

Sexual Size Dimorphism in Swine Denies Rensch's Rule

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ABSTRACT—Sexual dimorphism, defined as a phenotypic difference between males and females of a species, is a common phenomenon in animals. Rensch's rule describes the pattern of sexual size dimorphism, claiming that larger species generally exhibit higher male to female body size ratios. Offering domesticated animals excellent opportunities for testing predictions of functional explanations of Rensch's theory, we have tested in this paper whether the morphological size of domestic pig breeds follows this rule. We analysed the literature data on adult body size (live weight and withers height) of males and females in 130 contemporary domestic swine breeds and 4 wild *Sus* species. The analysis confirmed that the pattern of sexual size dimorphism in domestic swine does not conform to Rensch's rule. It is proposed that this is due to the fact that males and females have been subjected not solely to a sexual selection regimen, but also to environmental factors, interspecific competition with other domestic species, an increase of intersexual food competition, poor feeding resources, and reproductive functional constraints. Considering all of the breeds studied, it is also likely that different counteracting selective pressures exist worldwide.

Keywords— body mass, differentiation of breed, domestication, sexual selection, *Suidae*

1. INTRODUCTION

There is an extraordinary ability of domestic species to radiate into numerous morphologically and behaviourally distinct breeds within a few generations (see [3]). Nowadays, all over the world, there are hundreds of morphologically differentiated swine breeds that differ in size and shape; differences in size are currently very apparent, ranging from about 20 kilograms in the Bampudke (the smallest hog breed in the world, from Nepal) to about 350 kilograms in the well-known Large White, Mangalitza and Duroc breeds, as well as in the German Schwäbisch-Hall and Angeln Saddleback breeds.

As a morphological character, sexual differences is a common phenomenon (for a review see [2]), with body size being a conspicuous aspect. Sexual size dimorphism (SSD), defined as a phenotypic difference between males and females of a species, is a common phenomenon in animals. Of several evolutionary hypotheses proposed to explain the origin and maintenance of SSD, the most widely accepted one is based upon the theory of sexual selection [7]. The direction of these differences, i.e. 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 [20, 21] describes the pattern of SSD, claiming that larger species generally exhibit higher male to female body size ratios [1, 10]. 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 larger male SSD [10]. 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 (see [19] for an interesting review). It is of particular interest that Rensch's rule is not applicable to even-toed ungulates (Artiodactyla), which is a group exhibiting both great variation in body size and considerable SSD [15]. Nevertheless, artiodactyls are a heterogeneous group and thus the relationship between SSD and body size may be masked by great variation in mating systems and life histories among particular clades [8]. In contrast to previous studies of SSD in artiodactyls, in the present study we performed a particular analysis of a smaller and thus more homogenous model group. We not only considerably improved taxonomic sampling but, for the first time, we also included domestic breeds to test the generality of the results. Domestic breeds provide a unique opportunity to assess within-species allometries when sexual selection favouring large male body size under natural conditions is relaxed as a result of the domestication process [16, 17]. We focused on a single family, *Suidae*, which is a biphyletic group.

In fact, the domestication process involved the Eurasian Wild Pig (*Sus scrofa*), but also Sulawesi Warty Pig (*Sus celebensis*), which is the only other successfully domesticated species of pig [26]. There is evidence that local wild pigs were independently domesticated in Europe, Asia Minor, the Far East (including Japan) and various parts of South-east Asia [26]. Mitochondrial DNA studies of the dispersion of these domesticated forms agree on three major dispersal events, two involving *S. scrofa* and one involving *S. celebensis* [26]. Evidence supports an early human-mediated

translocation of *S. celebensis* to Flores and Timor and two later, separate human-mediated dispersals of domestic pig through the islands of SE Asia into Oceania [26]. It is well documented that Asian pigs were used to improve European pig breeds during the 18th and early 19th centuries [6, 12], but to what extent Asian pigs have contributed genetically to different European pig breeds is unknown. In a recent study, the divergence between major European breeds and the Chinese Meishan breed was estimated at ~2000 years using microsatellite markers [14]. Genetics indicate that, although many of today's pigs are related to the European wild boar, they are also related to the *Sus scrofa* of the Near East. Thus, in addition to the wild *Sus* species, there are hundreds of domestic breeds.

