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Rensch's rule is broken in Cervidae

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A regra de Rensch está quebrada em Cervidae

Resumo: A diferença de tamanho corporal entre machos e fêmeas é conhecida como dimorfismo sexual de tamanho (DST). O surgimento do DST é atribuído na maioria das vezes a processos de seleção sexual, entretanto a seleção natural também pode afetar o DST. Tem se observado em diversos grupos que a intensidade do DST está associada com o tamanho corporal das espécies, padrão conhecido como Regra de Rensch. Nós testamos a regra de Rensch na família Cervidae, um grupo com forte dimorfismo sexual. Analisamos o DST de 35 espécies utilizando análises de regressão tipo II (eixo principal reduzido) filogenética (RMA). Ao analisar a relação entre o tamanho dos machos vs o tamanho das fêmeas observamos que o DST se modifica isometricamente com o aumento do tamanho corporal (βRMA = 1.05, p = 0.18). Estes resultados evidenciam que a regra de Rensch não se cumpre nos membros da família Cervidae. Na última década, diversos estudos tem mostrado grupos taxonômicos que não seguem a regra de Rensch. Dado que o tamanho corporal está associado com diversas características ecológicas das espécies, é possível que a associação do tamanho corporal com o DST não seja sempre um efeito causal nos grupos que seguem a Regra de Rensch.

Palavras chave: Dimorfismo sexual de tamanho, mamíferos, RMA filogenético, seleção sexual, tamanho corporal.

Abstract: The difference in body size between males and females is known as sexual size dimorphism (SSD). The existence of SSD is usually attributed to processes of sexual selection, although natural selection can also affect SSD. In some animal groups the extension of SSD is associated with body size, a pattern known as Rensch's rule. We tested Rensch's rule in the members of the family Cervidae, a group with strong sexual dimorphism. We analyzed SSD of 35 species by means of phylogenetic reduced major axis regression (RMA). Analyzing the relationships between male size vs female size we observed that SSD changes isometricly with the increase of body size (βRMA = 1.05, p = 0.18). These result evidence that Rensch's rule does not operate among members of the family Cervidae. In the last decade, many studies have shown diverse taxonomic groups that do not follow Rensch's rule. Because body size is associated with many ecological characteristics, it is possible that the association of body size with SSD is not always a causal effect in those groups that follow Rensch's rule.

Key words: Sexual size dimorphism, mammals, phylogenetic RMA, sexual selection, body size.

Introduction

Sexual dimorphism is widespread in the animal kingdom. Males and females may differ in most secondary sexual traits (e.g., body size and shape, colour, antlers, feathers and behaviour) and sexual selection acts on those traits by maximizing individual reproductive success while not necessarily increasing survivorship (Darwin 1859, 1871; Emlen *et al.* 2005; Plard *et al.* 2011; Fairbairn 2013). Thereby, natural selection has also an important role on sexual dimorphism by limiting the growth of sexual display traits, increasing the competition between sexes and increasing differences between the reproductive and ecological roles of males and females (Clutton-Brock *et al.* 1977; Pérez-Barbería *et al.* 2002; Stuart-Fox & Ord 2004). Sexual size dimorphism (SSD) – the difference in body size between males and females of the same species - is among the most conspicuous and widely studied sexual differences (Emlen *et al.* 2005; Isaac 2005; Tobias *et al.* 2012). The SSD (either male-biased or female-biased) is common and highly variable in the most diverse animal groups, and even closely related phylogenetic lineages may show strikingly different levels of SSD. Additionally, both conditions (male and female-biased SSD) may occur within the same lineage indicating a great lability of SSD (Fairbairn *et al.* 2007).

