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DOES SEXUAL SIZE DIMORPHISM VARY WITH FEMALE LENGTH IN FOREST MILLIPEDES CENTROBOLUS COOK, 1897?

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Abstract

The objectives of this study were to determine what happened to Rensch's Rule if Sexual Size Dimorphism (SSD) and body size changed with a morphological character. The female length was correlated with SSD in the volume of the forest millipede genus Centrobolus. There was a significant correlation between SSD in volume and female length (r=0.44, Z score=2.05, n=22, p=0.02). Morphological variance in the polygynandrous reproductive systems occurs where higher SSD equals longer females.

Keywords*: Dimorphic; females; gradient; length; morphology; size; species.*

INTRODUCTION

Numerous studies are finding animal taxa have female-biased SSD and mostly disobey Rensch's rule including corvids and pinnipeds [1, 2, 4, 13, 15, 18-19, 22-31, 35, 356 38-41]. The finding of the converse or inverse Rensch rule implies SSD increases with body size when females are larger [1, 2, 4, 13, 15, 18-19, 22-31, 35, 356 38-41]. 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 was 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 corroborate Rensch's rule and illustrate patterns of decreasing (hypoallometric) 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 [41]. Sexual size dimorphism (SSD) is correlated with female length in the pachybolid millipede genus *Centrobolus* Cook, 1897 [5, 16, 21]. The null hypothesis is that there is an SSD correlation with female body length consistent with the Rensch rule [6-11].

MATERIALS AND METHODS

Morphometrics

Twenty-two of 39 valid species were identified as belonging to the genus *Centrobolus* Cook, 1897. Millipede-type localities were obtained from a checklist of southern African millipedes [2]. 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 length was obtained by calculating the lengths of the sex alongside a plastic rule [4]. SSD was calculated as the ratio of female volume to male volume. SSD and female length was checked for correlations using the Pearson Correlation Coefficient calculator (https://www.gigacalculator.com/calculators/correlation-coefficient-calculator.php).

Model

The major distinction between a linear increase in length and an exponential increase in width is they are functions that have different rates of their growth. The linear function for length increase models a constant rate of change. The exponential function for width increase, on the other hand, models a rate of increase or decrease that increases/decreases at consecutive intervals. The composition of these two functions is different from function multiplication (https://tutorial.math.lamar.edu/Classes/Alg/CombineFunctions.aspx). In most cases, we will get different answers in different order. Note, however, that there are times when we will get the same answer regardless of the order. In *Centrobolus* the composition of the linear and exponential increase models a constant rate of change combined with an increase/decrease at consecutive intervals. The ultimate changes may match the proximate changes and are given by the compositional function $v=\pi.r^2$; where v is the volume and r is half the dorsal tergite width.

RESULTS

There was a significant positive correlation (hypoallometric) between SSD in volume and female length (Fig. 1: r=0.43923738, Z score=2.05428583, n=22, p=0.01997395). Female length was normally distributed (D=0.10475, n=22, p=0.94864). SSD in volume was normally distributed (D=0.15168, n=22, p=0.63788). There was no difference between the correlation coefficient between SSD and female length and the correlation coefficient between SSD with species size (z-statistic=-1.1715, n=22, 18, p=0.2414) or with SSD and female width (z=0.43923738, n=22, 22, p=0.43923738).

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

Species	SSD	Location	Female length (mm)
C. albitarsis	2.89	Lochiel	50
C. angelicus		Makhanda	
C. anulatus	1.19	Umhlanga Rocks	76
C. atrophus		Signal Hill	
C. bifidus		Nkhandla	
C. coriaceus		caffraria	
C. decoratus	0.63	Ngome Forest	31
C. digrammus	1.01	Hout bay	34
C. dubius	1.35	Gans bay	51
C. formosus		caffraria	
C. fulgidus	1.65	Richards Bay	52
C. immaculuatus	2.72	Gorongosa	60
C. inscriptus	1.21	Scottburgh	63
C. inyanganus	1.44	Inyanga village	43
C. lawrencei	1.57	Pietermaritzburg	43
C. litoralis		Algoa Bay	
C. luctuosus		Inhambambane	
C. lugubris	2.18	Glenconnor	63

C. miniatomaculatus		Tsitsikamma	
C. pococki		Cape Peninsula	
C. promontorius	0.69	Little Lions Head	27
C. pusillus	2.08	Qolora River mouth	40
C. richardii	0.95	Richards Bay	50
C. ruber	1.62	Port Shepstone	62
C. rubricollis		Karkloof waterfall	
C. rugulosus	1.97	Hluhluwe	50
C. sagatinus	1.27	Between Uitenhage and Addo	48
C. sanguineomarginatus		Bain's Kloof	
C. sanguinipes		Qolora River mouth	
C. saussurii		caffraria	
C. silvanus	1.13	Kentani	44
C. splendidus		Masiene near Chai Chai	
C. strigosus		caffraria	
C. striolatus		Port St Johns	
C. titanophilus	1.15	DeHoop vlei	29
C. transvaalicus	1.26	Mariepskop	38
C. tricolor	1.10	Champaigne Castle	37
C. validus		Haroni River	
C. vastus	1.81	Port St Johns	63

