



E-ISSN: 2788-8428
 P-ISSN: 2788-8436
 ZEL 2022; 2(1): 30-35
 Received: 19-11-2021
 Accepted: 21-12-2021

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Does sexual size dimorphism vary with time in red millipedes *Centrobolus* Cook, 1897?

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Abstract

Sexual Size Dimorphism (SSD) variation with time was studied in red millipedes. Time (1964.7±29.4 years) was correlated with SSD in volumes in the red millipede genus *Centrobolus*. There was an marginal absolute difference ($T=1.271239$, $n=2$, 5 , $p=0.071465$) but not a relative difference ($T=0.914933$, $d.f.=5$, $p=0.201098$) between mean $\log SSD_{1+2}$ (0.065050 mm^3) and mean $\log SSD_3$ (0.156442 mm^3). This converted back into an absolute difference of $8.35 \mu\text{m}^3$ in mean volume. Neither an inverse Rensch's rule nor Rensch's rule pattern could be confirmed from $\log SSD$ with body size ($r=0.25608594$, $Z \text{ score}=0.69296229$, $n=10$, $p=0.24416654$). Systematic variation of SSD with time was shown in two examples in *Centrobolus* with higher SSD in more recent times being faster in the smaller *C. digrammus* (58% more female-biased after 32 years) and slower in the larger *C. ruber* (25% more female-biased after 60 years). There was a relative difference in size between *C. digrammus* and *C. ruber* compared to recent measurements of four species ($T\text{-score}=6.242725$, $d.f.=4$, $p=0.002$). *C. digrammus* and *C. ruber* were relatively larger sizes after the time ($T\text{-score}=3.858367$, $d.f.=2$, $p=0.030541$).

Keywords: Dimorphic, female, male, length, morphology, time, width

1. Introduction

Numerous studies are finding animal taxa have female-biased SSD and mostly disobey Rensch's rule including corvids and pinnipeds [1, 2, 5-11, 13-17, 19-26, 28-33, 35-38, 40-42]. The finding of converse or inverse Rensch rule implies SSD increases with body size when females are larger [1, 2, 5-11, 13-17, 19-26, 28-33, 35-38, 40-42]. This has implications in the genus *Centrobolus* because females are larger than males and SSD increases hypoallometrically with body size [5-10].

The forest genus *Centrobolus* of diplopods belonging to the Order Spirobolida found along the eastern coast of southern Africa was the subject of this study. Its northern limits are on the east coast of southern Africa being -17° latitude South (S) and its southern limits -35° S; from the Cape Peninsula to Beira in Mocambique in all the forests of the coastal belt [4]. As essentially shade-loving Diplopoda, the members of the genus are represented by 39 species in these litoral forests of the eastern half of the subcontinent [4]. Sexual size dimorphism (SSD) in volumes is compared across time [3, 4, 14, 18]. The hypothesis that there is no SSD correlation with time was tested.

2. Materials and Methods

Four valid species were identified as belonging to the genus *Centrobolus* Cook, 1897 (Table 1). Millipede localities were obtained from the Mating dynamics of South African forest millipedes *Centrobolus* (Diplopoda: Pachybolidae) [4]. SSD was calculated from the publication of collected material over three dates [4, 34, 39]. SSD was calculated as the ratio of female volume to male volume. SSD and differences in time were checked for correlations with female body size using the Pearson Correlation Coefficient calculator (<https://www.gigacalculator.com/calculators/correlation-coefficient-calculator.php>). Male and female collection dates were at the same time except for *C. ruber* where only male data is given [39]. Tests for normality were conducted (<https://www.socscistatistics.com/tests/kolmogorov/default.aspx>). A Lilliefors test was used to test for normality of time data at <http://www.statskingdom.com/kolmogorov-smirnov-test-calculator.html>. Six potential measurements for the time were 1928, 1934, 1966, 1967, 1995, and 1998. To test between divergent and convergent series a series integral test calculator was used (<http://www.symbolab.com/solver/series-integral-test-calculator>). Body sizes were tested for differences over time with a P-value Calculator (<https://www.gigacalculator.com/calculators/p-value-significance-calculator.php>).

