SHORT COMMUNICATION

# Domestic chickens defy Rensch's rule: sexual size dimorphism in chicken breeds

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## Abstract

Sexual size dimorphism (SSD), i.e. the difference in sizes of males and females, is a key evolutionary feature that is related to ecology, behaviour and life histories of organisms. Although the basic patterns of SSD are well documented for several major taxa, the processes generating SSD are poorly understood. Domesticated animals offer excellent opportunities for testing predictions of functional explanations of SSD theory because domestic stocks were often selected by humans for particular desirable traits. Here, we analyse SSD in 139 breeds of domestic chickens *Gallus gallus domesticus* and compare them to their wild relatives (pheasants, partridges and grouse; Phasianidae, 53 species). SSD was male-biased in all chicken breeds, because males were 21.5 ± 0.55% (mean ± SE) heavier than females. The extent of SSD did not differ among breed categories (cock fighting, ornamental and breeds selected for egg and meat production). SSD of chicken breeds was not different from wild pheasants and allies (23.5 ± 3.43%), although the wild ancestor of chickens, the red jungle fowl *G. gallus,* had more extreme SSD (male 68.8% heavier) than any domesticated breed. Male mass and female mass exhibited positive allometry among pheasants and allies, consistently with the Rensch's rule reported from various taxa. However, body mass scaled isometrically across chicken breeds. The latter results suggest that sex-specific selection on males vs. females is necessary to generate positive allometry, i.e. the Rensch's rule, in wild populations.

## Introduction

Differences between sexes in various morphological, ecological and behavioural traits have puzzled biologists for a long time. It was a subject of substantial interest for Darwin himself (Darwin, 1871). Although recent research has discovered a great deal about patterns of variation in sexual dimorphism among taxa at various phylogenetic levels, the genetic and physiological mechanisms (Bonduriansky & Chenoweth, 2009) as well as the selective processes that generate these patterns remain poorly understood (Shine, 1989; Andersson, 1994; Blanckenhorn, 2005; Fairbairn *et al.*, 2007).

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One of the most widespread patterns is an allometric relationship between body sizes of males and females, termed the Rensch's rule (Rensch, 1950; Fairbairn, 1997), whereby the extent of male-biased sexual size dimorphism (SSD) increases with overall body size across species, whereas the extent of female-biased SSD decreases with body size. Although well documented across diverse taxa, it is by no means universal (Abouheif & Fairbairn, 1997; Fairbairn, 1997; Cox *et al.*, 2003; Blanckenhorn *et al.*, 2007; Fairbairn *et al.*, 2007) and is particularly lacking in taxa with females larger than males (Webb & Freckleton, 2007; but see Fairbairn, 2005; Stuart-Fox, 2009).

The extent of SSD within species is usually viewed as resulting from sex-specific equilibrium of sexual, fecundity and viability selections (Andersson, 1994; Blanckenhorn, 2005; Cox & Calsbeek, 2009) possibly constrained by cross-sex genetic correlations (Poissant *et al.*, 2010).

However, why the extent of SSD systematically changes with body mass across related species is less clear, and many hypotheses were advanced to explain the occurrence and strength of the allometry (Abouheif & Fairbairn, 1997; Fairbairn, 1997, 2005). The most supported hypothesis at present is sexual selection, whereby intense sexual selection drives the evolution of body size of the selected sex, usually the males, with weaker correlated selection on body size in the other sex (Székely *et al.*, 2004, 2007; Raihani *et al.*, 2006; Dale *et al.*, 2007). However, the latter studies focused on a single animal clade, the birds, under natural conditions.

Studies of Rensch's rule, as far as we are aware, focused exclusively on animal populations in their natural environment with the exception of insects that have been investigated in the laboratory (e.g. water strider *Aquarius remigis*, dung flies *Scatophaga* spp and fruit flies *Drosophila* spp; reviewed in Fairbairn *et al.*, 2007) and domestic goats and sheep (Polák & Frynta, 2009). However, domesticated animals offer largely untapped resources for studies of SSD. First, excellent data exist on the body sizes of males and females from a large range of breeds. Second, the breeds underwent substantial diversification during their cohabitation with humans (Montgomerie, 2009), sometimes surpassing phenotypic diversification of their wild ancestors (Drake & 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 should reflect different artificial selection regimes.

