

Is sexual size dimorphism similar irrespective of the origin of the goose breed?

P.M. Parés-Casanova

Department of Animal Production; University of Lleida Av. Alcalde Rovira Roure, 19125198 Lleida (Catalunya, Spain)

Abstract

Sexual dimorphism, defined as a phenotypic difference between males and females of a particular species, is a common phenomenon in animals. Rensch's rule describes the pattern of sexual size dimorphism (SSD) and claims that larger species generally exhibit higher male to female body size ratios. Domesticated animals offer excellent opportunities for testing predictions of functional explanations of Rensch's theory. In this paper, predictions were tested in geese by evaluating SSD in 70 breeds of domestic geese from different geographic origins (34 from Asian origin and 36 from European origin) which were compared to their wild relatives (genus *Anser*, 12 species). The data indicated that the body mass of different goose breeds were consistent with the Rensch's rule, where the allometry of SSD was significantly positive. Second, despite varying selective forces, scaling of SSD with body mass did not diverge according to breed origins (*Anser anser* and *A. cygnoides* groups).

Keywords: *Anser anser*; *Anser cygnoides*; *Anserinae*; domestication; sexual size dimorphism

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Introduction

Sexual size dimorphism (SSD), defined as a phenotypic difference between males and females of a species, is a common phenomenon in animals (for a review see Andersson, 1994). Of several evolutionary hypotheses proposed to explain the origin and maintenance of SSD, the most widely accepted is based upon the theory of sexual selection (Darwin, 1871). The direction of these differences, that is whether males or females are larger, varies from one taxonomic group to another.

SSD has important consequences for ecology, behaviour, population dynamics, and evolution. Rensch's rule (Rensch, 1950 & 1959) describes the pattern of SSD, claiming that larger species generally exhibit higher male to female body size ratios (Abouheif and Fairbairn, 1997; Polák and Frynta, 2010). In recent years, this rule has attracted considerable research, and conforming patterns have been reported by interspecific comparisons for various animal taxa, especially or exclusively in taxa exhibiting

larger males (Frynta et al., 2012). Although well documented across diverse animals, this rule is by no means universal and is particularly lacking in some taxa.

Domesticated animals offer a largely untapped resource for studies on SSD (Remes and Széleky, 2001). First, complete biometric data normally exist for males and females from a large range of breeds (Remes and Széleky, 2001). Second, the breeds underwent substantial diversification during their cohabitation with humans (Montgomerie, 2009), sometimes surpassing phenotypic diversification of their wild ancestors (Drake and Klingenberg, 2010). Third, in many domestic breeds, the males, females or both sexes were selected for a particular set of traits, and therefore, the extent and direction of SSD and allometry would reflect selection regimes other than sexual.

Domestic species possess an extraordinary ability to radiate into numerous morphologically and behaviourally distinct breeds within a few generations (Arbuckle, 2005). Over thousands years of domestication, geese have been considerably

Corresponding author: P.M. Parés-Casanova, Department of Animal Production; University of Lleida Av. Alcalde Rovira Roure, 19125198 Lleida (Catalunya, Spain)

differentiated by natural and artificial selections (Romanov and Weigend, 2001) and the tendency has been to obtain domestic breeds which are much larger than their wild ancestors. Nowadays, world-wide there are hundreds of morphologically differentiated goose breeds which differ in size, colouring, etc. Differences in weight are very apparent, ranging from about 4.9 kg for Padoven geese to 12 kg for the African, Embden and Toulouse ganders (in addition to differences in egg production).

The goose belongs to the genus *Anser*, subfamily *Anserinae*, family *Anatidae* (del Hoyo et al., 1994). Most of the domestic geese are descended from the Greylag Goose (*Anser anser*) which was domesticated thousands of years ago (del Hoyo et al., 1994). Some Chinese Geese are descended from the Wild Swan Goose (*Anser cygnoides*) (Li et al., 2010) which lives in Siberia and Eastern Asia (Sambraus, 1992). There is some evidence that the domestic goose was present in Egypt about 5,500 BC (Farrell, 2004), though domestication may pre-date the great Mediterranean civilisations, as there is evidence that Germanic tribes domesticated geese (del Hoyo et al., 1994). In Egypt, it is likely that the Egyptian goose (*Alopochen aegyptiaca*) was present during the period of the Old Kingdom (around 2,500 BC) (del Hoyo et al., 1994).

This study investigated SSD and size-related allometry across domestic goose breeds by comparison with their origin and wild relatives (genus *Anser*). There were two specific objectives: (i) to test whether the extent and allometry of SSD differ between goose breeds according to their origin and (ii) to test whether goose breeds and their wild counterparts follow Rensch's rule. The expectation would be that if sexual selection had a primary role in generating Rensch's rule under natural conditions (Dale et al., 2007; Székely et al., 2007), SSD allometry consistent with Rensch's rule would be present in goose breeds. This expectation is based on the idea that artificial selection is unlikely to mimic sexually antagonistic selection for geese, a potential driver of Rensch's rule in wild populations, because humans were using directional selection to obtain the desired traits (Remes and Székely, 2001) such as increased meat production, "beauty" displays or egg production. Therefore, the non-targeted sex is allowed to track changes in the targeted sex (Remes and Székely, 2001).