Body size is a highly variable characteristic both at the intra-specific (e.g., Martinez *et al.* 2013, 2018) and inter-specific levels (Smith & Lyons 2011). Body size is strongly associated with multiple characteristics of the life history of organisms and is in turn affected by environmental (Peters 1983; Olalla-Tárraga *et al.* 2015; Gohli & Voje 2016) and genetic factors (Martinez *et al.* 2018). SSD is not an expeption to these factors, many studies show that SSD may be associated with variation of body size (Fairbairn *et al.* 2007; Fairbairn 2013). As a result of this dependence, in species where males are larger than females, when species body size is increased, SSD also increases. In contrast, in species whose females are bigger than males the increase in body size would lead to a decrease of SSD (Rensch 1950; Fairbairn 1997). This pattern is known as "Rensch's rule" and could be a result of a differential response to selection on body size in females and males (Fairbairn 1997). However, no completely satisfactory model of Rensch's rule exists up to this day (Kappeler & van Schaik 2004; Piross *et al.* 2019). Then, if Rensch's pattern is fulfilled, we expect a positive allometric association between SSD and body size. Body size is decisive for male success in polygenic species because bigger males are commonly the healthier, more aggressive and experienced ones (Miller 2013).

Understanding the mechanisms that modulate SSD is very relevant for the assessment of the evolutionary forces that drive species diversification. We analyzed SSD and the operation of Rensch's rule in Cervidae. We chose deer as a model system for the following reasons: data on male and female body size are available for many species, and the family present many obvious traits of male-biased sexual dimorphism as well as a variety of mating and social systems. We used phylogenetic comparative methods to analyse the relationship (scaling) between SSD data and body size for 35 cervid species.

Material and Methods

Data collection

We built a database of body mass for males (MBM) and females (FBM) of 35 cervid species (**Table 1**). We estimated SSD as log(MBM/FBM) (Fairbairn 2007), where positive values represent a male bias of SSD and negative values represent a female bias of SSD.

Table 1. Body mass (kg) of male (MBM) and female (FBM) cervids species used in this study.

Species	Common Name	MBM	FBM	LOG(M/F)	Reference
Alces alces	Moose	482.5	365	0.121204453	Plard *et al.* (2011)
Axis axis	Chital	89.5	39	0.360758428	Plard *et al.* (2011)
Axis porcinus	Hog Deer	41	31	0.121422163	Plard *et al.* (2011)
Capreolus capreolus	Western Roe Deer	28	26.5	0.023912157	Plard *et al.* (2011)
Capreolus pygargus	Eastern Roe Deer	42	39.5	0.026652195	Plard *et al.* (2011)
Cervus albirostris	White-Lipped Deer	204	125	0.212720154	Plard *et al.* (2011)
Cervus canadensis	Wapiti	350	250	0.146128036	Plard *et al.* (2011)
Cervus duvauchelii	Barasingha	236	145	0.211544001	Plard *et al.* (2011)
Cervus elaphus	Red Deer	250	125	0.301029996	Plard *et al.* (2011)
Cervus eldi	Eld's Deer	105	67	0.195114496	Plard *et al.* (2011)
Cervus nippon	Sika Deer	52	37	0.14780162	Plard *et al.* (2011)
Cervus timorensis	Timor Deer	95.5	33	0.461489432	Plard *et al.* (2011)
Cervus unicolor	Sambar	192	146	0.118948373	Plard *et al.* (2011)
Cervus mariannus	Philippine Deer	64	40.4	0.199798609	Wiles *et al.* (1999)
Dama dama	Fallow Deer	67	44	0.182622126	Plard *et al.* (2011)
Elaphodus cephalophus	Tufted Deer	18	18	0	Plard *et al.* (2011)
Elaphodus davidianus	Pere David's Deer	214	159	0.129016649	Plard *et al.* (2011)
Hippocamelus antisensis	Taruca	65	45	0.159700843	Barrio (2010)
Hippocamelus bisculus	Chilean Guemal	95	75	0.102662342	Plard *et al.* (2011)
Magammuntiacus vuquangensis	Giant Muntjac	45	34	0.121733597	Plard *et al.* (2011)
Mazama americana	Red Brocket	24.5	24.5	0	Plard *et al.* (2011)
Mazama goauzoupira	Gray Brocket	18	18	0	Plard *et al.* (2011)
Mazama rufina	Dwarf Red Brocket	12.5	12	0.017728767	Barrio (2010)
Moschus fuscus	Black Musk Deer	12.5	13	-0.017033339	Nowak (1999)
Muntiacus feae	Fea's Muntjac	19.5	22	-0.052388069	Geist (1998)
Muntiacus crinifrons	Black Muntjac	23	24.1	-0.020289207	Plard *et al.* (2011)
Muntiacus gonghanensis	Gongshan Muntjac	21	16	0.118099312	Plard *et al.* (2011)
Muntiacus muntjak	Muntjac	19	20	-0.022276395	Plard *et al.* (2011)
Muntiacus putaoensis	Leaf Deer	12	12	0	Plard *et al.* (2011)
Muntiacus reevesi	Chinese Muntjac	13.5	14	-0.015794267	Plard *et al.* (2011)
Muntiacus atherodes	Bornean Muntjac	18	16	0.051152522	Payne & Francis (1985)
Odocoileus hemionus	Mule Deer	112.5	55.5	0.306859539	Plard *et al.* (2011)
Pudu puda	South Pudu Deer	13	13.5	-0.016390416	Plard *et al.* (2011)
Pudu mephistophiles	Northern Pudu	13.16	13.84	-0.021880201	Geist (1998)
Tragulus javanicus	Lesser Mouse-Deer	2	1.5	0.124938737	Geist (1998)