Through domestication, humans manipulate animal genomes to enhance desirable traits [4]. These processes can produce rapid changes, and domestic species often differ markedly from their wild progenitors, both physically and behaviourally. SSD can demonstrate that larger species tend to exhibit higher ratios of male to female body size than smaller species. The aim of this paper is to examine the allometry of SSD and to test Rensch's rule among domestic swine breeds. We expected that if the artificial selection was not solely sexual, the allometry of SSD consistent with Rensch's rule would be decreased in swine breeds. This lack of relationship would be consistent with the hypothesis that the evolution of female body size is equally constrained compared to that of male size [9]. Agreement with Rensch's rule is manifested by the slope of the allometric relationship between male and female body size exceeding one [16,17].

2. MATERIALS AND METHODS

We collected data on 130 domestic swine breeds (including some topotypes and varieties), and 4 wild *Sus* species (*Sus barbatus*, *S. cebifrons*, *S. scrofa* -Romania, Spain, Sri Lanka and Pakistan populations- and *S. verrocosus*). Contemporary breeds were from different geographical origins. We collected data (withers height and live weight for adult males and females) from the literature, mainly from [22] and the FAO-DAD IS database (<http://dad.fao.org/>). Data for wild species were extracted mainly from [26]. Unfortunately, the authors did not find data for the Sulawesi Warty Pig (*Sus celebensis*), so no comparison with this ancestral trunk has been possible. Withers height was selected as a measure of body size for two reasons. First, body mass was available for more breed descriptions than body length or cephalic length. Second, there is normally a close relationship between withers height and the remaining linear body measurements or measurements of the skeleton.

It cannot be excluded that the breed descriptions can sometimes reflect oversimplification, and they do not rigorously adhere to morphological variation for all animals. It may also be somehow underestimated when "natural" breeds live in poor conditions. Therefore, data must be interpreted as a whole, in a general view, rather than from a specific breed point of view. The withers height was selected as a body measurement because (1) it does not depend on body condition, and (2) this measurement appeared to be closely correlated to live weight ($r_s=0.878$, $P<<0.001$, for domestic breeds). When the information provided was in ranges instead of means, we used average values.

To express SSD, it was decided to employ Lovich-Gibbons revised two-step ratio [13]:

- (1) if $M \geq F$, dimorphism = M/F
- (2) if $F \geq M$, dimorphism = $2 - F/M$

where M and F are the measures of male and female live weight, respectively.

SSD is a convenient and readily interpretable measure of sexual dimorphism; for instance, a value of 0.5 indicates that males are 50% or 1.5 times larger than females, whereas a value of 1 indicates monomorphism. This ratio assures both linearity and proportional symmetry of SSD index (for details, see [25]).

A two-tailed (Wilcoxon) Mann-Whitney *U* test was used to test whether the medians of domestic and wild specimens were different. We fitted the Ordinary Least Squares (OLS) of log₁₀ male mass against log₁₀ female mass, which assumes that the *x* values are fixed, and finds the line which minimises the squared errors in the *y* values. Agreement with Rensch's rule is manifested by the slope of the allometric relationship between male and female body size exceeding one. We tested the deviation of the slope from isometry (i.e. slope=1) using the one-way ANCOVA test. Deviations from the isometric relationship were considered significant when the expected isometric slope (1.0) fell outside the 95% confidence interval of the estimated slope. The non-parametric Wilcoxon signed rank test *W* was used to compare body mass between sexes. All calculations were performed using the PAST package [11].

3. RESULTS

3.1. Body mass dimorphism in domestic and wild *Sus*

In some domestic breeds (13% of the total, all being Asiatic, except the Black Majorcan from the Balearic Islands), female-biased SSD occurred, although males tended to be the most dimorphic sex (Figure 1). There were SSD differences among wild and domestic *Sus* (Mann-Whitney test, $U=144$, $P << 0.01$). In wild *Sus*, SSD was higher (1.51 ± 0.327 , mean \pm SE) than in domestic breeds (1.14 ± 0.237), with all wild species being male-heavier (Table 1). For domestic breeds, variance in male body size was higher (CV=57.6%) than in females (CV=55.2%), with these differences being significant (Wilcoxon, $W=7703$, $P <<< 0.001$).

3.2. Rensch's rule

Swine breeds exhibited an allometric sexual relationship in withers height ($r=0.894$, $P << 0.00001$), although it was not isometric because the confidence interval of the slope of OLS did not include 1 ($a=0.824$, 95% CI = 0.735 to 0.924) (Figure 2). Local Asian continental breeds (from China and Tibet) tended to present the lowest ratios, with the OLS slope being significantly different from the isometric regression ($F=143.1$, $P << 0.00001$, Figure 3). Different levels of SSD were observed in Asian breeds. Globally, female withers height showed no correlation with Lovich-Gibbons ratio ($r_s=0.06$, $p=0.433$), but slopes between wild *Sus* and domestic breeds were significantly different ($P << 0.0001$, Figure 4).

