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ECOLOGICAL SOUNDINGS

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Rensch's rule—Definitions and statistics

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Abstract

Issue: Sexual size dimorphism is thought to vary in a predictable manner with overall body size, a pattern named "Rensch's rule". The rule is thought to suggest different predictions for taxa with female- and male-biased dimorphism. This leaves taxa where both types of dimorphism are common in limbo. Rensch's rule is usually estimated using the reduced major axis (RMA) slope of a regression of male size on female size. A slope steeper than one shows support for the rule.

Evidence: We show that the predictions of Rensch's rule for male- and female-biased taxa are, in fact, the same and offer a unified definition of the rule. Using numerical examples and data from the literature, we show that RMA and ordinary least squares (OLS) methods of line fitting can produce conflicting results, suggesting that RMA is a less conservative way to test the rule.

Conclusion: We recommend that both line-fitting methods are used to estimate Rensch's rule, with strong support being claimed only when the results of both agree with each other. Alternatively, we suggest that tests are conducted in a way that agrees with the definition of the rule (i.e., that size dimorphism is regressed on the mean size of males and females of the species).

KEYWORDS

ordinary least squares, ratios, reduced major axis, regression, sexual size dimorphism, slopes, variance

1 | INTRODUCTION

Bernhard Rensch lived and breathed ecological and evolutionary rules. He named Allen's, Gloger's and Cope's rules (the last of these erroneously; Stanley, 1973) and did much to promote Bergmann's rule (Rensch, 1938). Therefore, it is perhaps surprising that the rule that now bears his name received such little attention from Rensch. The paper in which he introduces it (Rensch, 1950; in German) is mostly concerned with the sizes of differenct body parts rather than with body size per se. In his magnum opus, the book "Evolution above the species level" (Rensch, 1959), Rensch paid "his" rule little attention. Discussion of what is now termed "Rensch's rule" starts mid-paragraph at the bottom of page 157 and is interspersed with a long table taking all of page 158 and most of page 159 before ending a few short sentences later. He was involved in the study and naming of so many rules that it would appear he largely disregarded this one.

Rensch's rule is a pattern whereby size is more female biased (i.e., the female size to male size ratio is higher) the smaller the body size of the species, whereas it becomes increasingly more male biased the larger-bodied the species is (see "simpler definition"). Reference to this phenomenon as "Rensch's rule" gained momentum with the influential mid-1990s publications of Daphne Fairbairn and Ehab Abouheif (Abouheif, 1995; Abouheif & Fairbairn, 1997). Before 1995, the term "Rensch's rule" was rarely used. A Google Scholar search for "Rensch's rule" of pre-1995 papers yielded only 18 hits, and some of them use the term to describe other phenomena (e.g., Murrill, 1960; Precht et al., 1973; Pulliainen et al., 1981). Others refer to cases of increasing sexual size dimorphism (SSD) with size regardless of which sex was the larger (e.g., Earhart & Johnson, 1970; Kappeler, 1990; Nudds & Kaminski, 1984; Selander, 1966).

Abouheif and Fairbairn (1997) deserve credit for more than simply reviving the term "Rensch's rule". They carried out the first meta-analysis to assess its validity and pioneered the way it is studied today. They follow Rensch's (1959) definition of the rule (also cited by Abouheif, 1995; Fairbairn & Preziosi, 1994; Selander, 1966): "sexual size dimorphism (size of the larger sex/size of the smaller sex) will be positively correlated with mean body size (hyperallometry) in taxa in which males are the larger sex and negatively correlated with mean body size (hypoallometry) in taxa in which females are the larger sex" (Abouheif & Fairbairn, 1997).

2 | DOES IT MATTER WHETHER MALES OR FEMALES ARE THE LARGER SEX?

Abouheif and Fairbairn (1997) suggested that if females are larger in 80% of the species in a taxon then the SSD in this taxon can be characterized as being female biased, whereas in taxa where males are larger in > 80% of species the SSD can be characterized as being male biased. This, however, leaves much middle ground, consisting of taxa with no strong bias for either sex. Furthermore, 80% is arbitrary, and running separate regressions for female- and male-biased taxa limits sample size. We contend that defining a priori which sex is generally larger is unnecessary, because under Rensch's rule the same allometric pattern is predicted in all cases (Figure 1). We, therefore, suggest a simpler definition that, while perfectly retaining Rensch's rationale and making identical predictions to the widely accepted definition, does not necessitate defining which sex is larger:

> Rensch's rule is an empirical pattern whereby the ratio of female size to male size is larger the smaller the body size of the species.

