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## Discrete sexual size dimorphism in domestic sheep

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### ABSTRACT

Rensch's rule describes the pattern of sexual size dimorphism, claiming that in taxa where males are the larger sex, they exhibit higher body size ratios. Domesticated animals offer excellent opportunities for testing predictions of functional explanations of Rensch's theory. In this study, we tested the hypothesis that the morphological size of sheep breeds follows Rensch's rule. We have analysed data in the literature on adult body size (live weight and withers height) of males and females in 74 sheep breeds. The analysis confirms that the pattern of sexual size dimorphism conforms discretely to Rensch's rule among sheep breeds, with all breeds appearing to be dimorphic. We propose that this is due to the fact that rams and ewes have been subjected to different selection regimes, with a higher selective pressure on rams.

**Keywords:** body mass, differentiation of breed, domestication, *Ovinae*, sexual selection

### INTRODUCTION

There is an extraordinary ability of domestic species to radiate into numerous morphologically and behaviourally distinct breeds within a few generations. Nowadays, worldwide there are hundreds of genetically related but morphologically differentiated sheep breeds that may differ in size and shape even more than distinct species or even genera of wild *Ovis* ungulates. Differences in size are very apparent among sheep breeds, ranging from about 22 kilograms in the West African Dwarf to about 130 kilograms in the Mutton Merino, although domestic sheep (*Ovis aries*) is mammalian species with low morphologic variability, in comparison with other species such dog and horse. As a morphological character, sexual differences are a common phenomenon (for a review, see [1]), the most conspicuous aspect of which is body size. Of several evolutionary hypotheses proposed to explain the origin and maintenance of sexual size dimorphism (SSD), the most widely accepted one is based on the theory of sexual selection [2]. The direction of these differences, whether males or females are larger, varies from one group to another.

SSD has important consequences for ecology, behaviour, population dynamics, and evolution. Rensch's rule describes the pattern of SSD, claiming that in taxa where males are the larger sex, larger species generally exhibit higher male-to-female body size ratios [3, 4]. In recent years, this rule has attracted considerable research effort, and conforming patterns have been reported by interspecific comparisons in various animal taxa, especially or exclusively in taxa exhibiting SSD with larger males [5]. Although well documented across diverse animals, this rule is by no means universal and is particularly lacking in taxa with females that are larger than males.

The aim of this study was to examine the allometry of SSD and to test Rensch's rule among domestic sheep breeds. We expected that if sexual selection had the primary role in generating Rensch's rule under natural conditions, the allometry of SSD consistent with Rensch's rule would be absent in sheep breeds if the artificial selection had not been solely sexual. This expectation was based on two lines of argument. Firstly, heifers have been selected for desired traits that are often unrelated to sexual selection, for instance, meat quality and wool production. Therefore, sexual selection is expected to be weak in domestic stocks, at least in traditional extensive sheep farming systems.

Secondly, artificial selection is unlikely to mimic sexually antagonistic selection, a suspected driver of Rensch's rule in wild populations, because humans are using directional selection to obtain the desired traits, such as increased milk or meat production. Therefore, the non-targeted sex is allowed to track changes in the targeted sex.

## MATERIALS AND METHODS

We collected data on 74 sheep breeds and ecotypes/varieties for withers height and live weight. Adult male and female withers height and live weight were extracted from different published articles but standards were avoided as they provide a prototype ('the idealised form that serves as the selective type') rather than a typical morphotype ('the real existing form'). Moreover, it could not be excluded that the breed standard could sometimes oversimplification, and they did not adhere rigorously to morphological variation for all animals. Table 1 presents the studied breeds and ecotypes/varieties. The withers height was selected as a body measurement because: (1) it does not depend on body condition; and (2) this measurement appeared to correlate well with live weight. Where the information provided ranges instead of mean values, we used average values.

The SSD was expressed as an adapted Lovich-Gibbons ratio [6], calculated as follows: we divided the mass of the heavier sex by the mass of the lighter sex, and subtracted one and made the resulting figure high for breeds in which the males were the larger sex, whereas it let it is clearly lower or negative in breeds where the females were the larger sex. SSD is a convenient and readily interpretable measure of sexual dimorphism [7]; for instance, a value of 0.5 indicates that the males are 50% or 1.5 times larger than the females, whereas a zero value indicates monomorphism. This ratio assures both linearity and proportional symmetry of the SSD index (for details, see [8]. Effectively, the distribution of SSD did not significantly depart from normality ( $W=0.976$ ,  $p=0.175$ , Figure 1). The significance of SSD was tested by t-tests and two-way non-parametric multivariate analysis of variance (NPMANOVA), with sex and breed as factors. Relationships between SSD and withers height were tested by non-parametric or parametric correlations between the Lovich-Gibbons ratios and means of their naturally log<sub>10</sub>-transformed expressions.