4. DISCUSSION

Domestic swine are much less dimorphic than most of their wild relatives, and domestic breeds are still generally male-larger, even after the considerable reduction of SSD. However, although nearly all breeds appear to be dimorphic, the general pattern is not consistent with Rensch's rule. If the sexual selection hypothesis is considered a general explanation for SSD, whereby intense sexual selection drives the evolution of body size of the selected sex, usually males [5, 18, 23, 24], with weaker correlated selection on body size in the other sex, other selective forces will have clearly affected the evolution of their SSD. These forces may explain this deviation from Rensch's rule. Nevertheless, different levels in the reduction of SSD between domestic breeds may suggest that different mechanisms were involved, and that breeds were subjected to different counteracting selective pressures, rather than a similar constrained selection for all.

Artificial breeding of contemporary breeds implies different kinds of pressure than sexual selection occurring in natural conditions; therefore, it has different consequences on body size and thus on the magnitude of SSD. Although no exact data quantifying and comparing the strength of sexual selection in pig are available, relaxation of sexual selection in domestic forms can reasonably be expected. We propose intuitively three reasons for the reduced SSD in domestic swine breeds, which are not mutually exclusive. First, sex-specific or sexually antagonistic selection might be relaxed or lacking in captivity, with heifers having selected for desired traits that are not necessarily related to sexual selection; for instance, meat quality or fat production. Assuming that size is primarily controlled by loci without a sex-biased expression pattern, the genetic correlation between male and female body size should quickly eliminate their size difference. Second, their morphological changes may result from non-genetic, environmental effects. Moreover, interspecific competition with other domestic species, an increase in intersexual food competition and/or poor feeding resources could lead to poor nutrition, which can result in the reduction of body size. A third explanation could be the functional reproductive constraint, by which larger females are better mothers, but this hypothesis requires corroboration.

Although none of these factors has been well documented throughout the domestication process and their relationship to SSD is more or less hypothetical, all of these explanations seem fairly plausible.

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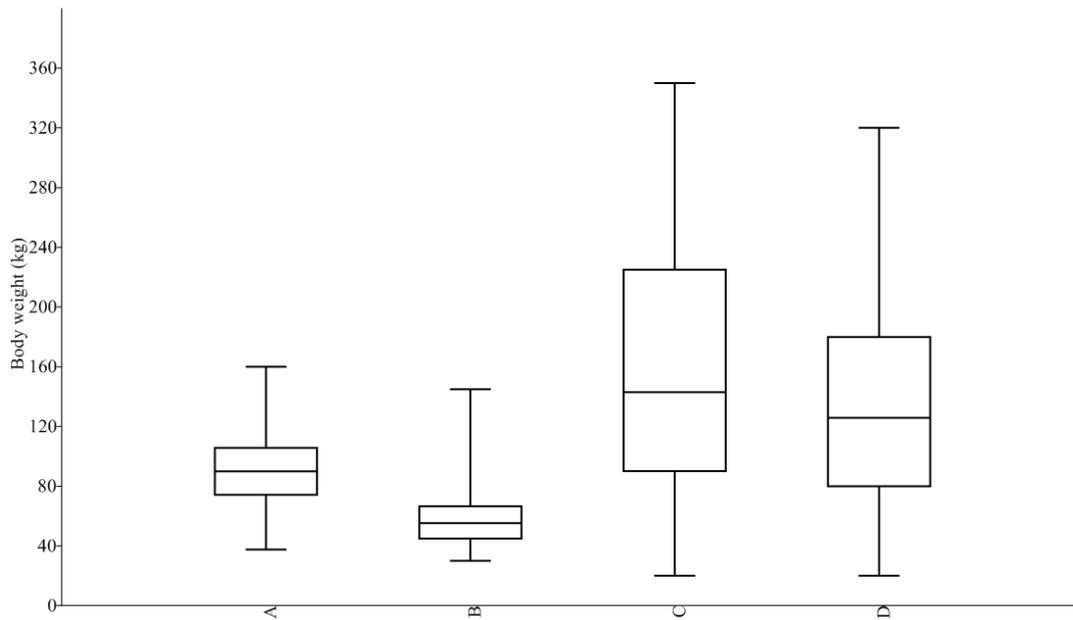


Figure 1: Comparison box plots of body weight in *Sus* wild species (4 species), and in domestic breeds (130 breeds), for males (A: *Sus* wild males, C: domestic males) and females, respectively (B: *Sus* wild females, D: domestic females). The median is shown with a horizontal line inside the box, which present the 25-75 per cent quartiles. The minimal and maximal values are shown with short horizontal lines ("whiskers")

