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HORN ANTISYMMETRY IN A LOCAL GOAT POPULATION

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ABSTRACT

Fluctuating asymmetry (FA) refers to small random deviations from perfect bilateral symmetry. Directional asymmetry (DA) is defined as population-level deviations from bilateral symmetry that are unimodal and significantly different from symmetry. Lastly, antisymmetry (AS) is a pattern of bilateral variation in which differences exist between sides, but the side that is larger varies randomly among individuals. FA reflects the ability of individuals to undergo stable development, so it may provide a potential measure of individual quality. FA is not likely to be adaptive but both DA and AS are developmentally controlled and are therefore likely to have adaptive significance. Twenty-seven adult females belonging to the Catalan goat population (NE Spain) were studied to assess horn perfect symmetries (in total length and base circumference) as indicators of their fitness. Symmetry was tested by means of Wilcoxon signed test and dispersion values. Platykurtic distributions and plotting the cumulative frequency was used to assess DA and AS. For horn length, but not for horn circumference, AS was revealed. Although AS has been considered to be developmentally controlled and possibly adaptive, the specific processes producing this pattern in Catalan goat horn remain a matter of discussion.

Keywords: Capra hircus; Catalan goat; directional asymmetry; fluctuant asymmetry; laterality.

1. INTRODUCTION

Horn size signals individual quality (von Hardenberg *et al*., 2007) and reflects the environmental conditions experienced both during early development (Côté *et al*., 1998; Toïgo *et al*., 1999) and throughout an animal's entire life, especially in species where substantial horn growth continues throughout life, such as goats. Horn growth is sensitive to changes in population density (Jorgenson *et al*., 1998), weather (Pérez-Barbería *et al*., 1996; Giacometti *et al*., 2002) and resource availability (Festa-Bianchet *et al*., 2004; Festa-Bianchet and Côté, 2008), as well as horn and antler size being heritable and genetically correlated with fitness-related traits in both sexes (Kruuk *et al*., 2002; Coltman *et al*., 2005). Males with greater horn growth obtain high-quality resources, are more resistant to parasites (Luzón *et al*., 2008) and have better sperm quality (Santiago-Moreno *et al*., 2007). All these facts explain why horn size in mountain ungulates has important and diverse implications for conservation biology and evolution (Coltman *et al*., 2002; Singer and Zeigenfuss, 2002), although not much work has been done in domestic ungulates.

Deviations from perfect symmetry may be measured as variances (or related measures of dispersion) of linear dimensions, shape variation involving landmarks, or continuous symmetry measures (Graham *et al*., 2010). The distribution of trait asymmetry may represent contributions from fluctuating asymmetry (FA), directional asymmetry (DA) and antisymmetry (AS) (Graham *et al*., 1998). The classic measure of FA is the variance (or standard deviation) of the difference

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between the values of a trait on the left and right sides. If $d_i = l_i - r_i$, where d_i is the *signed* left–right asymmetry of individual *i*, l_i is the value of the trait on the left side, and r_i is the value of the same trait on the right side, then a measure of FA is $Var(d_i)$ or its square root (standard deviation) (Graham *et al*., 2010). Ordinarily, FA is symmetrically distributed about a mean of zero, and in perfectly symmetrical objects, the traits will be mirror images of one another. DA is characterized by a symmetry distribution that is not centred around zero but is biased significantly towards larger traits on either the left or the right side. Finally, AS is characterized by having either a platykurtic or a bimodal distribution about a mean of zero (Graham *et al*., 2010). FA is not likely to be adaptive as symmetry is expected to be the ideal state (van Valen, 1962; Palmer, 1994; Gangestad and Thornhill, 1999) but it can provide useful information about individual quality (Cuervo *et al*., 2011). Both DA and AS are developmentally controlled and are therefore likely to have adaptive significance, although a number of cases clearly suggest that both DA an AS may reflect poor developmental conditions (Møller, 1998).

In this research, we studied the horn symmetry in a local goat breed, named "Cabra Catalana" (Catalan Goat), in the only herd that remains of this ancient population. This population had occupied Catalunya (NE Spain) until the mid 20^{th} century, and was well adapted to harsh interior Mediterranean areas in the Catalan Pre-Pyrenees region. The breed is medium-sized, has a slender neck and sloping rump, is relatively long-legged and short-haired with characteristic long hair on the upper thigh, and has a haired udder. Both sexes have horns, typically sharply backwards ("aegagrus" type), although some have corkscrew-shaped horns, curving back and out ("prisca" type). The breed is clearly different from other Catalan neighbouring breeds, e.g. Pyrenean and White de Rasquera. Some years ago, a group of volunteers from "Cultures Trobades" ("Slow Food Terres de Lleida") made an effort to gather the last individuals, and relocated them to a safer place under better management, starting a program to preserve them. Only two pure males remain, and they were excluded from this study.