To test for Rensch's rule, we fitted the reduced major axis regression (RMA) model of log<sub>10</sub> male live weight against log<sub>10</sub> female live weight, which accounts for error in both dependent and independent variables [9]. Agreement with Rensch's rule is manifested by the slope of the allometric relationship between male and female body size exceeding one [10]. We tested the deviation of the slope from isometry (i.e., slope=1) using the one-way analysis of covariance (ANCOVA) test. Deviations from an isometric relationship were considered significant when the expected isometric slope (1.0) fell outside the 95% confidence interval (CI) of the estimated slope. The calculations were performed using the PAST package [11].

## RESULTS AND DISCUSSION

Globally, differences between the sexes were statistically significant both for live weight ( $p<0.0001$ ) and for withers height ( $p<0.0001$ ) (Figure 2). The Lovich-Gibbons ratios ranged from 0.994 to 1.308 (mean=1.103, median=1.089), with the male being larger in all breeds except the West African Dwarf, Andalusian, and Castellana (Lovich-Gibbons ratios ranged from 0.015 to 0.055). No breed appeared to be monomorphic (i.e., SSD=0). No difference appeared when comparing each breed according to their productive purpose (meat, milk, or wool). SSD did not correlate with male in withers height ( $r^2=0.008$ ;  $p=0.444$ , 95% CI 0.597–2.312, Figure 3) but for females, the correlation was significant ( $r^2=0.183$ ;  $p<0.001$ , Figure 4), although their CI of the slope of Reduced Major Axis (RAM) (95% CI 0.497–0.794) did not include 1. One may argue that extreme SSD indicates intense sexual selection. Indeed, restricting the analyses to SSD=1 (1.0 to 1.09) produced a non-significant relationship for females. A clear linear relationship was found between the log-transformed male live weight against the log-transformed female live weight (Figure 5), with a RMA slope of the line of 0.911 (95% CI 0.839–0.968), significantly under the slope of 1.0 expected under isometry ( $F=16.26$ ,  $p<0.001$ ).

The pattern obtained in this study is not consistent with Rensch's rule, although all breeds appear to be dimorphic. The SSD pattern was found to be consistent with Rensch's rule by other authors [4]. Variance in SSD could be explained by greater changes in body size in males than in females.

Table 1. The studied breeds, ecotypes, and varieties

Abergelle (2 ecotypes)	Churra	Kengui	Romanov	Xisqueta
Andalusian	Coburg Fox	Latxa	Roussillon Red	Yankasa
Apennine	East Friesland Milk	Leine	Santa Ines	Zwartbles
Aragonesa	Finnish	Lourdaise	Scottish Blackface	
Aranesa	Flemish	Manchega	Segureña	
Bellay	Forest	Mandya	Skudde	
Bentheim	Gallega	Spanish Merino (3 varieties)	Soay	
Black Milk	Ganjam	Merino Land	Suffolk	
Black-brown Mountain	Garut	Moor	Texel	
Black-headed Mutton	Gotland	Morada Nova	Tyrolean Stone	
Blue de Maine	Grey Horned Heath	Mutton Merino	Valais Black-nosed	
Brown Mountain	Hampshire	Pelibuey Bahamas	West African Dwarf	
Brown-headed Mutton	Hassan	Pelibuey Tabasco	West African Dwarf from Abia State	
Cakiel	Hu-Yang	Pomeranian	White Alpine	
Carinthian Spectacled	Jacob	Racka	White Horned Heath	
Castellana	Kalarritiko	Rampur Bushair	White Mountain	
Charollais	Karakul	Rhön	White-headed Mutton	

Figure 1. Frequency distribution of sexual size dimorphism as measured by Sexual Size Dimorphism (SSD, see Materials and Methods for explanation) in domestic sheep (74 breeds). The distribution of SSD did not significantly depart from normality (W=0.976, p=0.175)