Materials and Methods

Data was collected for 70 goose breeds around the world, 36 originating from *Anser anser* and 34 from *Anser cygnoides* (Breeds from China and Africa, except the Chinese Yili breed). Adult body mass data for males and females was collected from published literature.

The Greylag Goose (*Anser anser*) and the Wild Swan Goose (*Anser cygnoides*) were used as ancestor for

comparison. Sexual size dimorphism was calculated as follows: the mass of the male was divided by the mass of the female, subtracted 1, and the resulting figure was labelled positive for breeds (or species) in which the males were the larger sex or negative in breeds (or species) where the females were the larger sex (Lovich and Gibbons, 1992). SSD is a convenient and readily interpretable measure of sexual dimorphism (Fairbairn et al., 2007); for instance, a value of +0.3 indicates the males are by 30%, or 1.3 times, larger than females, whereas a zero value indicates monomorphism (Remes and Székely, 2001).

Goose breeds were categorized according to their origin: *Anser anser* and *Anser cygnoides* (Chinese and Africans breeds, except the Yili breed from China). No differentiation was done for domestic breeds descending from the western (*Anser anser anser*) or eastern goose (*Anser anser rubrirostris*) (Farrell, 2004). As the distribution of body mass and SSD significantly departed from normality for goose breeds and wild species ($P < 0.05$), a nonparametric ANOVA Kruskal-Wallis test was used to compare median values.

To test for Rensch's rule, the Reduced Major Axis (RMA) of log transformed male mass was fitted against female mass for goose breeds and two wild *Anser* ancestor species, and the fitting and standard error was estimated according to Warton et al. (2006). An ANCOVA (Analysis of covariance) test was used to test the deviation of the slope from isometry (i.e. slope=1) and all calculations were performed using the PAST package (Hammer et al. 2001). The level for statistical significance was set at 5%.

Results

Body mass dimorphism in domestic and wild geese

In all goose breeds, males were heavier than females ($P < 0.05$) (Table 1). The median SSD did not differ among goose breed origins (Kruskal-Wallis test, $H = 0.096$, $P = 0.755$), having an average value of -0.193 ± 0.118 (mean \pm SE) for *Anser cygnoides* breeds and an average value of -0.190 ± 0.134 for *Anser anser* breeds (Figures 1 and 2).

Rensch's rule

Goose breeds exhibited a positive allometric relationship for sexual body mass consistent with the Rensch's rule ($R = 0.942$, $P < < < 0.001$) (Fig. 3) showing an isometric relationship for both groups. RMA slopes were not significantly different among goose breed origins ($P = 0.069$), where the regression slope among *A. anser* goose breeds was 0.1% less than among *A. cygnoides* breeds. If SSD was restricted to values between -0.1 and -0.5, allometry remained significant ($R = 0.942$, $P < < < 0.001$, $n = 58$).

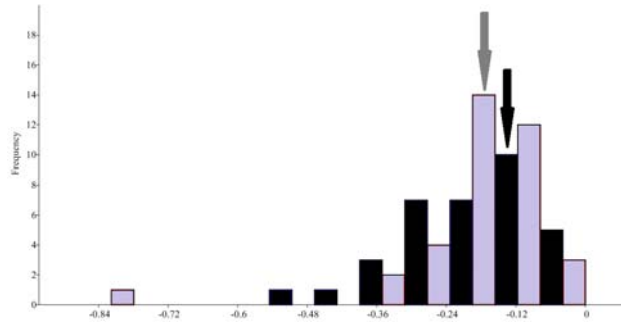


Fig. 1: Frequency distribution of sexual size dimorphism (SSD) as measured (see Materials and Methods for explanation) for 36 breeds of *Anser anser* origin and 34 breeds of *Anser cygnoides* origin (Chinese and African breeds, except the Yili breed from China). Arrows indicate the average SSD for *Anser cygnoides* breeds (black; -0.193 ± 0.118) and *Anser anser* breeds (grey; -0.190 ± 0.134).