Comparative analyses

We performed a phylogenetic reduced major axis regression (RMA) analysis between log10 (MBS) and log10 (FBS), with the phytools package (Revell 2012) in R 3.2.2 (R Core Team 2018). If Rensch's rule is verified, the slope (β) must be significantly higher than 1, but if β < 1 the rule is inverted, and if β = 1 the rule is not supported (Abouheif & Fairbain 1997; Fairbairn 1997). Comparative methods allow us to correct for statistical non-independence of biological data (Felsenstein 1985). Due the non-independence of species-level data, the use of comparative methods is necessary. Additionally, the use of RMA is appropriate because ordinary model I regressions are inadequate when both variables (response and predictors) are estimated with errors (Fairbairn 1997). In this case, regression models of type II are the best and recommended option (Sokal & Rohlf 1995).

To perform comparative analyses, we used the phylogenetic hypothesis from Hassanin *et al.* (2012). Since we have some species with size information that are not included in the phylogeny, we included them randomly from the genus node where they occur. This procedure was repeated 100 times, generating 100 phylogenetic trees and allowing us to account for phylogenetic uncertainty in our analyses (Rangel *et al.* 2015). Thus, the RMA phylogenetic analyses were conducted 100 times for each phylogenetic tree, as proposed by Martinez *et al.* (2015).

Results

Data overview

The body weight of analysed cervid species varied between 2 to 482.5 kg (mean = 87.70 kg) for males, and between 1.5 to 365 kg for females (mean = 60.58 kg) (**Table 1**). We observed a strong prevalence of male-biased sexual dimorphism (~70% of species). The highest male-biased SSD were found for *Cervus timorensis* (male = 95.5 kg, female = 33 kg). Conversely, from female-biased SSD species the difference between females and males were small, with the most dimorphic species being *Muntiacus feae* (male = 19.5 kg, female = 22 kg). When analysing the scaling of sexual dimorphism with body size, we found no evidence that SSD increases in relation to body mass in deer species. We analysed the relationship of log10 (MBM) versus log10 (FBM) and from these results we observed a mean of βRMA equal to 1.05 (p = 0.18) (**Figure 1**). This result do not support Rensch's rule in cervids.