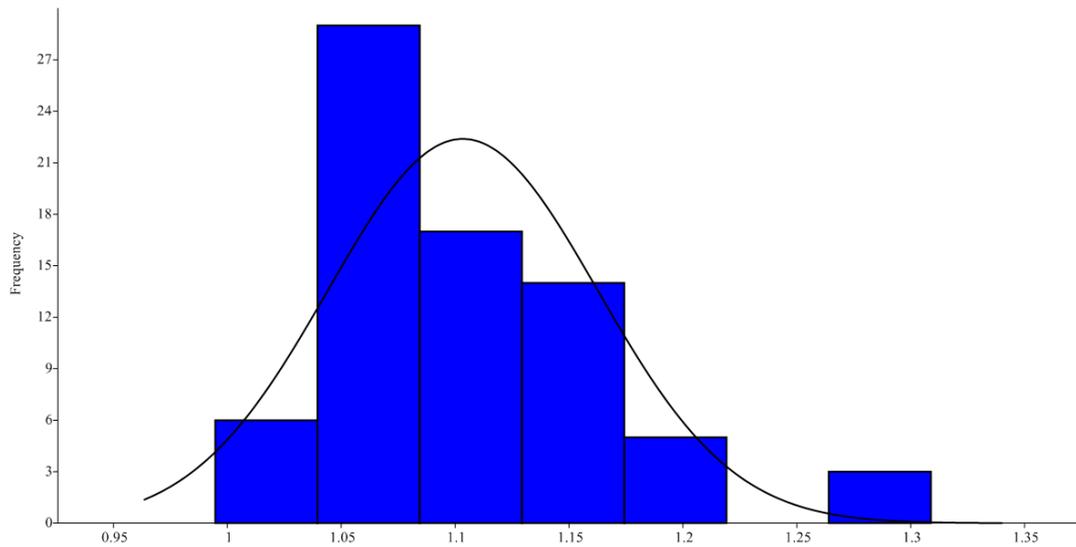
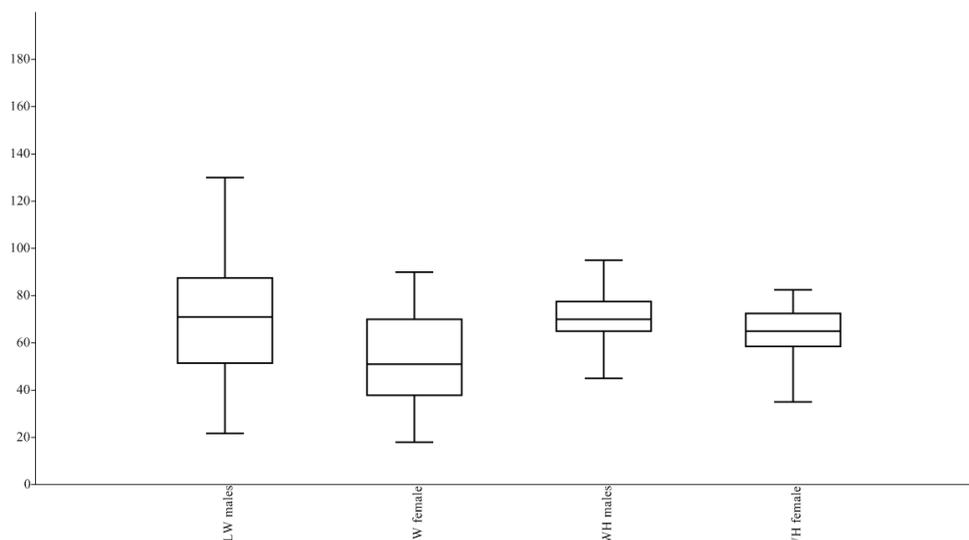
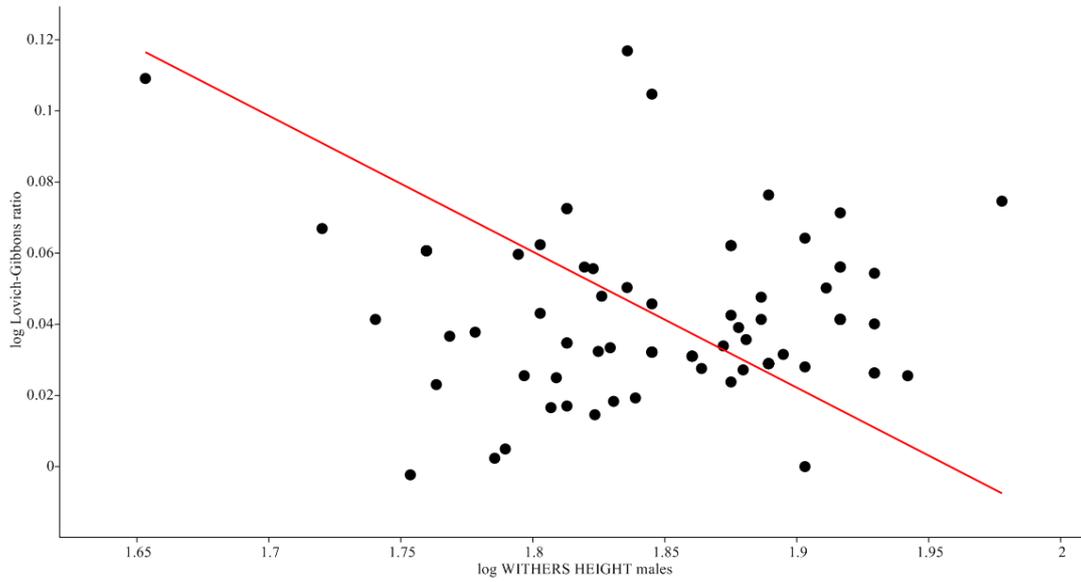