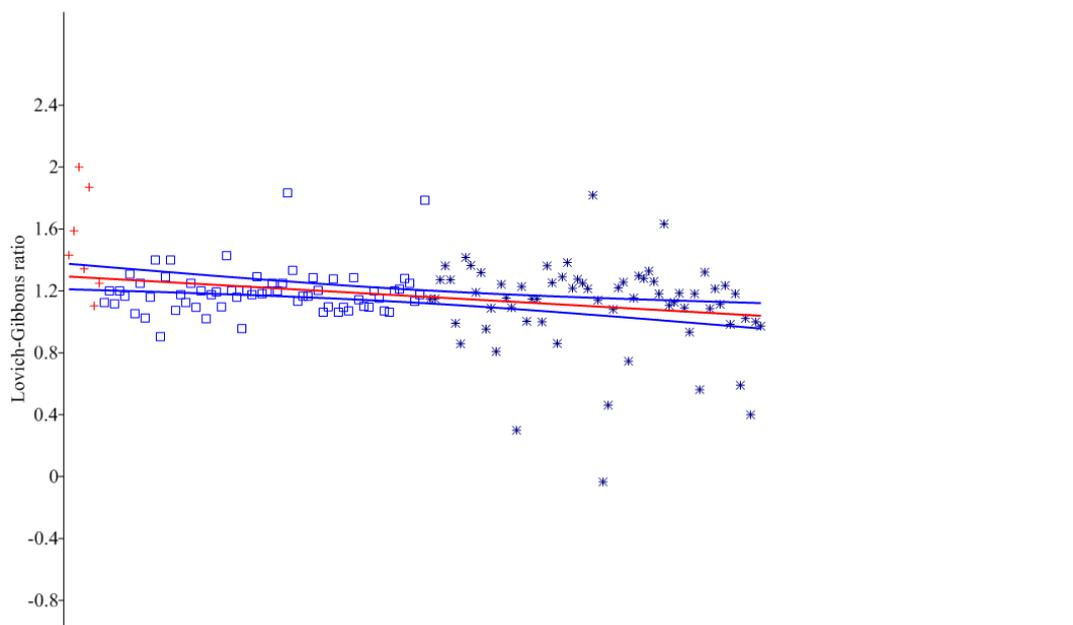


Figure 2: SSD (expressed as Lovich-Gibbons ratio) for wild *Sus* (crosses) and domestic pigs (squares, and stars from local Asiatic continental breeds from China and Tibet). Curved lines show 95% confidence ellipse