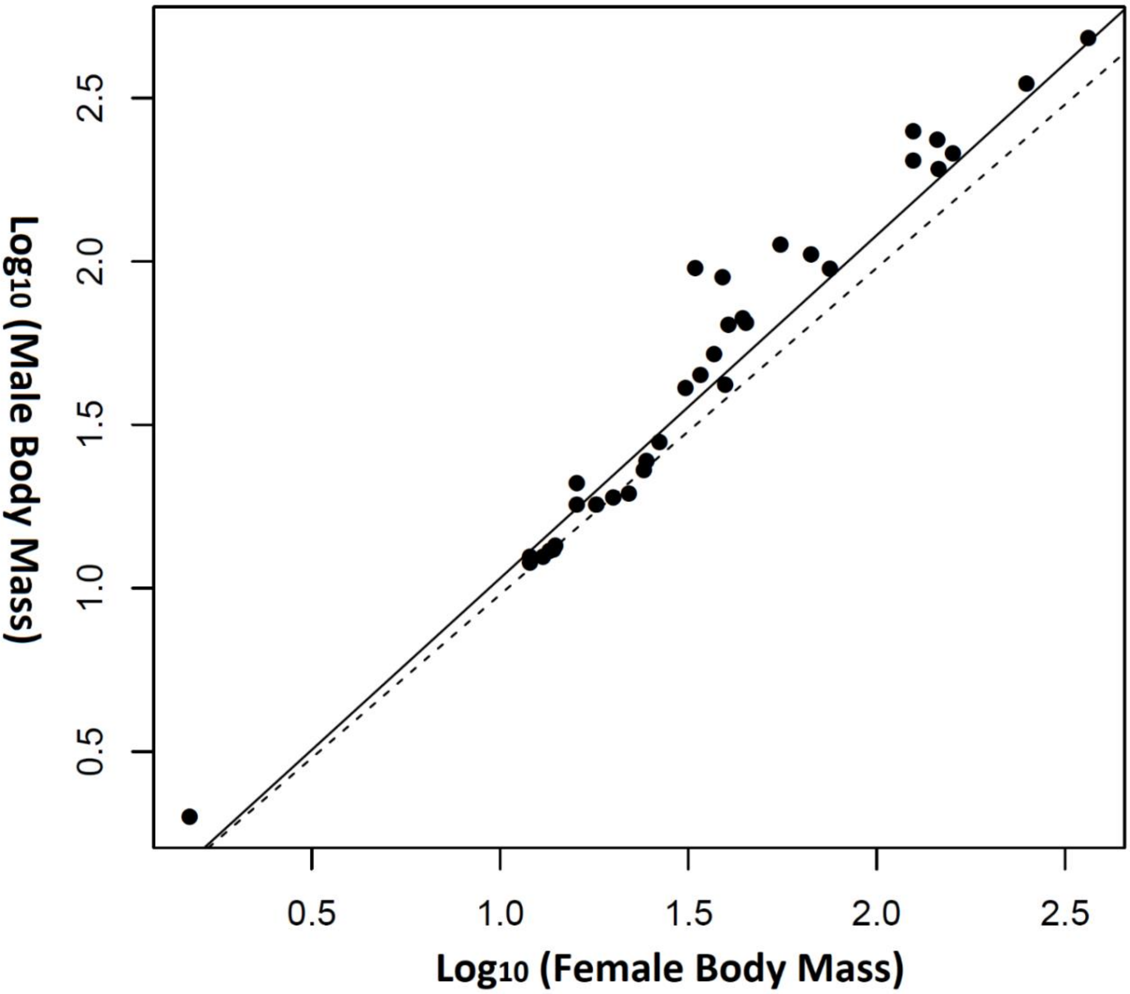

Figure 1. Reduced Major Axis (RMA) regressions between male body mass (log10) vs female body mass (log10) of 35 species of cervids. The solid line show the slope of regression and dashed line show de slope = 1.