Figure 2. Median values for live weight and withers height for males and females. Differences between the sexes were statistically significant both for live weight (p<0.0001) and withers height (p<0.0001)



**Figure 3.** Sexual size dimorphism (SSD) (defined here as log Lovich-Gibbons ratio, see Materials and Methods for explanation) against log (withers height) for sheep breeds (males). SSD did not correlate with males in log withers height ( $r^2 = 0.008$ ;  $p=0.444$ )



**Figure 4.** Sexual size dimorphism (SSD) (defined here as log Lovich-Gibbons ratio) against log (withers height) for sheep breeds (females). SSD correlates with females in log withers height ( $r^2 = 0.183$ ;  $p < 0.001$ )

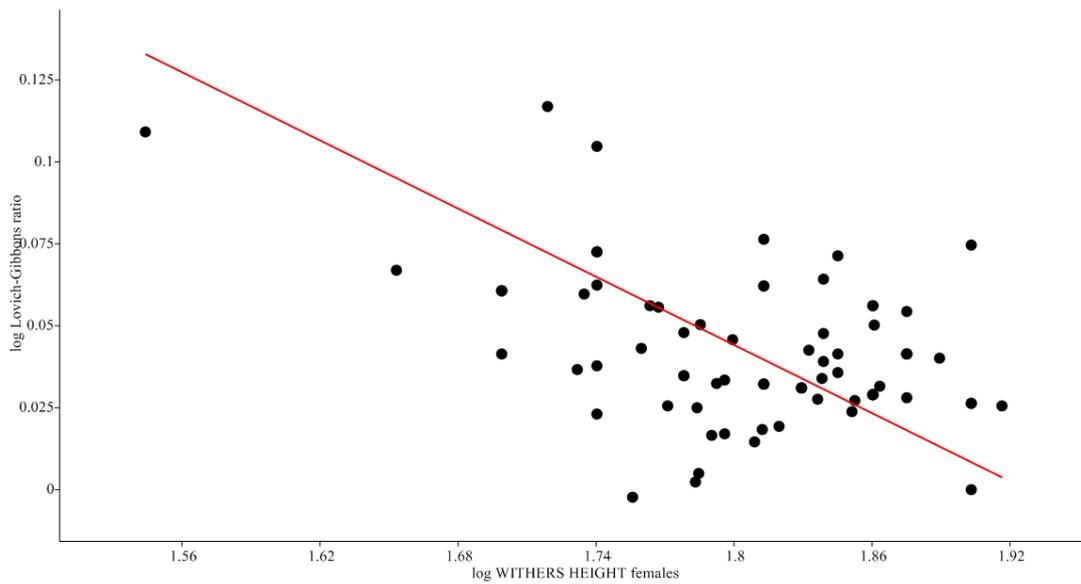
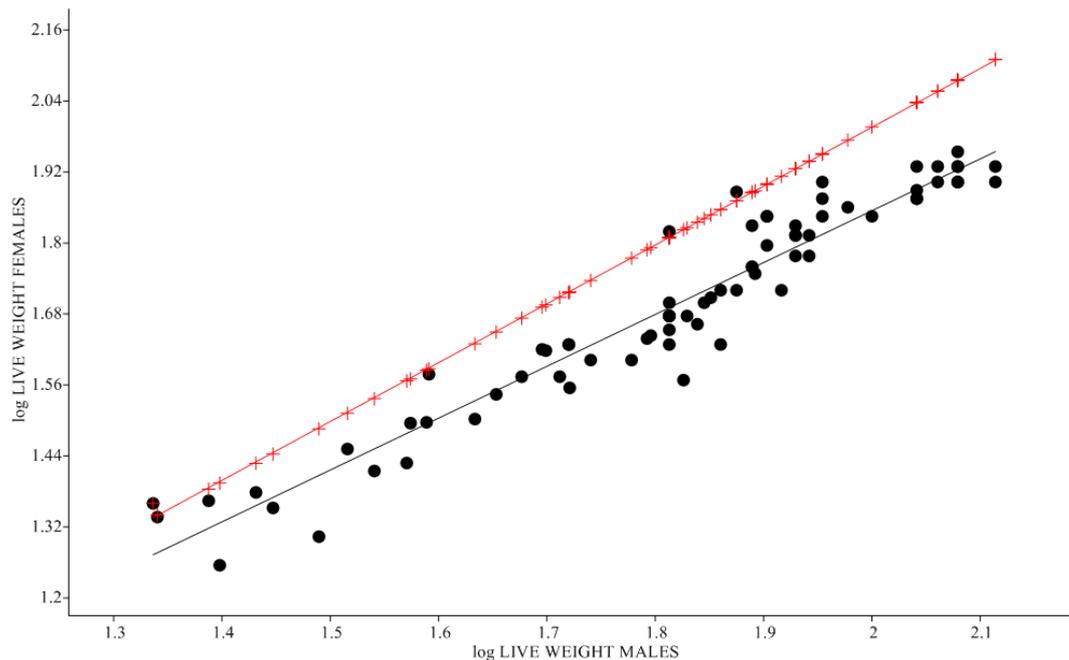