We note that this implicitly suggests that this definition can be reversed to state that size becomes increasingly more male biased the larger-bodied the species is, and authors will choose which sex to focus on in any particular study. We stress, however, that this definition is only a rewording of previous definitions (Abouheif & Fairbairn, 1997; Rensch, 1959), but potentially one that is somewhat clearer and easier to implement.

3 | REDUCED MAJOR AXIS REGRESSION IS LESS CONSERVATIVE

Abouheif and Fairbairn (1997) also set the stage on the way Rensch's rule is tested to this day. They argued against using size dimorphism against the size of one or both sexes, because this encounters the well-known problem of regressing a ratio against its denominator. The solution offered by Abouheif and Fairbairn (1997) was elegant: they suggested regressing male size on female size (or vice versa, but

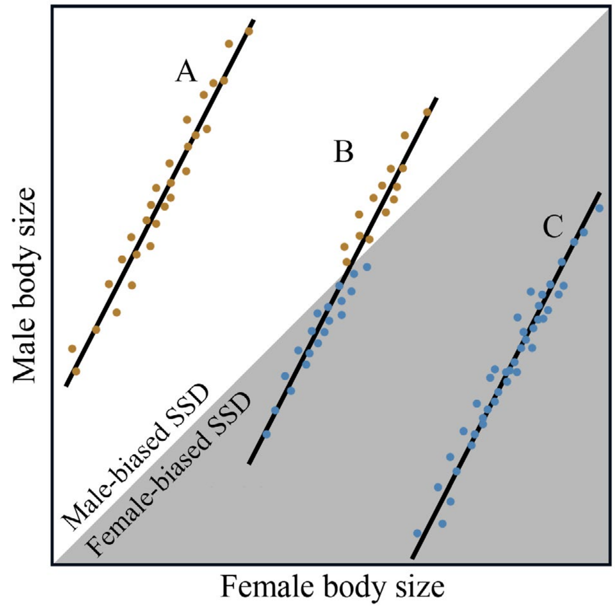

FIGURE 1 The predictions of Rensch's rule (modified from Portik et al., 2020). A cartoon depicting three hypothetical taxa (A–C), all of which follow Rensch's rule. Male size is on the *y* axis and female size on the *x* axis. In the grey region (blue dots), females are larger than males, whereas in the white region (brown dots), males are larger. Where the two regions meet, sexes are of equal size (intercept of zero and isometric slope = 1). For taxon A, sexual size dimorphism (SSD) is always male biased. For taxon B, SSD is female biased in small-bodied taxa and male biased in large-bodied taxa. For taxon C, SSD is always female biased. All share a male versus female regression slope steeper than one (hyperallometry), with SSD becoming more female biased as size decreases. Therefore, treating the three scenarios differently is unwarranted. Note that the same data with female size depicted on the *y* axis and male size on the *x* axis will result in all slopes being shallower than one (hypoallometry).

this version seems much more commonly used); a slope steeper than one is indicative of Rensch's rule.

Furthermore, Abouheif and Fairbairn (1997) advocated using reduced major axis regression (RMA), rather than ordinary least squares (OLS) regression, because they correctly pointed out that "Rensch's rule predicts a greater evolutionary divergence in male size than in female size, regardless of which sex is larger". Indeed, RMA regression has the added benefit of its slope being the ratio of the variance on the *y* axis divided by the variance on the *x* axis (i.e., the variance in male size divided by the variance in female size; Fairbairn, 1997; Price & Phillimore, 2007; Smith, 2009). Thus, an RMA slope steeper than one also implies higher size variance in males, as Rensch's rule predicts (e.g., Starostová et al., 2010).