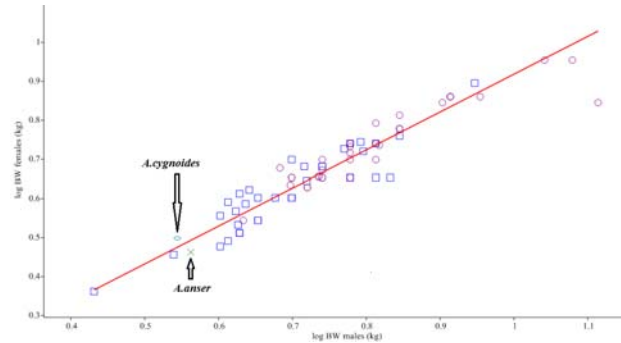


Fig. 2: Reduced Major Axis for goose breeds ($n=70$), shown as the relationship between log-transformed male (X axis) and female body (Y axis) weights ($R=0.942$). Circles correspond to breeds of *A. anser* origin while squares to those of *A. cygnoides* origin.

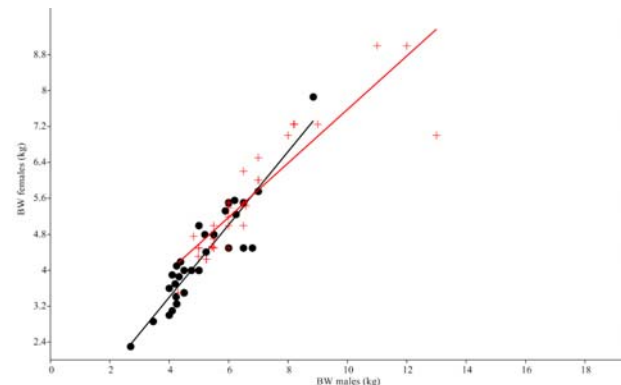


Fig. 3: Comparison of regression slopes for body mass according to sex between goose breeds of *Anser anser* origin (blades) and *A. cygnoides* origin (filled dots). RMA slopes were not significantly different among goose breed origins ($p=0.069$).

Table 1: Body mass (in kg) for 36 domestic goose breeds of *Anser anser* origin and 34 of *Anser cygnoides* origin (Chinese and African breeds, except the Yili breed from China). For all goose breeds, males (σ) were heavier than females (ϕ) ($P<0.05$)

	σ Ac	ϕ Ac	σ Aa	ϕ Aa
Min	2.7	2.3	4.3	3.5
Max	8.9	7.9	13.0	9.0
Average	5.1	4.3	6.7	5.6
Std. error	0.208	0.183	0.327	0.219
Variance	1.471	1.141	3.847	1.728
Stand. dev	1.213	1.068	1.961	1.315
Median	4.875	4.050	6.000	5.420
Skewness	0.889	1.020	1.778	0.977
Kurtosis	1.470	2.473	3.199	0.607
Geom. mean	4.954	4.160	6.488	5.476

Discussion

This study yielded two major results - the body mass of goose breeds were consistent with Rensch's rule and allometry was equal across breed origins (*Anser anser* group and *A. cygnoides* group). Although ganders were usually easier to differentiate for Chinese and African breeds because they tend to have larger knobs on their heads than females, this group had less SSD than *A. anser* breeds, though the differences were not significant and attributed to similar selective forces between both groups.

Two reasons were proposed for the maintenance of allometry in domestic geese. First, male-male competition in captivity was not reduced because ganders may be housed together. Domestic ganders were frequently associated with a group of females and vigorously defended all of these females, their preferred nest sites and offspring against competitors or predators, while greylag geese were more monogamous (Hirschenhauser et al., 2013). Strong sexual selection for large males leads to, under natural conditions, a large male body size, with a weaker selection for female body mass (Kolm et al., 2007), which results in SSD allometry consistent with Rensch's rule (Dale et al., 2007). Selection for strong, heavy males would thus be conserved. Second, in the wild, males and females are exposed to natural and sexual selections of different strengths, resulting in different net selection acting on males and females for the same traits which may be either sex-specific (different strengths but the same direction) or sexually antagonistic (different direction). Similarly, humans have used directional selection for geese to achieve the desired characteristics in the targeted sex. In domestic geese, males and females differed substantially in the direction and magnitude of trait selection, where selection for egg and down production was to improve female traits and ornamentation and meat production aimed to improve male traits, where the key factor was sexual selection related to body size. Evolution of SSD allometry in domestic geese was not prevented by prohibitively high

cross-sex genetic correlations, because they were similar in magnitude, or even slightly lower, in domestic geese compared to the Greylag Goose and Wild Swan Goose. Other aspects of body mass selection could also have changed with domestication (resource competition, predators).

As goose breeds exhibited a wide range for body mass and SSD, additional types of sensitivity analyses were performed. First, if body mass variation was restricted, breeds still exhibited positive allometry. This analysis showed that when breeds with extreme SSD in either direction were removed, extreme SSDs were not critical for generating positive allometry, which was similar to that demonstrated by Remes and Székely (2001) for chicken.

In conclusion, extant domestic stocks were excellent resources for testing SSD hypotheses. Using domestic goose breeds, this study showed that domestic breeds do show positive allometry in body mass irrespectively of their origin and domestic geese exhibited a similar allometric relationship for both regional origins and ancestors.

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