

Mastication in goats shows a chewing side preference

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Abstract

Developmental instability theory suggests that variation in some body parts in part can reflect the ability to buffer development from key environmental and genetic perturbations. Support for this approach comes mainly from assessment of fluctuating asymmetry, or deviations from symmetry of body features that are symmetric at the population level. In order to study dental asymmetry in domestic goats, we sampled 22 adult goat skulls. Bucco-palatine and mesio-distal distances (width and length) of the second molar on each side for each skull, on their occlusal aspect, were measured and compared using standard lineal methods. There was evidence of directional asymmetry, that is, unilateral mastication habits, being the left teeth of the arch slightly but systematically longer than the right. This directional change supported a right chewing side preference in the sample. It is important to highlight that the sample comes from non-pathological specimens. Therefore, it does depict the sample population of animals used in general. The observed asymmetries was not associated with any other cranio-facial abnormalities.

Introduction

Animals body tends to present bilateral symmetric skeletal development, which implies that both right and left sides have the same size and shape [1]. However, this is no more than a tendency, as asymmetry is commonly found and reported in biological literatures both at species, organ, tissue cellular and genetic levels and are not necessarily associated with syndromes, traumas, or pathologies [2].

Developmental stability (DS) is defined as the ability of organisms to withstand genetic or environmental disturbances during their development [3]. As DS reflects the capacity of organisms to produce an optimum phenotype despite perturbations during development, its appraisal can be used to evaluate these stresses [3], which may be environmental or genetic in origin [3]. For the former, a large number of stressor factors -food deprivation, temperature, pollution, and so on- have been shown to contribute significantly to the DI (developmental instability) of organisms [4].

But most of bilateral asymmetries are subtle and go unnoticed on casual clinical appraisal, so they require precise comparisons to be detected [5]. Fluctuating asymmetry (FA) is frequently used to appraise DI [3]. The idea behind this concept is that individuals of low genetic quality cannot control their development precisely, and consequently more often develop different phenotypes on both sides [6]. Low levels of FA are then seen as indicators of overall quality or general health condition of individuals. Asymmetry of an individual is measured as the right minus the left value (L-R) of a bilaterally paired trait (homologous dimensions) [3,7], occurring when the sample distribution of the left-right differences is centered on zero [5]. The small random deviations in FA result in a normal or leptokurtic distribution of asymmetry around a mean of zero [7]. Although subtracting the measurement of the right side of a trait from that of the left side forms the basis of the analysis, accurately quantifying FA is not simple [7]. The measurement of FA is complicated by the distribution of measurement error (that component of the overall variance due to imprecision of measurements)

[7]. Therefore, in order to establish that real differences in symmetry rather than just measurement error are being reported, it is imperative to establish that the measures of FA explain statistically significant proportions of the observed total variance between both sides [7].

FA needs to be distinguished from two other types of asymmetry: directional asymmetry (DA) and antisymmetry (AS) [3,7], two conspicuously other asymmetrical forms in animals [8]. DA occurs when one side of a bilateral character is systematically larger/smaller than the other, so the mean of the (L-R) normal distribution of the population is different from zero [3,5,9]. On the other hand, a typical antisymmetry (AS), which can be considered a macroscopic form of FA, trait leads to a bimodal (L-R) distribution centred on zero [3,9]. A prediction of AS is that the mean value of unsigned residuals from a linear regression of unsigned asymmetry against trait expression is subtle or absent as expression increases [10]. Prior assessment of DA and AS must be done in studies of symmetries, not only for the biological information it provides, but also to estimate if FA is potentially biased [1].

Mammalian molar teeth are designed to function by making species specific contacts with each other on the upper maxillas and lower mandibles [11]. Molars cannot function without such occlusion [11], each tooth aligning precisely with its counterpart on the opposing jaw [11]. In the absence of any asymmetric constraints, tooth wearing on opposing jaws is coordinated, so there were only slight differences in shape between opposing teeth. Asymmetry between bilateral teeth in

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the dental arch in laboratory animals shows increased expression after exposure to external stress during development [12], but in humans, sometimes they are acquired, an example is observed in chewing side preference or trauma. Few documented evidence exists in this regards on domestic mammals. The aim of this investigation was to study bilateral asymmetry in teeth of domestic goats, and concretely of the second upper molars.