Figure 5. Relationship between mean male and female withers heights among the 74 domestic sheep breeds studied. Each point represents a breed. The data are naturally log-transformed. The slope of the fitted line is 0.911 (95% confidence interval 0.839 to 0.968), significantly under the slope of 1.0 expected under isometry ( $F=16.26$ ,  $p<0.001$ ). The crossed upper line indicates the estimated isometric scaling of Sexual Size Dimorphism with live weight



On the other hand, the hypothesis by Polák and Frynta [4], that breeds of sheep from the tropics tend to be sexually less dimorphic than breeds living in temperate regions, was not demonstrated here. For instance, Pelibuey Tabasco, a Cuban breed, presented a SSD of 1.040, close to Romanov, the prolific well-known Russian breed; and Yankasa, from Nigeria, and Blue de Maine, from France, presented both the same SSD (1.060). No correlation of the Lovich-Gibbons ratio with aptitude (milk or meat) or origin was found either (results not shown here).

## CONCLUSION

The sexual selection hypothesis is considered as a general explanation for SSD, whereby intense sexual selection drives the evolution of body size of the selected sex, usually the males [12, 13, 14], with weaker correlated selection on body size in the other sex. Although no data quantifying and comparing the strength of sexual selection in sheep are available, the relaxation of sexual selection in domestic forms can be reasonably expected. Artificial breeding of ancient and contemporary breeds implies different kinds of pressures than sexual selection occurring under natural conditions and, therefore, it has different consequences on body size and thus on the magnitude of SSD. We propose three reasons for the reduced SSD in domestic sheep breeds. First, male-male competition is usually relaxed in captivity. Thus, selection on strong, heavy rams is much reduced. Assuming that the size is primarily controlled by loci without a sex-biased expression pattern, the genetic correlation between male and female body size should quickly eliminate the size difference caused by the higher selection pressure on a single sex. The use of directional selection to achieve desired characteristics in the targeted sex allows for a phenotypic response in the other sex. This response is likely to be in the same direction in a homologous trait (e.g., body mass) as in the targeted sex because of high genetic correlations between the sexes. Second, sex-specific or sexually antagonistic selection might be relaxed or lacking in captivity. Under an artificial environment, males and females are exposed to natural and sexual selections of lesser strengths, resulting in different net selection. Third, shepherds probably have not always selected only for body size but for other morphological or behavioural characteristics, related to the product (wool, milk and/or lamb production).

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