The purpose of this study is not only a study of horn symmetries as indicators of fitness but also to increase the literature of these animals in order to strength its future recognition as an official breed.

2. MATERIAL AND METHODS

2.1. Studied animals

Twenty-seven adult females with good body condition, belonging to the Catalan goat population, were studied. All of them belonged to the same – and, at the moment, only – herd that holds this kind of animal, in the village of Vilanova de Meià (630 m altitude, lat. 41.9º and long. 1.03º).

2.2 Studied parameters

Information collected was total horn chord length (not arch length) and basal circumference. Both traits were measured on both sides using a flexible ruler. The same researcher (Irina Kucherova) always measured each animal once and, therefore, we cannot estimate the error in horn measurements.

Although seemingly simple, in practice the study of bilateral variation as a measure of developmental noise has been laden with methodological concerns. This is due in part to the diversity of procedures that have been used to analyse asymmetry data, which sometimes obscured the meaning of results and made comparisons among studies nearly impossible. Normality was assessed according to Shapiro and Wilk (1965). We tested the type of horn asymmetry by means of the distribution plots. FA is modelled as a normal distribution centred at 0, whereas DA has a normal distribution with a non-zero mean, and AS has two normal distributions that are identical except that they have non-zero means of opposite sign. For some authors (e.g. Palmer and Strobeck, 1986) FA was assessed by determining whether signed right-minus-left character values did not deviate significantly from normal frequency distributions with a mean of zero. We assessed it with the non-parametric Wilcoxon signed rank test. As $n<26$, an exact *p* value was computed, by complete enumeration of all possible reassignments. Empirically, as a graphical method to assess bimodality (and thus AS), we plotted the cumulative frequency against the subtracted mean of the differences. In a bimodal distribution, this graph consists of two reasonably straight lines.

Skewness and kurtosis were also obtained. A zero value indicates that the tails on both sides of the

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mean balance out, which is the case both for a symmetric distribution and for asymmetric distributions in which one tail is long but thin and the other is short but fat. Positive skew indicates that the tail on the right side is longer or fatter than the left side. In a similar way to the concept of skewness, kurtosis is a descriptor of the shape of a probability distribution. A high kurtosis distribution has a sharper peak and longer, fatter tails, while a low kurtosis distribution has a more rounded peak and shorter, thinner tails. The relationships between horn asymmetry and horn measures were determined using Spearman correlation analysis.

2.3. Statistical analyses

All procedures were done using the PAST software (Hammer *et al.*, 2001).

3. RESULTS

There was no variation in horn differences with increasing length or circumference ($p<0.05$). For both traits, the geometric mean was 0 (Table 1). For horn length differences, a clear, low peak with a negative value (platykurtic) distribution appeared. Frequency distributions of signed right-minus-left character values for horn length did not deviate significantly from normal distributions (Table 1) but horn circumference differed significantly ($W=0.837$, $p<<0.01$) (Figure 1). Wilcoxon signed rank test showed statistically significant differences in right-left values for horn length but not for horn circumference (Table 2). So, if horn length did not deviate significantly from normal frequency distributions, asymmetries can be suspected, as Wilcoxon demonstrated differences between sides (differences in right-left sides) and as there is a low kurtosis value, a bimodal distribution can be suspected. If, finally, we plot the cumulative frequency against the subtracted mean of the differences (Figure 2), the distribution gives two different straight-line plots. So, for horn length antisymmetry was revealed.

4. DISCUSSION

Non-adaptive departure from bilateral symmetry may reveal how well development is buffered against environmental influences that could perturb growth. More symmetrical individuals may have greater mating success, possess greater resistance to stress and parasites, and be capable of greater feats of physical performance. Heterozygosity, inbreeding or environmental stress have all been hypothesized to affect development stability (see Palmer, 1996, for a review). Skeletal asymmetry is related to both exogenous (e.g. mechanical) and endogenous (e.g. genetic) factors (Auerbach and Ruff, 2006). Although a great many studies of subtle bilateral variation have revealed FA, it has not been shown in the Catalan breed, and the detected AS is not supposed to indicate "phenodeviants" (Møller, 1998), but probably the reflection of poor developmental conditions for animals (as said in the introduction, they were rescued from different scattered herds, where it can be supposed that they were not always subject to the best management).