Here, we investigate SSD and size-related allometry across domestic chicken breeds. By comparison with their wild relatives (pheasants, partridges, grouse; 172 species; family Phasianidae; del Hoyo *et al.*, 1994), we are contrasting the patterns between domestic breeds and Phasianidae. We have two specific objectives: (i) to test whether the extent and allometry of SSD differ between chicken breeds and wild pheasants and allies (Aves: Phasianidae) and (ii) to test whether chicken breeds and their wild counterparts exhibit the Rensch's rule. We expected that if sexual selection had the primary role in generating Rensch's rule under natural conditions (Dale *et al.*, 2007; Székely *et al.*, 2007), the allometry of SSD consistent with Rensch's rule would be absent in chicken breeds. This expectation is based on two lines of argument. Firstly, in domestic breeds, humans select for desired traits that are often unrelated to sexual selection, for instance milk production, meat quality or egg production. Therefore, sexual selection is expected to be weak in domestic stocks. For instance, in traditional extensive poultry farming systems, the farmer may choose one (or a few) cocks so that female poultry can only exert a limited, if any, choice (Verhoef-Verhallen & Rijs, 2009). 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 egg or meat production. Therefore, the nontargeted sex is allowed to track changes in the targeted sex.

## Materials and methods

We collected data on chicken breeds and wild pheasants, partridges and grouse from the literature. We obtained data on adult male and female body mass, and the number of eggs produced per year in traditional chicken breeds from Europe, Americas and Asia (Pavel & Tuláček, 2006). As a wild avian group for comparison, we used family Phasianidae as reconstructed by modern molecular phylogenetics (Crowe *et al.*, 2006a,b; Kriegs *et al.*, 2007). This family includes the wild ancestor of chicken breeds, the red jungle fowl (*Gallus gallus*; Liu *et al.*, 2006), and also a congeneric species, the grey jungle fowl (*Gallus sonneratii*), which was a potential source of introgression into domestic chicken lines (Eriksson *et al.*, 2008). We collected male and female body mass from a comprehensive source on avian life histories (Lislevand *et al.*, 2007): mean body masses of adult males and females preferentially taken during the breeding season. We calculated sexual dimorphism index (SDI) as follows: we divided the mass of the heavier sex by the mass of the lighter sex, subtracted one and made the resulting figure negative for breeds (or species) in which the males were the larger sex whereas we let it positive in breeds (or species) where the females were the larger sex (Lovich & Gibbons, 1992). SDI 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. The distribution of SDI significantly departed from normality in both chicken breeds and wild species (Fig. 1), and it was not
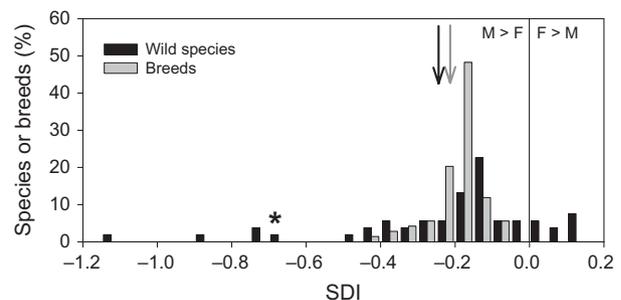


**Fig. 1** Frequency distribution of sexual size dimorphism as measured by SDI (see Materials and methods for explanation) in pheasants, partridges and grouse (53 species), and in chicken breeds (139 breeds). Asterisk indicates the ancestor of domestic chicken, red jungle fowl. Arrows indicate average SDI of pheasants and allies (black) and chicken breeds (grey). M > F: male heavier than female and vice versa.

possible to normalize it by any transformation. Therefore, we used nonparametric Kruskal–Wallis tests to compare median values of SDI between classes.