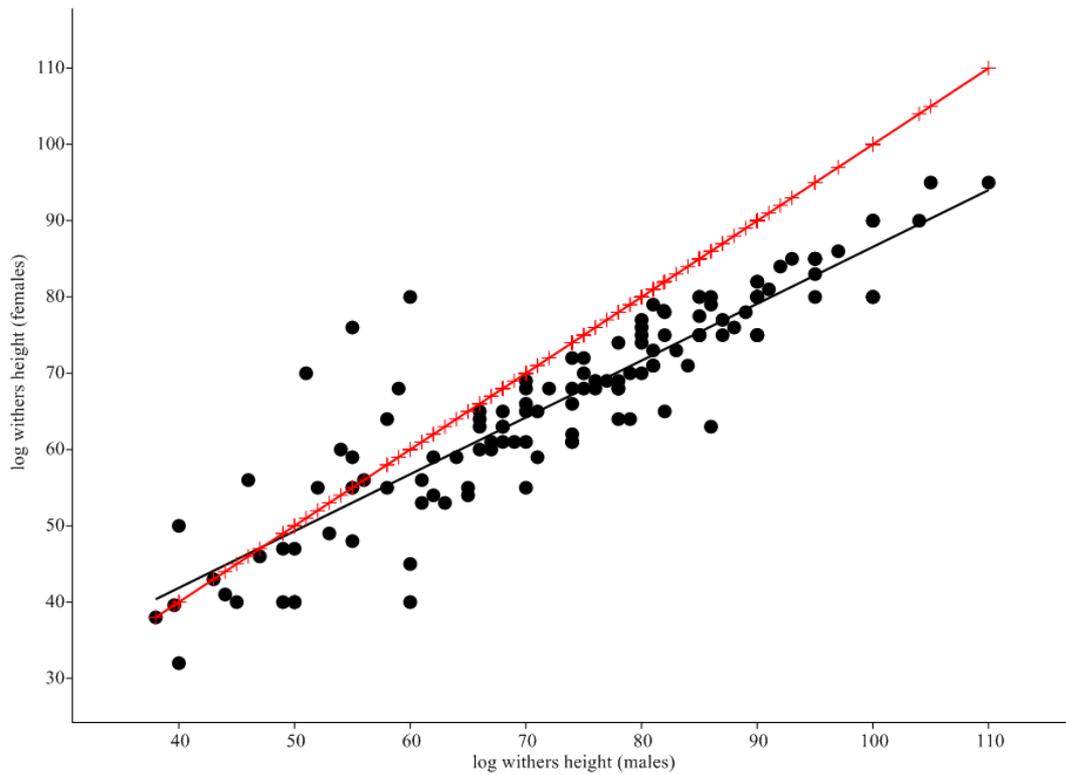


Figure 3: Regression of log(male mass) against log(female mass) for domestic swine breeds (dotted line). The regression was different from isometry ($F=143.1, p << 0.00001$, crossed upper line). Dots represent breeds

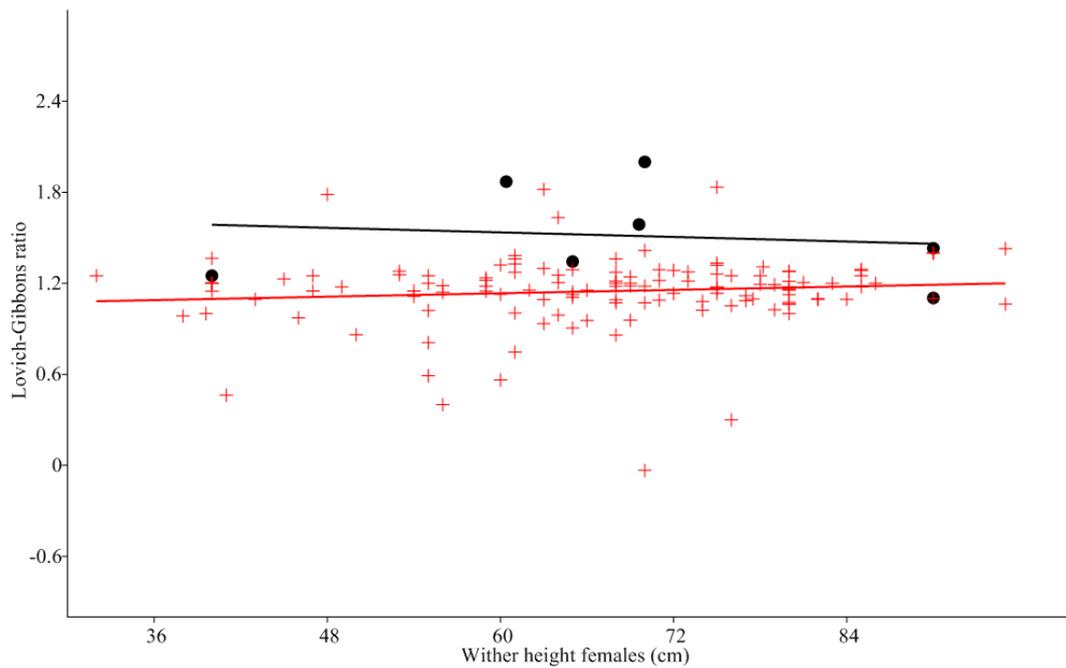


Figure 4: Slope regression of withers height for females with Lovich-Gibbons ratio for domestic and wild *Sus* differed ($p < 0.0001$). Crosses are for domestic breeds, and filled dots for wild species

| | N | | Male body mass (kg) | Female body mass (kg) | SSD |
|--|-----|----------|---------------------|-----------------------|-------------|
| Domestic <i>Sus</i> (male heavier) | 111 | Mean±SE | 177.3±8.48 | 145.5±7.10 | 1.215±0.01 |
| | | Range | 31;350 | 27;320 | 1.00; 1.83 |
| Domestic <i>Sus</i> (female heavier) | 17 | Mean±SE | 67.2±10.29 | 79.6±9.90 | 0.720±0.07 |
| | | Range | 22.5;152.3 | 32.1;153.7 | -0.03;0.99 |
| Domestic <i>Sus</i> (males and females of same weight) | 2 | Mean±SE | 55±35 | 55 ± 35 | 1.00 |
| | | Range | 20;90 | 20;90 | |
| Wild <i>Sus</i> | 7 | Mean ±SE | 93.0±14.01 | 64.8±14.05 | 1.512±0.123 |
| | | Range | 37.5;160 | 30;145 | 1.10;2.00 |

Table 1: Body mass and sexual size dimorphism as measured by SSD (see Materials and methods for explanation) in domestic and wild *Sus*.