As annual horn growth is driven by a complex interaction of age, energetic demands, genetic variation and habitat quality (Festa-Bianchet *et al*., 2004), the presence of horn symmetry in the Catalan goat population may indicate a good individual quality. However, surprisingly, subtle AS appears. The value of this alternative pattern of bilateral variation as measures of developmental precision remains open to debate (as stated by Graham *et al*., 1993, in general). It has been described that animals in the subfamily Caprinae can both break the tips of their horns and also wear them down over time (Brandborg 1955; Schaller 1977). We believe horn wear did not bias our results because we did not include animals with broomed or broken horns. Moreover, assuming tip wear is constant over time, we found no differences in the lengths of goats sampled. The authors are aware that FA measures are especially sensitive to measurement error because the magnitude of FA is usually small (often 1-5% of the total variation in a given trait) and is random by definition.

Future genetic studies that are ongoing will help to give more information and this will be taken into account for future reproductive schemas. New research on individuals born in the "rescued herd" and fully grown animals will indicate if the level of AS corresponds to poor development conditions or a mere adaptive state. Evidently, studies of males are also needed. Finally, we would like to emphasize that measures of developmental stability under field conditions may provide important and readily accessible information on the well-being of domestic organisms.

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Table 1. Summary statistics of signed right-minus-left character values (length and circumference) of horns of the Catalan goat breed (females, n=27). Lineal measurements are in centimetres. Horn length demonstrated that frequency distributions of signed right-minus-left character values did not deviate significantly from normal distributions but horn circumference did, although for both traits geometric mean was 0.

	Horn length	Horn circumference
Average value	1.51 (0.297)	0.09 (0.08)
Skewness	0.240	0.560
Kurtosis	-0.694	2.980
Shapiro-Wilk	0.954	0.837
P (normal)	0.269	<<0.01
Geometric mean	0	0

Average (SE)

Table 2. Wilcoxon signed rank test of values (length and circumference) of horns of the Catalan goat breed (females, n=27). There appeared statistically significant differences in right-left values for horn length but not for horn circumference.

	Horn length	Horn circumference
Wilcoxon signed rank	261.5	50.5
P (normal)	<<0.01	0.425

Figure 1. Histogram for right-left differences of horn circumference of the Catalan goat breed (females, n=27), which were not significantly different between sides.

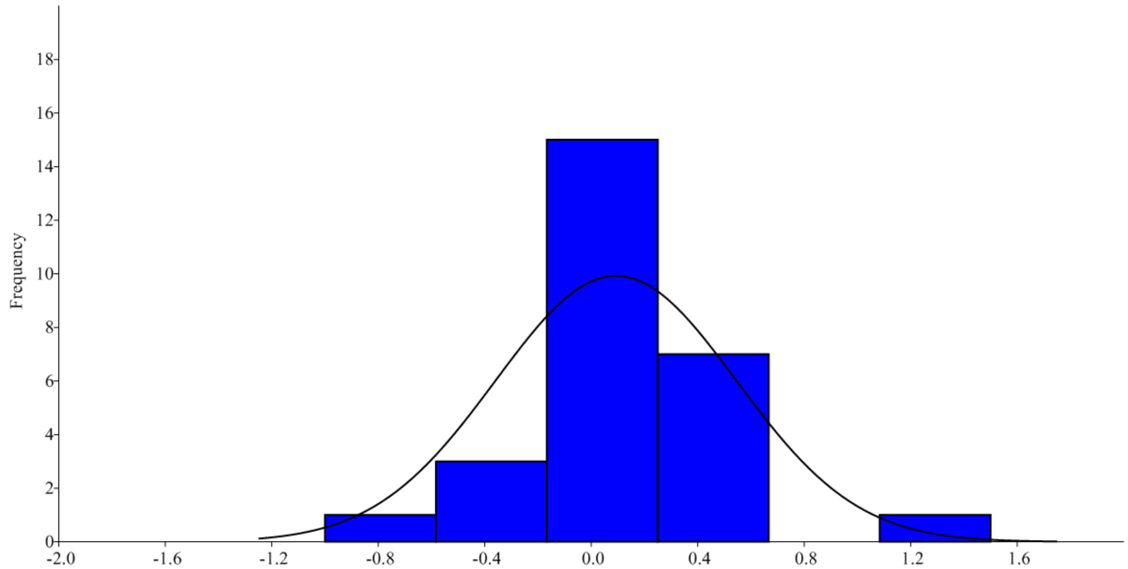

Figure 2. Cumulative frequency against the subtracted mean of the differences in right-left lengths. It shows two different straight-line plots and the inflection point is the change of modal distributions.