We categorized chicken breeds according to Pavel & Tuláček (2006) based on desired characteristics that have been targeted by the breeders in different breeds. First, fighting breeds ($n$ = 19) were traditionally kept and bred for cock fighting. The desired characteristic was fighting ability in cocks, somehow analogous to the outcome of male–male competition in the wild. Second, ornamental breeds ($n$ = 15) were kept for decorative purposes and pleasure. Here, selection for aesthetic characteristics in both sexes, perhaps analogous to the outcome of mate choice acting on both sexes in the wild, prevailed. Third, there were dual-purpose breeds ($n$ = 105) kept for small-scale subsidy of eggs and meat. Although individual breeds in this group differ in their primary use (i.e. production of eggs, meat or both), most of them are used as universal breeds and many of them include both egg and meat producing lines within the breed. Thus, we made no attempt to split this category into breeds used predominantly for the production of eggs vs. meat. The common theme among dual-purpose breeds is artificial selection for female fecundity and meat production. These two traits (egg production per year and female body mass) were positively related in dual-purpose breeds ($r$ = 0.74, $P$ < 0.001, $n$ = 98) indicating no trade-off between fecundity and body mass. The desired characteristics of the latter breeds appear to include the analogue of the outcome of fecundity selection in wild species. Our final data set included 139 chicken breeds and 53 wild species of pheasants, partridges and grouse.

To test for Rensch's rule, we fitted major axis regression (MAR) of $\log_{10}$ male mass against $\log_{10}$ female mass both for chicken breeds and wild pheasants and allies in smatr package for R (Warton et al., 2006). We tested the deviation of the slope from isometry (i.e. slope = 1; smatr test statistic $r$), and for heterogeneity of slopes among breed categories (smatr likelihood ratio test statistic LR). We also adjusted the analysis of wild pheasants and allies for phylogenetic relationships among species using phylogenetically independent contrasts (Felsenstein, 1985) as suggested by Abouheif & Fairbairn (1997). We fitted MAR to independent contrasts forced through zero in the smatr package. For the calculation of phylogenetically independent contrasts, we used a working phylogeny based on the most recent molecular phylogenies (Bloomer & Crowe, 1998; Crowe et al., 2006b; Lislevand et al., 2009). Our phylogenetic hypothesis for the family Phasianidae is presented in Appendix S1. The phylogenetic positions of three species (*Francolinus lathami*, *Francolinus nathani* and *Francolinus psilolaemus*) were uncertain, and therefore, these species were excluded from the phylogenetic analyses. We used a composite phylogeny with all branches set to the same length. We calculated the independent contrasts in the CAIC package for R (Orme et al., 2009) and checked that there was

no relationship between the absolute values of contrasts and (i) the estimated nodal values and (ii) the square root of the expected variance at the node (Garland et al., 1992). Because the CAIC package for R does not allow polytomies in the phylogeny, we resolved the polytomies (two polytomies in total) randomly.

## Results

### Body mass dimorphism in chickens and wild pheasants and allies

In all chicken breeds, the male was heavier than the female (Table 1, Fig. 1). The median SDI was not different among chicken breed categories (Kruskal–Wallis test, $\chi^2$ = 4.1, $P$ = 0.127), although cock fighting breeds tended to be the most dimorphic (SDI = −0.248 ± 0.020, mean ± SE), followed by ornamental (−0.224 ± 0.018) and dual-purpose breeds (−0.208 ± 0.006).

In wild pheasants and allies, however, both male-biased and female-biased SSD occurred (Table 1, Fig. 1). The median SDI of chicken breeds and wild pheasants and allies did not differ (Kruskal–Wallis test, $\chi^2$ = 3.0, $P$ = 0.082). However, SDI was significantly more variable in wild species than in chicken breeds (Bartlett test: $F_{1,190}$ = 155.9, $P$ < 0.001). The red jungle fowl had one of the most extreme male-biased dimorphisms (SDI = −0.688, Fig. 1).

### Rensch's rule

Chicken breeds exhibited an isometric relationship in body mass, because the confidence interval of the slope of MAR included one ($\beta$ = 1.011, 95% CI = 0.9959–1.0257, $n$ = 139; Fig. 2). Furthermore, the MAR slopes were not significantly different among chicken breed categories (LR = 2.4, $P$ = 0.308). Wild pheasants and allies, however, exhibited strong allometry consistent with the Rensch's rule using both species-level data ($\beta$ = 1.151, 95% CI = 1.1000–1.2049, $n$ = 53; Fig. 2) and phylogenetically independent contrasts ($\beta$ = 1.148, 95% CI = 1.0706–1.2309, $n$ = 48). These patterns remained

**Table 1** Body mass and sexual size dimorphism as measured by SDI (see Materials and methods for explanation) in chicken breeds and wild pheasants, partridges and grouse.