Materials and methods

Measurements and statistics

A sample of 22 edentulous Rasquera goat skulls, representing animals of above 10 months of age was studied. Maximal bucco-palatine distance (width) and maximal mesio-distal distance (length) of second upper molar (M²) for each skull, for each side, on occlusal aspect, were measured two times in two temporally separated sessions by the second author by using a digital-readout sliding caliper precise to 0.01 mm.

As distribution of measurements (replicas pooled) appeared as being not-normally distributed for length ($W=0.952, p=0.002$, assessed by a Shapiro-Wilk W test), non-parametric tests were performed for the analysis. Measurement error and differences between sides were analysed by a two-way-model NPMANOVA including all measurements as dependent variables, replica and side as factors, and Gower distances and 9,999 permutations. The error of the method was also determined through intraclass correlation coefficient (ICC) to assess intra-observer reliability. Then, averaged values were obtained, and a Wilcoxon W paired test was used for comparing signed left-right (L-R) matched values. A Kolmogorov-Smirnov D test was used for comparing overall equal distribution of both sides. Finally, a new Wilcoxon W paired test was applied to signed relative differences $\{(L-R)/(L+R)\}$ to know their departure from 0 value.

All statistics were performed using the PAST software [13]. Confidence level was established at 0.05.

Results

With mean squares values clearly below values for sides (Table 1). In other words, measurements for both populations were shown to be highly repeatable indicating a very low influence of error on measurements. Intra-observer ICC was 0.96 for the evaluated measurement, thus reinforcing reliability of two replicas, with an average difference between observations of 0.28 mm. Signed right-left (L-R) side measurements appeared also not statistically significant both for width as for length (Table 1). Average for each measurement and side were obtained (Table 2). Kolmogorov-Smirnov test demonstrated different overall distributions for both measurements ($D=0.454, p=0.013$). They showed (L-R) statistical differences for length ($W=198, p=0.018$) but not for width ($W=170, p=0.163$) in the Wilcoxon W paired test. A new Wilcoxon test for signed relative differences $\{(L-R)/(L+R)\}$ corroborated differences for length ($W=199, p=0.017$) but not for width ($W=169, p=0.176$). Signed relative differences for length presented a positive sign (median of 0.005) (Figure 1).

Discussion

The two sides of the mammalian body are assumed to have similar genetic information [5]. During development many environmental issues may cause FA, such as side differences in times of primary tooth exfoliation and or germination, the position and orientation of the developing successor's tooth buds, differences such as seen in eruptive tempos and pathways, differences in tooth emergence and sequence, positions of antagonists [5]. None of these seem to have any effects on the present investigation since there were no detected FA in M² in goats.

Table 1. Two-way-model NPMANOVA including all measurements as dependent variables, and replica (R) and side (S) as factors, to detect error and differences between sides, for M² length and width (n=22). The between-replicas variation for all teeth was not statistically significant. Right-left side measurements appeared also not statistically significant, either.

Length	Sum of squares	Degrees of freedom	Mean squares	F	P
R	2.52E-05	1	2.52E-05	0.001	0.981
S	0.022338	1	0.022338	0.483	0.500
Interaction	0.000107	1	0.000107	0.002	0.960
Width					
R	0.005891	1	0.005891	0.123	0.734
S	0.007898	1	0.007898	0.164	0.694
Interaction	0.001133	1	0.001133	0.024	0.878