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3. Results

There was a marginal absolute difference between mean log SSD₁₊₂ (0.065050 mm³) and mean log SSD₃ (0.156442 mm³) (Figure 1: T=1.271239, n=2, 5, p=0.071465) but not a relative difference of mean log SSD₁₊₂ (0.065050 mm³) and mean log SSD₃ (0.156442 mm³) (T=0.914933, d.f.=5, p=0.201098) (Table 1). There was also a marginal absolute difference (0.135919 mm³) between the past (0.065050 mm³) and present (0.200969 mm³) SSD for pooled *C. digrammus* + *C. ruber* (T=1.994615, n=2, 2, p=0.092119). SSD was normally distributed (D=0.15168, n=22, p=0.63788). Time was normally distributed (D=0.2067, n=6, p=0.91609). Mean time was 1964.66667 Anno Domini (A. D.). and median time was 1966.5 A. D. Standard deviation in time was 29.405215 years. An integral test showed both the SSD₁₊₂ and SSD₃ series (Table 2) diverged. Neither a Rensch nor an inverse Rensch's rule pattern was confirmed here (r=0.35728793, Z score= 0.74754699, n=7 pairs, p=0.22736665) (Table 3). *C. digrammus* male length was normal (D=0.3, n=7, p=0.664); male width was normal (D=0.24906, n=7, p=0.69292); and female width was normal (D=0.27926, n=7, p=0.55343). The mean SSD of *C. digrammus* was 1.28 (S.D.=0.41012, n=2) and *C. ruber* was 1.45 (S.D.=0.21213, n=2). There was no difference in SSD between *C. digrammus* and *C. ruber* (t=-0.521, n=2,2,

p=0.6545). Mean SSD were not absolutely different (T-score=-0.630358, d.f.=2, p=0.296440) and not relatively different (T-score=-0.622882, d.f.=2, p=0.298460). The mean size of *C. ruber* was 1704.575 (S.D.=164.22555, n=2) and *C. digrammus* was 751.465 (S.D.=331.97956, n=2). Mean size differences between *C. digrammus* and *C. ruber* were marginally significant (t=3.643, d.f.=2, p=0.0678). There was no absolute difference in size between *C. digrammus* and *C. ruber* compared to recent measurements of four species (T-score=1.144381, d.f.=1.5154, p=0.102870). There was a relative difference in size between *C. digrammus* and *C. ruber* compared to recent measurements and four species (Figure 2: T-score=6.242725, d.f.=4, p=0.001678). *C. digrammus* and *C. ruber* were relatively different in time (Figure 3: T-score=3.858367, d.f.=2, p=0.030541). The two *C. inscriptus* SSD means were not significantly different (t=0.308, d.f.=133, p=0.7585). *C. fulgidus* SSD was not different to *C. inscriptus* mean SSD (t=0.047, d.f.=11, p=0.9634). *C. ruber* SSD was not different to *C. inscriptus* mean SSD (t=0.055, d.f.=18, p=0.9566). *C. fulgidus* SSD did not differ from *C. ruber* SSD (t=0.032, d.f.=27, p=0.9744). *C. fulgidus* SSD did not differ from *C. digrammus* mean SSD (t=-0.035, d.f.=11, p=0.9730). *C. inscriptus* SSD did not differ from *C. digrammus* SSD (t=0.040, d.f.=2, p=0.9719).

Table 1: Species in the millipede genus *Centrobolus* Cook, 1897, with SSD recorded at three different times (1-3). Two mean measurements are included for *C. inscriptus*.

Species	SSD ₃	SSD ₂	SSD ₁
<i>C. fulgidus</i>	1.48947444		
<i>C. inscriptus</i>	1.20538504 1.33693499		
<i>C. ruber</i>	1.60428011		1.35849057
<i>C. digrammus</i>	1.57274594	0.993214801	-

Table 2: Four species in the millipede genus *Centrobolus* Cook, 1897, with log SSD recorded at three different times (1-3). Two mean measurements are included for *C. inscriptus*.

Species	log SSD ₃	log SSD ₂	Log SSD ₁
<i>C. fulgidus</i>	0.173033055		
<i>C. inscriptus</i>	0.0811257971 0.12611029		
<i>C. ruber</i>	0.205280199		0.133056628
<i>C. digrammus</i>	0.196658573	-0.00295681716	

Table 3: Four species in the millipede genus *Centrobolus* Cook, 1897, with log SSD and female body size recorded at four different times (1-4). Two mean measurements are included for *C. inscriptus*.

