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Does sexual size dimorphism vary with female size in forest millipedes *Centrobolus* Cook, 1897?

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Abstract
This study aimed to determine whether the variation responsible for breaking Rensch's Rule when Sexual Size Dimorphism (SSD) increased with body size was due to male-biased or female-biased variation by studying a sex-based set of morphological characters. Variation in female volume based on length and width measurements was associated with the SSD in the forest millipede genus *Centrobolus*. There was a significant positive correlation between SSD and female size (r=0.56, Z score=2.76, n=22, p<0.01). The correlation coefficient between SSD and female size did not differ significantly from the correlation coefficient between SSD and species size (z-statistic=-0.7078, p=0.4790). The morphological differences among the polygynandrous reproductive systems occurring in *Centrobolus* with higher SSD and larger females were discussed.

Keywords: Dimorphic, females, gradient, morphology, size, species.

1. Introduction
Numerous studies are finding animal taxa having female-biased SSD and mostly disobey Rensch's rule including corvids and pinnipeds [1, 2, 4, 13, 15, 18-19, 22-30, 34, 35, 37-40]. The finding of converse or inverse Rensch rule implies SSD increases with body size when females are larger [1, 2, 4, 13, 15, 18-19, 22-30, 34, 35, 37-40]. This has implications in the class Diplopoda because females are larger than males and SSD increases with body size [6-11].
The forest genus *Centrobolus* of the diplopod Order Spirobolida diplopod found along the east coast of southern Africa were the subject of this study. The millipede genus *Centrobolus* is located in the temperate region of South Africa, with its northern boundary on the east coast of southern Africa [15]. Millipedes of the *Centrobolus* genus break Rensch's rule and illustrate converse patterns of increasing female-biased sexual dimorphism variation with body size [6-11]. The problem with these and other tests of Rensch's rule is that they combine male and female variation among two sexes into species body size. In an attempt to resolve this problem I question whether the variation observed in *Centrobolus* is only because of female variation or due to a combination of male and female variation [40]. Sexual size dimorphism (SSD) is correlated with female size in the pachybolid millipede genus *Centrobolus* Cook, 1897 [5, 16, 21]. The null hypothesis is that there is an SSD correlation with female body size consistent with an inverse Rensch rule [6-11].

2. Materials and methods
Twenty-two valid species were identified as belonging to the genus *Centrobolus* Cook, 1897. Millipede type localities were obtained from a checklist of southern African millipedes [16]. These were tabulated and known type localities also listed in Microsoft Word online (https://office.live.com/start/Word.aspx) (Table 1). GPS coordinates were obtained from internet sources for known type localities using google (https://www.google.co.za/maps/place). Mean female size was obtained by calculating the volumes (cylindrical) using the lengths and widths of the sex which were inputted into the formula for a cylinder's volume (https://byjus.com/volume-of-a-cylinder-calculator) [12]. SSD was calculated as the ratio of female volume to male volume. SSD and female size was checked for correlations using the Pearson Correlation Coefficient calculator (https://www.gigacalculator.com/calculators/correlation-coefficient-calculator.php).
Correlation coefficients between SSD and female size were compared to SSD and species size [6].

3. Results

There was a highly significant positive correlation between SSD and female size (Fig. 1: r= 0.55969609, Z score=2.75652643, n=22, p=0.002921). There was no correlation between SSD and male size. Female size was normally distributed (D=0.12448, n=22, p=0.84383). SSD was normally distributed (D=0.15168, n=22, p=0.63788). The correlation coefficient between SSD and female size did not differ significantly from the correlation coefficient between SSD and species size (z-statistic=-0.7078, n=22,18, p=0.4790).

Table 1: Species in the millipede genus *Centrobolus* Cook, 1897, with SSD, type or collected localities, and female size.

Species	SSD	Location	Female size
C. albitarsis	2.89	Lochiel	1414
C. angelicus		Makhanda	
C. anulatus	1.19	Umhlanga Rocks	2059
C. atrophus		Signal Hill	
C. bifidus		Nkhandla	
C. coriaceus		caffraria	
C. decoratus	0.63	Ngome Forest	429
C. digrammus	1.01	Hout Bay	523
C. dubius	1.35	Gans bay	1389
C. formosus		caffraria	
C. fulgidus	1.65	Richards Bay	1888
C. immaculuatus	2.72	Gorongosa	2309
C. inscriptus	1.21	Scottburgh	2245
C. inyanganus	1.44	Inyanga village	913
C. lawrencei	1.57	Pietermaritzburg	1176
C. litoralis		Algoa Bay	
C. luctuosus		Inhambambane	
C. lugubris	2.18	Glenconnor	3491
C. miniatomaculatus		Tsitsikamma	
C. pococki		Cape Peninsula	
C. promontorius	0.69	Little Lions Head	231
C. pusillus	2.08	Qolora River mouth	1021
C. richardii	0.95	Richards Bay	1187.915
C. ruber	1.62	Port Shepstone	1850
C. rubricollis		Karkloof waterfall	
C. rugulosus	1.97	Hluhluwe	2209
C. sagatinus	1.27	Between Uitenhage and Addo	1855
C. sanguine marginatum		Bain's Kloof	
C. sanguinipes		Qolora River mouth	
C. saussurii		caffraria	
C. silvanus	1.13	Kentani	793
C. splendidus		Masiene near Chai Chai	
C. strigosus		caffraria	
C. striolatus		Port St Johns	
C. titanophilus	1.15	DeHoop vlei	421
C. transvaalicus	1.26	Mariepskop	746
C. tricolor	1.10	Champaigne Castle	786
C. validus		Haroni River	
C. vastus	1.81	Port St Johns	3327