4 | EVIDENCE

We contend that showing that male size is more variable than female size is, in itself, insufficient to support Rensch's rule. Table 1 shows

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TABLE 1 Hypothetical numerical examples where larger male size variance does not necessarily imply that Rensch's rule holds

		Male size						
Species	Female size	a	b	c	d	e	f	g
A.								
א	1	8	0.25	2	2	4	7.5	0.5
ב	2	6	0.25	4	3	6	5.5	1.5
ג	3	4	0.25	6	4	6	4.5	2.5
ד	4	2	0.25	8	5	4	4	3.5
ה	1	8	4	0.25	3	0.25	0.5	1.5
ו	2	6	4	0.25	4	0.67	2.5	2.5
ז	3	4	4	0.25	5	1.5	3.5	3.5
ח	4	2	4	0.25	6	4	4	4.25
B.								
Variance	1.43	5.71	4.02	9.30	1.71	5.08	4.21	1.58
OLS slope	NA	−2.00	0.00	1.00	1.00	0.60	0.00	0.96
RMA slope	NA	−2.00	0.00	2.55	1.10	1.89	0.00	1.05
R^2	NA	1.00	0.00	0.15	0.83	0.10	0.00	0.84

A. Seven datasets (a–f) of eight species (Hebrew letters א–ח) each. Female sizes are identical in all datasets (varying from one to four), but male sizes are dataset specific.

B. The size variances of females (1.43 in all cases) and males, and the slopes of OLS and RMA regressions of male size on female size in each dataset (R^2 values are for the OLS regression).

NA = not assessed; OLS = ordinary least squares; RMA = reduced major axis.

seven hypothetical numerical examples of datasets in which female size is less variable than male size. The RMA slopes, however, are shallower than one in three of these cases, and the OLS slopes are never steeper than one. Furthermore, in two cases the OLS slope is shallower than one, whereas the RMA slope is steeper (Table 1; see supplementrary Figures S1 for OLS and RMA graphs of male vs. female size in these examples).

The regression of ratios is not as problematic as is usually perceived. Smith (1999) has shown that this becomes much less of an issue the more tightly the sizes of males and females are correlated, as is usually the case in large-scale studies of SSD, where very small and very large animals are compared (elephant females might be smaller than males, but they are still elephant sized, not elephant shrew sized). RMA regression enjoys a reputation of being more adequate when both the *x* and *y* variables are measured with error, as is certainly the case in studies of size and size dimorphism. This perception, however, has often been challenged (e.g., Kilmer & Rodríguez, 2017; Smith, 2009; Warton et al., 2006).

A significant drawback of RMA line fitting, in comparison to OLS fitting, in tests of Rensch's rule is that it is less conservative. The RMA slope equals the OLS slope divided by the correlation coefficient, *r* (Gould, 1974, 1975; Smith, 2009). Thus, RMA will tend to produce slopes consistent with Rensch's rule more often than when using OLS. The closer the slope is to one, the more acute the problem. Thus, in taxa where Rensch's rule is a weak pattern, an OLS regression is likely to fail to reject a null (or even show a slope significantly shallower than one), whereas RMA regression might well provide support for Rensch's rule even in cases where sexual dimorphism does not vary with size. In our recent study of Rensch's rule (T. Liang, S. Meiri, & L. Shi, unpublished observations), we found evidence for Rensch's rule across lizards and in most lizard clades, using RMA. In contrast, OLS regressions on the same datasets suggested either no significant deviations from the null or even the opposite patterns, but they never supported Rensch's rule. For example, for the Pleurodonta we obtained an RMA slope of 1.038, which is significantly steeper than one ($p = .021$, $n = 742$ species in a phylogenetic RMA analysis, with regression lines fitted by RMA) whereas a phylogenetic generalized least squares slope (using OLS for line fitting) calculated for the same dataset was significantly shallower than one (0.933 ± 0.017, 95% confidence interval of 0.900–0.966). Likewise, Jiménez-Arcos et al. (2017), reported support for Rensch's rule in *Sceloporus* lizards, based on an RMA slope of 1.17 [$p_{(\text{slope}=1)} = .02$] and a correlation coefficient (*r*) of 0.8. With such a correlation the OLS slope is 0.94. Thus, had they used OLS, the conclusion would be qualitatively different. We do not contend that the use of OLS is inherently preferable to RMA, and the relationship of the RMA and size variance is compelling, but if we are not sure whether a pattern holds, a conservative approach might be preferable. Rensch's rule, however, is nearly invariable examined with RMA alone. If the pattern is strong (i.e., if it has real and interesting evolutionary drivers behind it), it would be apparnet even in the more conservative OLS. We, therefore, suggest that both methods are used when studying the rule, to ensure that the evidence for (or against) the rule is more compelling (e.g., as is done in the studies by Blanckenhorn et al., 2007, Frýdlová & Frynta, 2010, 2015; Frynta et al., 2012).