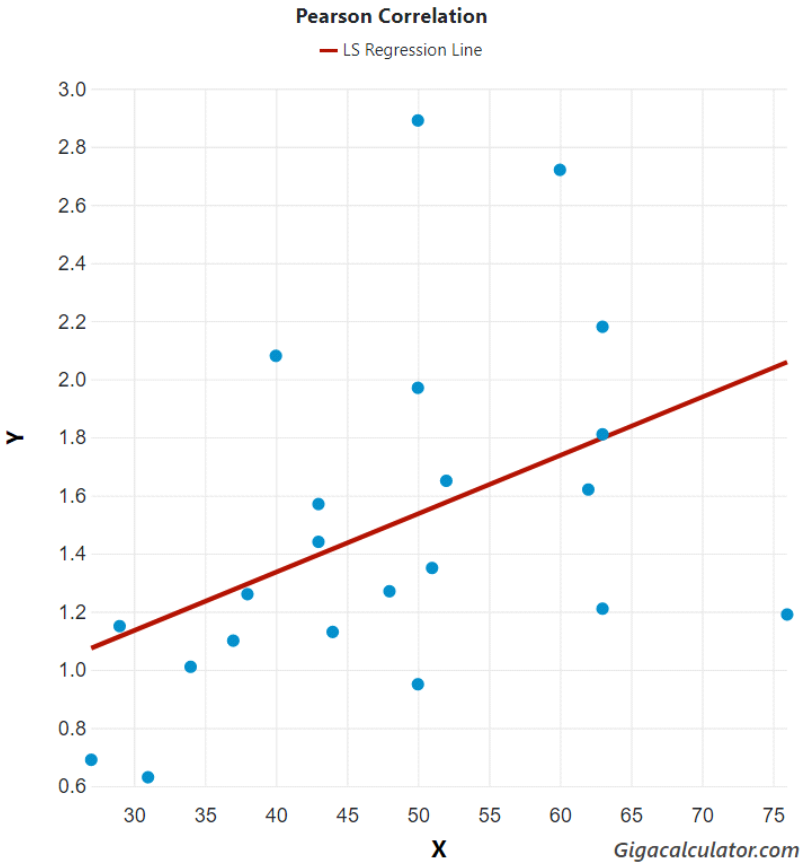

Fig. 1. Relationship between Sexual Size Dimorphism (y-axis) and female length (x-axis) in *Centrobolus* Cook, 1897 [2].

DISCUSSION

A relationship between female length and SSD in volume was found. *C. albitarsus* has the highest SSD (2.89) and the fifth-longest female length (50 mm). SSD was lowest in *C. promontorius* (0.69) which was among the three shortest female lengths with *C. decoratus* (0.63). This study supports female length as a predictor of SSD in volume in *Centrobolus*. 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 [2]. The correlation coefficient between SSD and female length 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 length [5, 6-10] and female body length alone. The correlation coefficient between SSD and female length did not differ significantly from the correlation coefficient between SSD and female width suggesting there was no difference between the combined effect of female length and width as opposed to either length or width alone. Thus all the volumetric sexual size dimorphism measured in this paper and the regression with which it was compared (Cooper, 2017) is due to variation in female width and female length.

Size-assortative mating based on female length determines the variance in millipede polygynandrous mating systems across a male size gradient with higher SSD in volume occurring in longer females. SSD volumes increase with female length explains greater fecundity selection. Female length is an explanation for skewed sex ratios in species showing sexual size dimorphism, such as millipedes and spiders [6]. Change in sexual size dimorphism is a correlated response between female length and width to selection on fecundity [5]. Although not as powerful in maximizing the volume of a cylinder, the significant additive effect of length on the surface area together with its complementary effect on volume explain longer females as being selected to maximize female size.

Female-biased SSD has been successfully accepted in *Centrobolus* [5, 6-10]. Numerous other studies have rejected Rensch's rule and these include newts [30], melanine grasshoppers [1], salamanders [3], stoneflies [14], spiders [16, 19, 31], sticklebacks [17], flying lizards [18], Chinese lizards [21], frogs [22-24, 29, 41], red flour beetles [27], molluscs [28], waterstriders [32, 33], chicken breeds [34], lizards [35], ground beetles [36], dwarf chaleleons [37], dog breeds [38], and tinamous [39]. *Centrobolus* is not one of these as it follows the rule.

CONCLUSION

SSD increased systematically with female length in *Centrobolus*. Morphological variance in the polygynandrous reproductive systems occurs with a linear relationship between (longer) female length and (higher) SSD occur together.

COMPETING INTERESTS

The author has declared that no competing interests exist.

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