Species	log SSD ₃	Female size ₃	log SSD ₂	Female size ₂	Log SSD ₁	Male size ₁
<i>C. fulgidus</i>	0.173033055	1917.11		1888.47		
<i>C. inscriptus</i>	0.0811257971 0.12611029	2221.16		2221.16		
<i>C. ruber</i>	0.205280199	1820.70		1811.93	0.133056628	1588.45
<i>C. digrammus</i>	0.196658573	986.21	-0.00295681716	516.72		

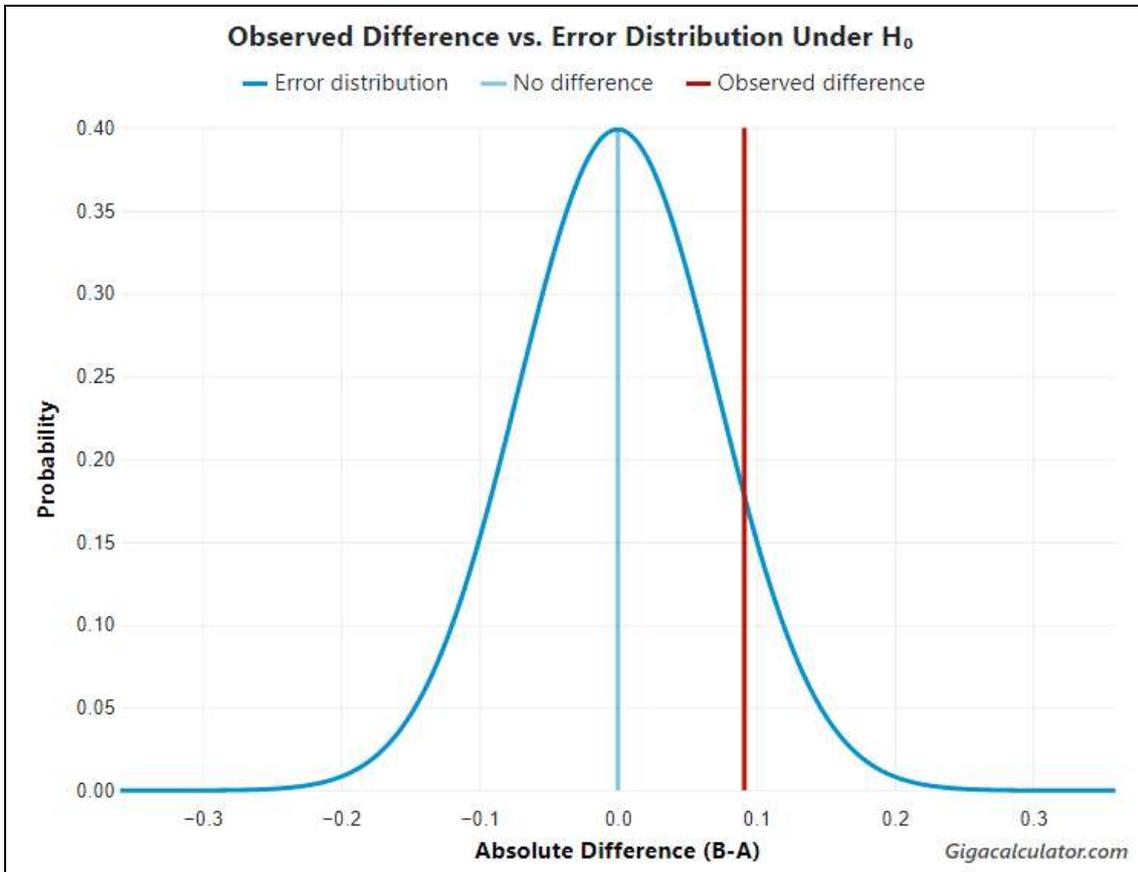


Fig 1: P-value showing marginal absolute difference (0.091392 mm^3) in \log Sexual Size Dimorphism (x-axis) over time in *Centrobolus* Cook, 1897.