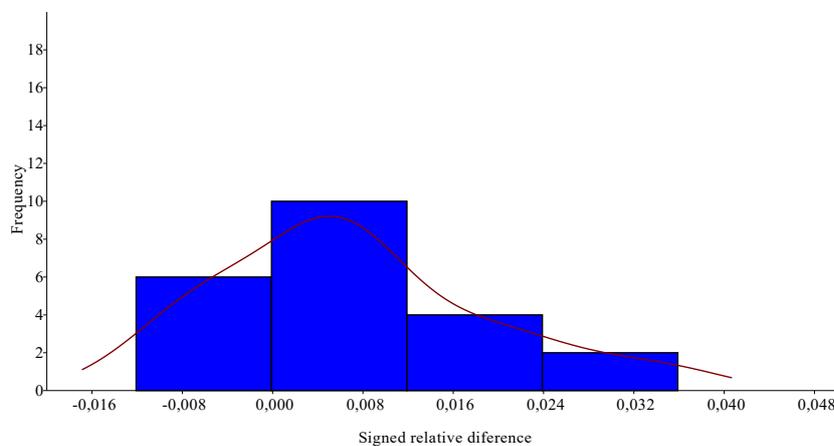


Figure 1. Histogram for signed relative differences $\{(L-R)/(L+R)\}$ of M² lengths (n=22 pairs). Data presented a positive sign (median of 0.005). The asymmetry distribution made for each of the two dimensions demonstrated that the measurements of length explicitly dominates on the left side.

Table 2. Main descriptive statistics for length and width of second upper molar (n=22). Linear measurements in mm. Kolmogorov-Smirnov test demonstrated different overall distributions for both measurements ($D=0.454$, $p=0.013$). They presented (L-R) statistical differences for length ($W=198$, $p=0.018$) but not for width ($W=170$, $p=0.163$) in the Wilcoxon W paired test.

	Length left	Left width	Length right	Width right
Minimal value	12.5	11.0	12.4	10.6
Maximal value	18.9	15.1	19.2	15.3
Mean	15.4	13.0	15.2	13.1
Standard deviation	1.410	0.904	1.474	1.142
Median	15.0	13.0	14.8	13.3
Skewness	0.597	-0.107	0.891	-0.318
Kurtosis	0.472	0.184	0.945	-0.266
Geometric mean	15.3	13.0	15.1	13.0
Coefficient of variation (%)	9.1	6.9	9.6	8.7

This study detected DA in the left M^2 length tending to exceed the right. Detected M^2 asymmetries did not present association with apparent pathologies, denoting a normal rostro-caudal masticatory force different for both sides. The wear process on the surface of teeth is a complex phenomenon that depends on diet type of individuals, captivity [14] and breed variation in the hardness of dental tissues, the ingestion of hard phytoliths (grit) in the diet influence the pattern, force and the direction of the chewing actions. The sizes, shapes, and angles of the opposing occlusal surfaces, and the relationship of cusps and crest patterns to the occlusal motion of cheek teeth contribute to tooth wear mappings [15]. Goats survive on coarse grass, the ingestion of large quantities of coarse foodstuffs containing much abrasive silicates predisposes to dental abrasion due to force demands on the teeth. Side preferences in chewing motion may also be due to innervation differences between both facial segments due to injuries or difficult access to preferred food choice [16]. So, if there are unbalanced attritive (wear) forces due to a chewing side preference, and if animals tend to chew the hard food mostly with their left side and soft food with both left and right [17], teeth wearing will be exacerbated, although not enough to cause pathological disharmonies between masticatory right and left sides.

In conclusion, we think that obtained DA length is explained by a differential masticatory use, that is, unilateral mastication habits, in the believing that molar FA would reflect environmental stress and variability while DA would reflect an asymmetrical biomechanical loading.

It has been suggested that some ungulates are one-sided chewers, a condition that could significantly affect attrition patterns [18,19,20,21], but none have measured bilateral teeth variables on goats, so for comparative purposes, data are inexistent. Moreover, further studies should be conducted to better comprehend the factors that could be related to skeletal asymmetries, as well as to attempt to determine the weight of genetics as an etiological factor of such alterations.

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