| | Male body mass (g) | Female body mass (g) | SDI |
|---|---|---|---|
| Chicken breeds ($n$ = 139) | | | |
| Mean ± SE | 2103.2 ± 102.65 | 1727.3 ± 83.71 | −0.215 ± 0.006 |
| Range | 600–5650 | 500–4650 | −0.089 to −0.469 |
| Pheasants and allies ($n$ = 53) | | | |
| Mean ± SE | 876.2 ± 161.00 | 636.9 ± 90.62 | −0.235 ± 0.034 |
| Range | 41–7400 | 35.6–4222 | 0.118 to −1.136 |

SDI, sexual dimorphism index.
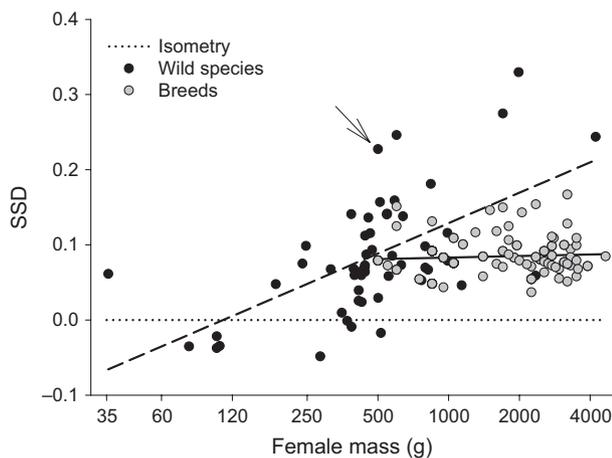
**Fig. 2** Sexual size dimorphism (SSD) (defined here as log(male mass/female mass)) against log(female mass) for chicken breeds (continuous line) and wild pheasant, partridges and grouse (hatched line). The dotted horizontal line indicates no scaling of SSD with size. For illustration, shown are ordinary least squares lines of the relationship between SSD and log(female mass). Note that this plot is equivalent to plotting log(male mass) against log(female mass), but it is easier to see differences between chicken breeds and wild pheasants on this scale. The major axis regression of log(male mass) on log(female mass) in chicken breeds was not different from isometry ($r = 0.12$, $P = 0.158$), whereas in wild pheasants, partridges and grouse it was different for both species-level data ($r = 0.66$, $P < 0.001$) and phylogenetically independent contrasts ($r = 0.50$, $P < 0.001$). The arrow indicates the ancestor of domestic chicken, the red jungle fowl.

consistent when we restricted body mass variation to that exhibited by chicken breeds (from 500 to 5650 g), which more than halved the sample size (species-level data: $\beta = 1.209$, 95% CI = 1.0206–1.4412, $n = 23$; independent contrasts: $\beta = 1.205$, 95% CI = 0.9883–1.4813, $n = 21$). One may argue that extreme SDI indicates intense sexual selection: indeed, restricting the analyses of wild phasianids to SDI exhibited by chicken breeds (−0.089 to −0.469) produced isometric relationships (species-level data: $\beta = 1.018$, 95% CI = 0.9757–1.0616, $n = 35$; independent contrasts: $\beta = 1.003$, 95% CI = 0.9602–1.0481, $n = 31$).

## Discussion

Our study provided two major results. First, we showed that the body masses of chicken breeds were not consistent with the Rensch's rule, and the lack of allometry was consistent across breed categories. Second, in pheasants and allies, the allometry of SSD was significantly positive, consistent with previous studies of Phasianidae (Drovetski *et al.*, 2006; Lislevand *et al.*, 2009; Fig. 2).

Both the extent of SSD and its isometry across chicken breed categories remained remarkably conservative

regardless of the selection targets (cock fighting, ornamentation, or egg and meat production) and whether the selection was aimed to improve male traits (cock fighting), female traits (egg and meat production) or traits in both sexes (ornamentation). Thus, despite varying selective forces, scaling of SSD with body mass did not diverge across breed categories. The regression slope (male mass: female mass) among chicken breeds was 12.2% less than the comparable slope among wild pheasants and allies. The reduced slope among domestic chickens is comparable to domesticated goats and sheep, in which the slopes decreased by 16.5% and 8.6%, respectively, when compared to the wild relatives, although both domestic goats and sheep still showed positive allometry, i.e. the Rensch's rule (Polák & Frynta, 2009).