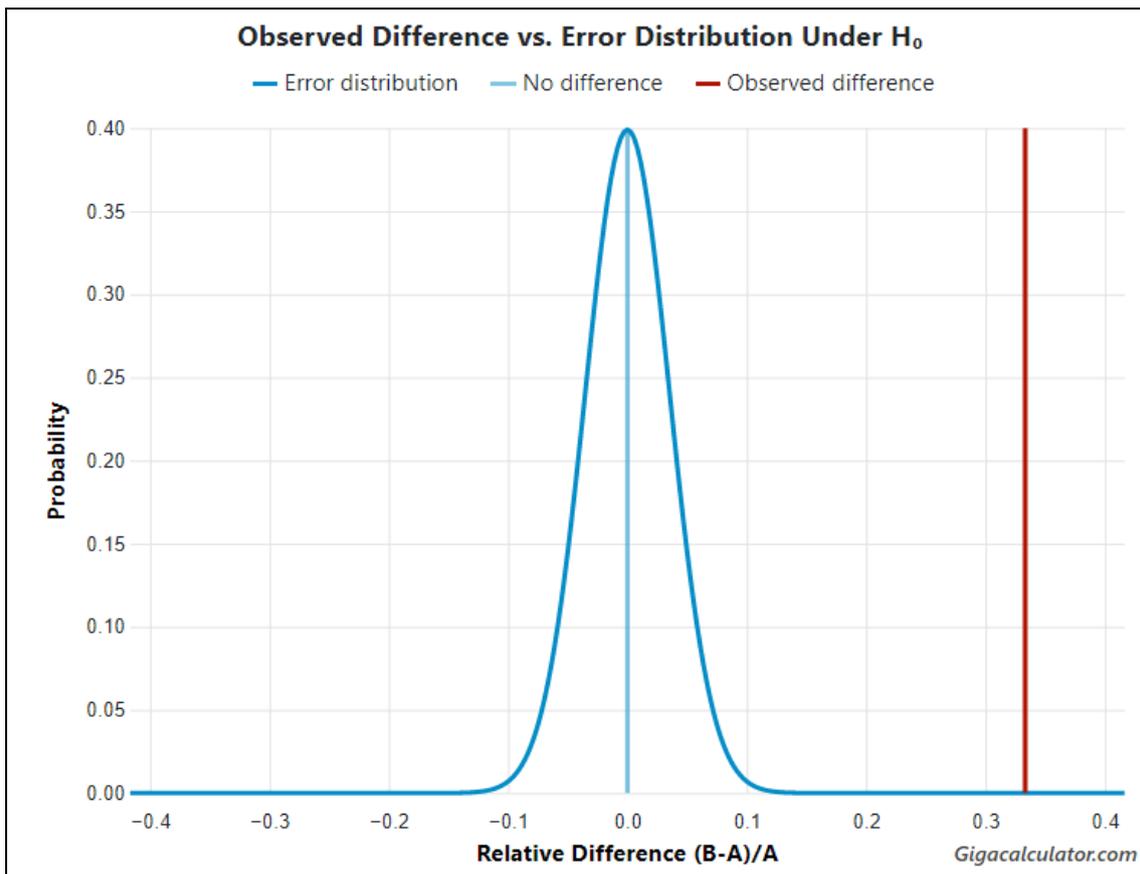


Fig 2: P-value showing relative size differences (0.333341 mm^3) between *C. digrammus* and *C. ruber* pooled over time (1052.5850 mm^3 to 1403.4550 mm^3).