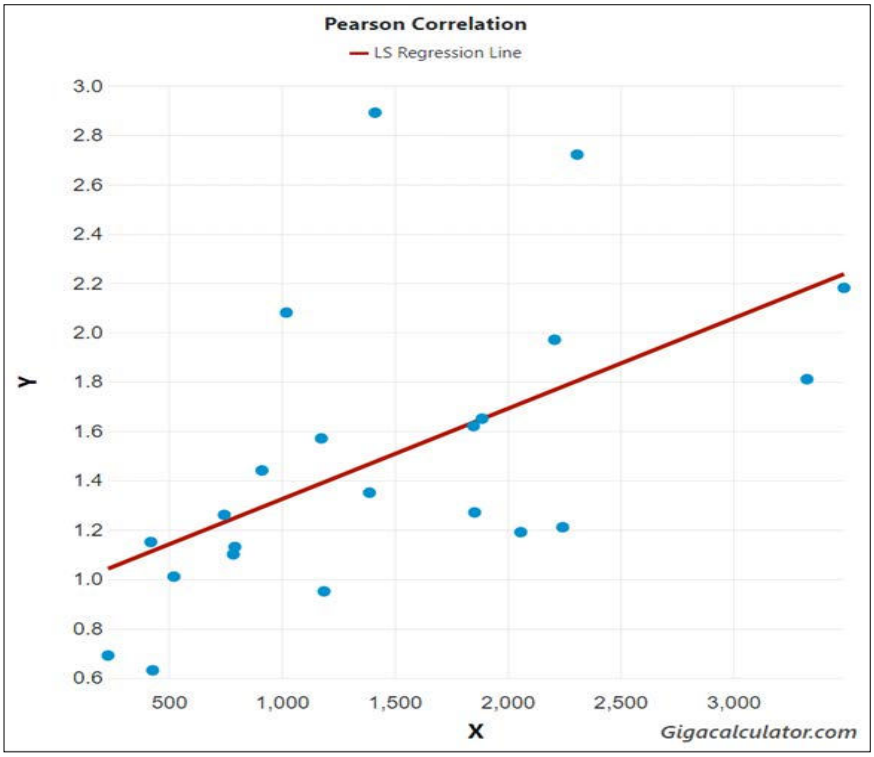

Fig 1: Relationship between Sexual Size Dimorphism (y-axis) and female size (x-axis) in *Centrobolus* Cook, 1897 [5].

4. Discussion

A relationship between female body size and SSD was found confirming the null hypothesis. *C. immaculatus* has the highest SSD (2.72) and the third-largest female size (2309 mm^3). SSD was lowest in *C. promontorius* (0.69) which had the smallest female size at 231 mm^3 and *C. decoratus* (0.63) which had the third smallest female size (429 mm^3). Only three species displayed male-biased SSD in this genus (*C. decoratus, C. promontorius, C. richardii*) and these were the exceptions to the rule of female-baised SSD among the other 19 species examined here. This study supports female size as a predictor of SSD in *Centrobolus* and helps to disentangle the size and shape components of SSD [3]. The correlation coefficient between SSD and female size did not differ significantly from the correlation coefficient between SSD and species size suggesting there was no difference between the combined effect of male and female body size [6-11] and female body size alone. Thus all the volumetric sexual size dimorphism measured in this paper and the regression with which it was compared [6] is due to variation in female width and female length.

Size-assortative mating based on female width and length is associated with variance in millipede polygynandrous mating systems across a female size gradient with higher SSD occurring in larger females [6-11]. SSD increase with female size may be explained by greater fecundity selection [6-11, 14, 32]. Female size and its components may be an explanation for skewed sex ratios in species showing sexual size dimorphisms, such as ground beetles, millipedes, scorpions, spiders, and water striders [14, 17, 20, 31-33]. Length and width components are useful reference characters because they both vary significantly with SSD and have correlated responses on female fecundity selection [8, 9].

Female-biased SSD has been successfully accepted in *Centrobolus* [6-11]. Numerous more studies have successfully rejected Rensch's rule and these include newts [1], melanine grasshoppers [2], salamanders [4], stoneflies [15], spiders [17, 20, 30], sticklebacks [18], flying lizards [19], Chinese lizards [22], frogs [23-26, 29, 40], red flour beetles [27], molluscs [28], waterstriders [31, 32], chicken breeds [33], lizards [34], ground beetles [35], dwarf chaleleons [36], dog breeds [37], and tinamous [38].

5. Conclusion

SSD increased systematically with female size in *Centrobolus*. Morphological variance in the polygynandrous reproductive systems occurs where larger females and higher SSD occur together.

Competing interests

The author has declared that no competing interests exist.

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