We propose two reasons for the reduced allometry in domestic breeds. First, male–male competition is usually relaxed in captivity because breeders often allocate particular sires to dams. Selection on strong, heavy males would be thus much reduced. Second, sex-specific or sexually antagonistic selection might be relaxed or lacking in captivity. In the wild, males and females are exposed to natural and sexual selections of different strengths, resulting in different net selection acting in males and females on the same traits (Cox & Calsbeek, 2009) that may be either sex-specific (different strengths but the same direction) or sexually antagonistic (different direction; Bondurianski & Chenoweth, 2009). On the contrary, humans use directional selection to achieve desired characteristics in the targeted sex and allow for a phenotypic response in the other sex. This response will be likely 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 (Lande, 1980; Poissant *et al.*, 2010). Strong sexual selection for large males leads under natural conditions to large male body size, with weaker, correlated selection on female body mass (Kolm *et al.*, 2007), resulting in allometry of SSD consistent with Rensch's rule (Dale *et al.*, 2007). The same is true for selection for small males (Székely *et al.*, 2004). Full correlated response in female body mass is often, although not always, prevented by sex-specific selective optima. A recent review of selection in wild animal populations found out that males and females often differed substantially in the direction and magnitude of the selection on shared traits (Cox & Calsbeek, 2009). In captive populations, however, full correlated phenotypic responses in homologous traits in males and females may manifest themselves given the lack of opposing selective forces.

As chicken breeds exhibited a small range of body mass and SDI compared to wild species (Figs 1 and 2), we carried out two types of sensitivity analyses. First, we restricted body mass variation in wild species to fall within the range of domestic breeds and found that wild species still exhibited positive allometry. Second, we restricted SDI and found that allometry was no longer

significant. The latter analysis, where all species with extreme SSD of either direction were removed (Fig. 2), shows that extreme SSDs are critical for generating positive allometry. To some extent, this is not too surprising because these are the very species subject to intense sex-specific selection – a process suspected to underlie Rensch's rule.

Although other aspects of selection on body mass also change with domestication (loss of resource competition, lack of predators), we suggest that changes in sexual selection regimes were more important. The reason is that the role of differential sex-specific selection pressures in generating diverse SSD in wild populations has been recently supported by various studies (Blanckenhorn, 2005). First, strong sexually antagonistic selection was present in strongly sexually dimorphic species (Cox & Calsbeek, 2009). Thus, SSD responds to sex-specific selection, although it fails to resolve fully the intralocus sexual conflict (Bonduriansky & Chenoweth, 2009). Second, sexual selection may act on either females or females to generate allometry of SSD. A key factor is the aspect of sexual selection related to body size, i.e. intrasexual competition for mating opportunities (Dale *et al.*, 2007). Evolution of the allometry of SSD in domestic chickens is certainly not prevented by prohibitively high cross-sex genetic correlations, because they are similar in magnitude, or even slightly lower, in domestic chickens when compared to red jungle fowl (Poissant *et al.*, 2010). What is perhaps missing in captivity is selection pressures connected with sexual competition and sex-specific reproductive roles. Thus, our study adds to the available evidence and points to the importance of sexual selection (Dale *et al.*, 2007; Lislevand *et al.*, 2009) and sex-specific selection pressures for generating positive allometry for SSD and its great variability in the wild (see also De Mas *et al.*, 2009).

In conclusion, we argue that domestic stocks are excellent yet rarely used resources for testing hypotheses of SSD. Using domestic chicken breeds, we show that unlike their wild relatives, the domestic breeds do not show positive allometry in body mass. This is a somehow tantalising result, because domestic chickens originated from one of the most strongly allometric groups among all birds (Fairbairn, 1997; Dale *et al.*, 2007; Székely *et al.*, 2007; Webb & Freckleton, 2007). We propose that domestic poultry fail to exhibit an allometric relationship because unlike in wild populations male and female poultry were not subject to different selection regimes towards different optima in body sizes of adult males and females.

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## Supporting information

Additional Supporting Information may be found in the online version of this article:

**Appendix S1** Composite phylogenetic hypothesis of the family Phasianidae used in our analyses.

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