Discussion

Our results showed that cervids display a large variation in body size and SSD. Because of the predominance of male-biased SSD we expected that, if Rensch's rule operates in this family, a hyperallometric relationship between male and female size (β > 1.0) indicating an increase in SSD with increasing body size. Nevertheless, our results showed an isometric relationship (β = 1.0) which means that SSD does not scale with body size in cervids which in consequence do not follow Rensch's rule.

Most mammal species show male-biased SSD (Fairbairn 2007). As known, sexual selection could not only drive SSD, but also be responsible for a significant fraction of the evolution of male bias (Jarman 1983; Isaac 2005; McPherson & Chenoweth 2012). The pattern recognized as Rensch's rule proposes that SSD increases when the body size in a male-biased species also increases (Rensch 1950; Abouheif & Fairbairn 1997). However, our results indicate that there is no significant increment in SSD with body size growth. Although some comparative analyses suggest the opposite (Abouheif & Fairbairn 1997; Fairbairn 1997, 2007), Rensch's rule has been widely questioned due the lack of clear mechanisms that may explain this pattern (Reiss 1989; Fairbairn 2013).

Different hypotheses were proposed to account for the covariation between SSD and body size (Martinez & Bidau 2016). Many studies that attempted to find evidences for Rensch's rule have serious methodological flaws and inappropriate statistical analyses (Abouheif & Fairbairn 1997). As proposed by many biologists, allometry consistent with Rensch's rule evolves as a response to sexual selection of male size (Fairbairn 1997, 2007, 2013). Thus, selection will happen more often in taxa with male biased size, as in cervids. Nevertheless, the rule lacks in consistency and the reproductive success of larger males may not increase the size difference between of males and females. Alternatively, some researchers suggest that SSD would emerge due a correlated evolutionary response in one sex to stronger sexual selection in another sex (Dale *et al.* 2007). In this case, SSD evolves as a by-product of genetic differences between males and females and their different responses to similar selective pressures. Another possible explaination is when females and males use different resources, being the natural selection the force that promotes the differentiation (Fairbairn 1997). When exist a strong stabilizing selection on female body size than on male size can lead to increased SSD when resources are plentiful, independent of sexual selection (Colwell 2000). Therefore, our fail to detect this pattern in extant species may due to our inability to directly analyse these differences between males and females across lineages (Blanckenhorn *et al.* 2007).

Rensch's rule is thus strongly controversial and numerous exceptions exist in mammals (e.g., Canidae, Felidae, Ctenomyidae) (Lindenfors *et al.* 2007; Martinez *et al.* 2014; Martinez & Bidau 2016; Stevens & Platt 2015; Bidau & Martinez 2017). The trend to follow or not Rensch's rule seems not to be phylogenetically structured. This is evident in some recent studies of domesticated animals. In a recent study, Bidau & Martínez (2017) showed that domesticated mammals such as dogs and cats, follow Rensch's rule while their ancestors (species of Canidae and Felidae) do not. Possible reason for the existence of taxa that follow Rensch's rule and other that do not may be the intrinsic complexity of the regulation of body size. Body size has a strong phylogenetic component (Diniz-Filho *et al.* 2007) but it is also deeply affected by natural and sexual selection (Smith & Lyons 2013). Furthermore, the size of a species is related to many ecological traits (e.g. number of offspring, home range, thermal tolerance, number of parasites) (Morand & Poulin 1998; Olalla-Tárraga *et al.* 2015). In carnivores for example, the number of parasites can increase SSD (Huang *et al.* 2015), while species with larger body size may also host more parasites (Morand & Poulin 1998). The association of body size with multiple ecological traits may lead reserachers to find an association between body size and SSD. However, these relationships not necessarily indicate that body size affects the species SSD. In this sense, studies of Rensch's rule must consider the direct and indirect effects of body size on SSD. Thus, an alternative to this approach is to use ecological characteristics jointly with body size to understand the ultimate causes that modulate SSD.

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