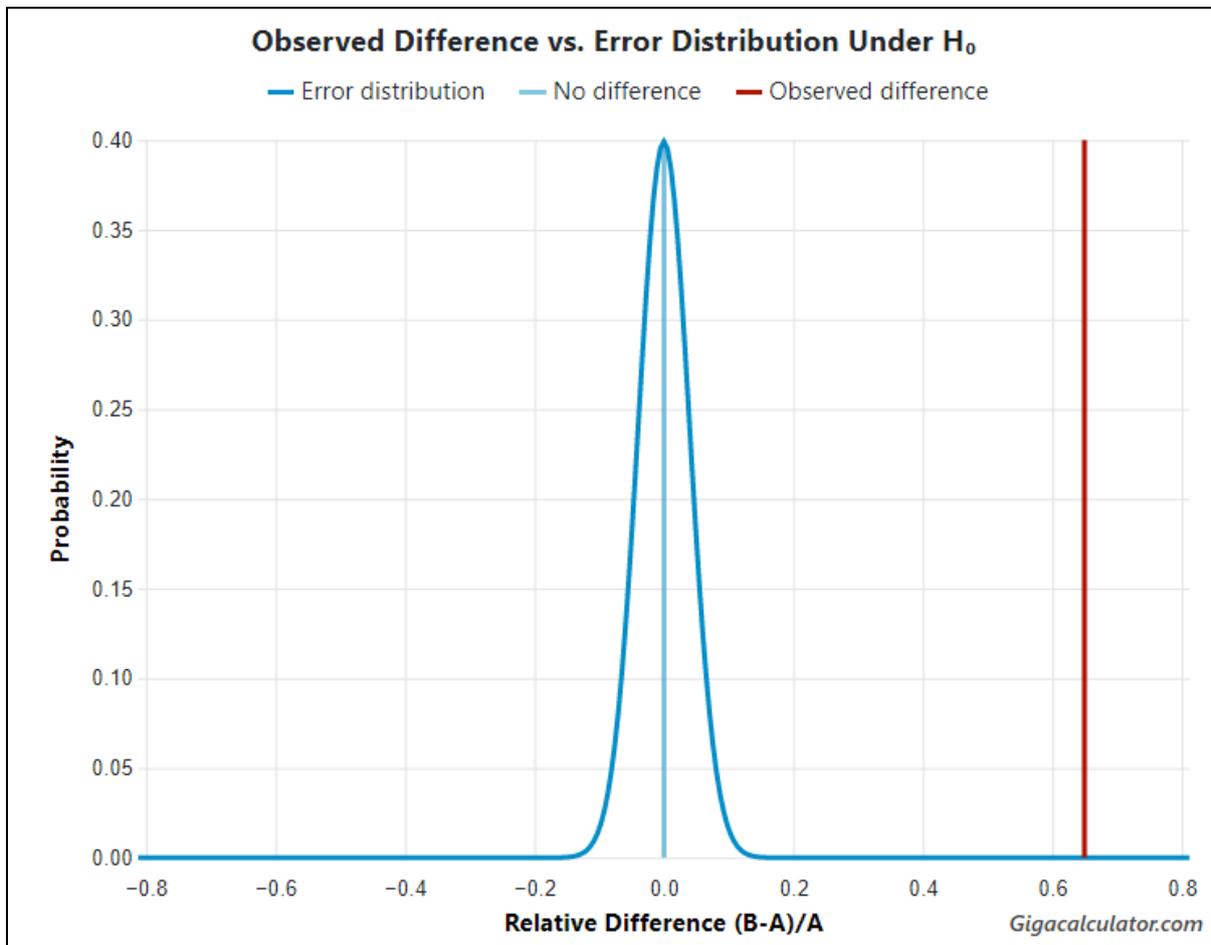


Fig 3: P-value showing a significant relative difference (0.649553 mm³) between past size (1052.5850 mm³) and present size (1736.2950 mm³) in *Centrobolus* Cook, 1897.

4. Discussion

The null hypothesis that SSD did not change over time was falsified. A marginal absolute difference in SSD and a relative difference (increase) in size values with time (1928-1998) were found. The species were relatively smaller in the past. This study supports time as a reference character and as a predictor of SSD and size in *Centrobolus*. SSD and size increase over time and tends towards female-biased dimorphism in *C. digrammus* and *C. ruber*. SSD increase with time is only directly comparable in these two species and is explained as a positive relationship between past and present SSD. *C. digrammus* had female-biased SSD (1.57) and this was lower in the past (0.99). *C. ruber* also had female-biased SSD (1.60) and was lower in the past (1.36). This does not concur with the shifts in SSD found in ostracods across mass extinctions [27].

In this study, neither a Rensch nor an inverse Rensch rule was confirmed [31-32]. This is possibly due to the small sample size or the likelihood that an (inverse) Rensch rule is not evident over the time frame. Rensch's rule and Inverse Rensch's rules are both generalizations that fail to consider true variation across time [31-32]. This study successfully illustrates SSD variation across time in two species where females have become large due to a fecundity advantage [43]. Furthermore, this study supports the finding that both niche and fitness differences increase with size differences [12].

The finding of a temporal change in SSD is consistent with r/K selection theory because it was faster in the smaller *C. digrammus* (58% more female-biased after 32 years) and slower in the larger *C. ruber* (25% more female-biased after

60 years). These two exemplar species are not extremes and represent moderate SSD within the genus *Centrobolus*. A range of similar long-term SSD variations with time probably occurred in the past with the majority of the SSD being evolution towards female-biased SSD [43]. The finding of a temporal change towards female-biased SSD is also consistent with hypoallometry which is already established in this genus [5-10]. *C. digrammus* and *C. ruber* were relatively larger sizes after the time intervals (32 and 60 years) and are consistent with a hypoallometric function. The finding of a marginal absolute difference in SSD and a relative difference (increase) in size values with time is consistent with hypoallometric increases in SSD with size.

