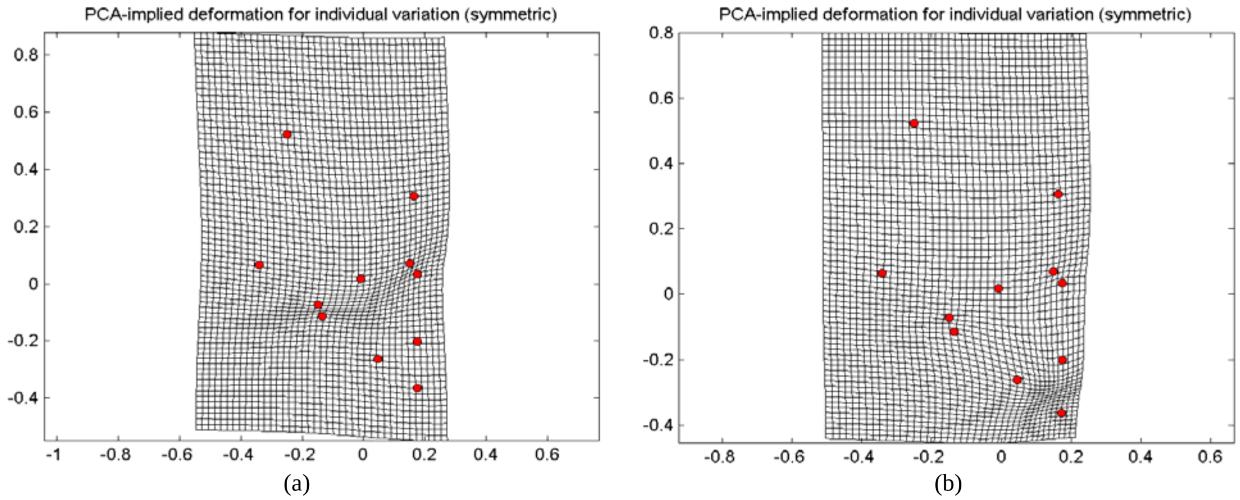
Table 1 shows the ANOVA table with expected mean squares for the mixed-model ANOVA (Table 1). The effect called “individuals” is the variation among individual animals and can be interpreted as a size/shape variation; the “individuals” mean square is a measure of total phenotypic variation and is random. The effect called “sides” is the variation between the two sides; it is a measure of DA. The “individual by sides interaction” is the failure of the effect of individuals to be the same from side to side; it is a measure of FA and AS. It is a mixed effect. The error term is the “measurement error”; it is a random effect. Procrustes ANOVA indicated that asymmetry variations in the samples were due to FA and that no DA existed.

The PCA axis 1 of skull FA is shown as deformation grids (Fig. 2). This axis explained 39.3% of the total variation in FA. Axis 2 explained 31.6% of the total variation in FA.

Table 1 Procrustes two-way, mixed model ANOVA results. The number of sides has been treated as a constant. Expected mean squares have been associated with Model 2.

Source	*SS*	*df*	*MS*	*F*	*P*
Individuals	0.2306	207	0.0011	6.9512	0.001
Sides	0.0079	9	0.0009	5.4724	0.006
Individuals × sides	0.0332	207	0.0002	2.5144	0.001
Measurement error	0.0275	432	0.0001	-	-

Sides: side-directional asymmetry; individual × sides interaction: fluctuating asymmetry. Significance was tested with 1,000 permutations.



(a) (b)

Fig. 2 Deformation grid of skull shape fluctuating asymmetry for PC1 (a) and PC2 (b).

4. Discussion

Asymmetry is a common phenomenon in nature [12] but is a rare phenomenon in mammalian skulls [13]. Few studies, if any, exist on goat skull symmetries. A low level of FA in skulls of “White Rasquera” goats reveals the weak influence of developmental stress on the contemporary population and its strong ability to compensate stress.

Any individual with high FA has probably experienced deficient developmental control, but a relationship between FA and health (not studied in our case) would imply that deficient developmental control has consequences for fitness. This is important, since any phenotypic variation not having consequences for fitness would be of little evolutionary or ecological interest. Obviously, a connection between FA and health does not mean that FA itself is caused by any disease. It could simply mean that an organism, under certain environmental and genetic conditions, experiences deficiencies in both developmental control and control of other functions leading to illness.

5. Conclusion

The low detected level of FA in skulls of “White Rasquera” goats reveals the weak influence of developmental stress on the contemporary population and the strong ability of the breed to compensate it. Nevertheless, the possible effects on individual fitness are still unknown, and further studies are needed.

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