Another issue with any regression of male size on female size is that it does not test sexual dimorphism directly. We cannot tell, for example, whether much of the variance in SSD is explained by body size. Whether the worry about regression of a ratio against its denominator is justified or not, especially when SSD is defined in complex ways [e.g., the common Lovich & Gibbons (1992) ratio, whereby SSD is defined as (female size/male size minus one) if females are the larger sex and as minus (male size/female size minus one) if males are the larger] needs to be demonstrated (see Supplementary Figure S2 and Supplementary Table S1 for examples based on data in Table 1). This should be done not with random numbers but with randomizations that are realistic with respect to the variance of female and male sizes, in addition to the correlation between them. In one of the most elegant presentations of this issue of which we are aware, Smith (1999) showed that spurious correlations between the nominator and denominator were not an issue in any of the datasets of SSD he examined and any of the SSD indices he tested. As Smith (1999) has demonstrated, "If there is a high correlation between X1 and X2 and approximately equal CVs in the numerator and denominator (both of which are common with sexual dimorphism data), the X1/X2 ratio is nearly independent of X2" (note that CV refers to the coefficient of variation).

A return to analyses of SSD, the response variable of interest, in terms of its relationship with body size, the predictor of interest (perhaps as the average size between males and females of the same species), might thus be warranted. In the data of Table 1, regressing the Lovich–Gibbons index against (female size + male size)/2 will give a negative slope, supporting Rensch's rule, in all cases except dataset d (where the OLS slope is 0.296). Dataset d, however, is the most realistic, because it is the only one in which female and male sizes are positively and tightly correlated (as is likely to occur within taxa in nature).

Rensch's rule is not the only controversial generalization in which the use of RMA might influence analytical results. In tests of the island rule, Lomolino (1985) has advocated the use of regressions of body sizes of island animals on the sizes of their mainland counterparts to avoid regressing a ratio against its denominator. One of us (S.M.) has advocated the use of RMA regressions, arguing that this is appropriate in cases where both variables are measured with error (Meiri, 2007; but see Warton et al., 2006). Price and Phillimore (2007) recommended using RMA regressions because under the island rule, size variance is lower on islands, which will manifest, if true, in an RMA slope shallower than one. The difference between analyses of the island rule and Rensch's rule in this respect is that whereas RMA regression is a liberal test of Rensch's rule (where the expected slope is > 1), it is a conservative test of the island rule (where the slope is expected to be shallower than one). In both cases, the correlation between body sizes (on islands versus the mainland, or of females versus males) is likely to be tight. The OLS and RMA slopes should thus be similar (because *r* is close to one; also see Blanckenhorn et al., 2007). Therefore, if the two techniques do not yield consistent results, the phenomena tested are likely to be weakly supported, at best.

5 | CONCLUSIONS

We find that a definition of Rensch's rule that does not make a distinction between male-biased and female-biased taxa is clearer than Rensch's original and still commonly used definition. We suggest that both OLS and RMA regression are used when testing Rensch's rule, because RMA is less conservative than OLS. Tests of size ratio against body size might, one way or another, be at least as informative as regressing the size of one sex against the sex of the other when studying this rule.

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DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this article because no datasets were generated or analysed during the present study, except the one given in full in Table 1. Supporting Information figures and Supporting Information Table S1 are archived in Dryad (datadryad.org), https://doi.org/10.5061/dryad.rv15dv476.

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BIOSKETCH

Shai Meiri is interested in tetrapod evolution, natural history, macroecology, biogeography and conservation.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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