5. Conclusion

SSD increased systematically faster in smaller *C. digrammus* and slower in larger *C. ruber*. This is consistent with the r/K selection theory. Neither a Rensch nor an inverse Rensch rule was confirmed in this study.

6. Acknowledgements

Marié Theron from Stellenbosch University assisted [34, 39].

7. References

1. Bidau CJ, Martí DA, Castillo ER. Rensch's rule is not verified in melanopline grasshoppers (Acrididae). *Journal of Insect Biodiversity*. 2013;1(12):1-14.
2. Colleoni E, Denoël M, Padoa Schioppa E, Scali S, Ficetola GF. Rensch's rule and sexual dimorphism - in

- salamanders: patterns and potential processes. *Journal of Zoology*. 2014;293:143-151.
3. Cook OF. New relatives of *Spirobolus giganteus*. *Brandtia* (A series of occasional papers on Diplopoda and other Arthropoda). 1897;18(2):73-75.
 4. Cooper M. Mating dynamics of South African forest millipede *Centrobolus* (Diplopoda: Pachybolidae). Thesis, University of Cape Town, 1998, 1-141.
 5. Cooper M. Re-assessment of Rensch's rule in *Centrobolus*. *Journal of Entomology and Zoology Studies*. 2017;5(6):2408-2410.
 6. Cooper M. Allometry in *Centrobolus*. *Journal of Entomology and Zoology Studies*. 2018;6(6):284-286.
 7. Cooper M. *Centrobolus* size dimorphism breaks Rensch's rule. *Arthropods*. 2018;7(3):48-52.
 8. Cooper M. *Centrobolus* size dimorphism breaks Rensch's rule. Scholars' Press, Mauritius. 2018, 1-48. ISBN: 978-3-659-83990-0.
 9. Cooper MI. Sexual size dimorphism and the rejection of Rensch's rule in Diplopoda (Arthropoda). *Journal of Entomology and Zoology Studies*. 2018;6(1):1582-1587.
 10. Cooper MI. Trigoniuclid size dimorphism breaks Rensch. *Journal of Entomology and Zoology Studies*. 2018;6(3):1232-1234.
 11. De Lisle SP, Rowe L. Correlated Evolution of Allometry and Sexual Dimorphism across Higher Taxa. *The American Naturalist*. 2013;182(5):630-639.
 12. Gallego I, Venail P, Ibelings BW. Size differences predict niche and relative fitness differences between phytoplankton species but not their coexistence. *The ISME Journal*. 2019;13:1133-1143.
 13. Guillermo-Ferreira R, Novaes MC, Lecci LS, Bispo PC. Allometry for sexual size dimorphism in stoneflies defies the Rensch's rule. *Neotropical Entomology*. 2014;43:172.
 14. Hamer ML. Checklist of Southern African millipedes (Myriapoda: Diplopoda). *Annals of the Natal Museum*. 1998;39(1):11-82.
 15. Herczeg G, Gonda A, Merilä J. Rensch's rule inverted – female-driven gigantism in nine-spined stickleback *Pungitius pungitius*. *Journal of Animal Ecology*. 2010;79(3):581-588.
 16. Husak JF, McGuire JA. Does 'gliding while gravid' explain Rensch's rule in flying lizards? *Biological Journal of the Linnean Society*. 2014;113:270-282.
 17. Jannot JE, Kerans BL. Body size, sexual size dimorphism, and Rensch's rule in adult hydropsychid caddisflies (Trichoptera: Hydropsychidae). *Canadian Journal of Zoology*. 2003;81:1956-1964.
 18. Lawrence RF. The Spiroboloidea (Diplopoda) of the eastern half of Southern Africa*. *Annals of the Natal Museum*. 1967;18(3):607-646.
 19. Liang T, Shi L, Bempah G, Lu CH. Sexual size dimorphism and its allometry in Chinese lizards. *Evolutionary Ecology*. 2021;35:323-335.
 20. Liao WB. Evolution of sexual size dimorphism in a frog obeys the inverse of Rensch's rule. *Evolutionary Biology*. 2013;40:493-499.
 21. Liao WB, Chen W. Inverse Rensch-rule in a frog with female-biased sexual size dimorphism. *Naturwissenschaften*. 2012;99:427-431.
 22. Liao WB, Zeng Y, Zhou CQ, Jehle R. Sexual size dimorphism in anurans fails to obey Rensch's rule. *Frontiers in Zoology*. 2013;10(10):1-7.
 23. Liao WB, Liu WC, Merilä J. Andrew meets Rensch: sexual size dimorphism and the inverse of Rensch's rule in Andrew's toad (*Bufo andrewsi*). *Oecologia*. 2015;177:389-399.
 24. Lindenfors P, Tullberg BS, Biuw M. Phylogenetic analyses of sexual selection and sexual size dimorphism in pinnipeds. *Behavioural Ecology and Sociobiology*. 2002;52:188-193.
 25. Lu D, Zhou CQ, Liao WB. Pattern of sexual size dimorphism supports the inverse Rensch's rule in two frog species. *Animal Biology*. 2014;64:87-95.
 26. Martin OY, Michalczyk L, Millard AL, Emerson BC, Gage MJG. Lack of support for Rensch's rule in an intraspecific test using red flour beetle (*Tribolium castaneum*) populations. *Insect Science*. 2017;24(1):133-140.
 27. Martins MJF, Hunt G, Thompson CM, Lockwood R, Swaddle JP, Puckett TM. Shifts in sexual dimorphism across a mass extinction in ostracods: implications for sexual selection as a factor in extinction risk. *Proceedings of the Royal Society B*. 2020;287(1933):28720200730.
 28. Monnet JM, Cherry MI. Sexual size dimorphism in anurans. *Proceedings of the Royal Society of London B Biological Sciences*. 2002;269(1507):2301-2307
 29. Peñalver Alcázar M, Galán P, Aragón P. Assessing Rensch's rule in a newt: Roles of primary productivity and conspecific density in interpopulation variation of sexual size dimorphism. *Journal of Biogeography*. 2019;46:2558-2569.
 30. Remeš V, Székely T. Domestic chickens defy Rensch's rule: sexual size dimorphism in chicken breeds. *Journal of Evolutionary Biology*. 2010;23:2754-2759.
 31. Rensch B. *Evolution above the Species Level*. Columbia, New York, 1947, 419.
 32. Rensch B. Die Abhängigkeit der relativen Sexualdifferenz von der Körpergrösse. *Bonn Zoological Bulletin*. 1950;1:58-69.
 33. Rutherford PL. Proximate mechanisms that contribute to female-biased sexual size dimorphism in an anguillid lizard. *Canadian Journal of Zoology*. 2004;82(5):817-822.
 34. Schubart O. *Diplopoda III*. *South African Animal Life*. 1966;12:33-77.
 35. Stuart-fox D. A test of Rensch's rule in dwarf chameleons (*Bradypodion* spp.), a group with female biased sexual size dimorphism. *Evolutionary Ecology*. 2009;23:425-433.
 36. Sutter NB, Mosher DS, Ostrander EA. Morphometrics within dog breeds are highly reproducible and dispute Rensch's rule. *Mammalian Genomics*. 2008;19:713-723.
 37. Teder T, Tammaru T. Sexual size dimorphism within species increases with body size in insects. *Oikos*. 2005;108:321-334.
 38. Tubaro PL, Bertelli S. Female-biased sexual size dimorphism in tinamous: a comparative test fails to support Rensch's rule. *Biological Journal of the Linnean Society*. 2003;80:519-527.
 39. Von Attems CMTG. *The Myriopoda of South Africa*. *Annals of the South African Museum*. 1928;26:1-431.

40. Webb TJ, Freckleton RP. Only half right: Species with female-biased sexual size dimorphism consistently break Rensch's rule. PLoS ONE. 2007;2(9):e897.
41. Werner Y. Bergmann's and Rensch's rules and the spur-thighed tortoise (*Testudo graeca*). Biological Journal of the Linnean Society. 2015;117:796-811.
42. Yu TL, Li Y, Zhang JD. Evolution of sexual dimorphism in the plateau brown frog fails to obey Rensch's rule. The Herpetological Journal. 2022;32(1):27-33.
43. Zamudio KR. The Evolution of Female-Biased Sexual Size Dimorphism: A Population-Level Comparative Study in Horned Lizards (*Phrynosoma*). Evolution. 1998;52(6):1821-1833.