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Sexual size dimorphism and the rejection of Rensch's rule in Diplopoda (Arthropoda)

Mark Ian Cooper**Abstract**

Rensch's rule predicts the negative associations between sexual size dimorphism (SSD) and body sizes for relatively larger females. This prediction was tested for forest and savanna diplopods using a geometric morphometric approach using calculations of length and width to derive shape volume based on the mathematical formulae for estimated cylindrical worm-like millipede size ($l \cdot \pi \cdot r^2$) and spherical pill millipede size ($4/3 \cdot \pi \cdot r^3$): (i) *Centrobolus* (were collected in February 1996, South Africa) SSD was 0.63-2.89 (1.52 ± 0.35 ; 267) (ii) *Sphaerotherium* (extracted from literature) SSD was 1.49-5.36 (2.96 ± 1.40 ; $n \geq 7$); (iii) savanna (*Calostreptus*, *Doratogonus*, *Odontopyge* and *Spinotarsus* were collected in February 1989, Zimbabwe) and forest helminthomorphs (collected in February 1996, South Africa) SSD was 0.88-1.62 (1.26 ± 0.23 ; 1233). Interspecific variation regressed was SSD (0.63-5.36) on body sizes ($n=1273$) with no significant negative correlations rejecting Rensch's rule. Eco-morphological patterns were discussed.

Keywords: Allometry, Diplopoda, forest, myriapod, savanna**1. Introduction**

Diplopoda are underrepresented in allometric analyses of sexual size dimorphism (SSD), although sexual size differences are known in body mass, length, width and leg dimensions of over half the taxa studied [1-6]. Size differences correlate with factors such as color, sexes, species, urbanisation and water relations [7-11]. Diplopoda resemble the majority of invertebrates where SSD is reversed [12]. SSD has consequences for outcomes of sexual encounters in diplopod mating [13-19]. The allometry of SSD involves the detection of a relationship between body size and SSD and is known by Rensch's rule [20-21]. Rensch's rule may be explained by sexual selection and fecundity selection [22-29]. The macro-evolutionary pattern is unresolved in Diplopoda [30]. Here, Rensch's rule was tested in predicting SSD was not negatively correlated with diplopod body size in African forest and savanna taxa. SSD in the forest genera *Sphaerotherium* and *Centrobolus* was investigated. The Sphaerotheriida genus *Sphaerotherium* consists of a large number of pill millipedes with some 54-60 described tropical and subtropical species extending to the Cape Peninsula in South Africa [31-33]. Individuals of both sexes roll into a spherical ball, which is part of the mating system [34]. Females are known to weigh up to three times more than males [35]. SSD has been studied in the Spirobolida genus *Centrobolus* with a relationship between the log of male and female volumes for 18 of 39 species suggesting corroboration of Rensch's rule [30]. SSD in the genus *Centrobolus* was re-investigated and re-tested. SSD in the savanna Spirostreptida genera *Calostreptus*, *Doratogonus*, *Odontopyge* and *Spinotarsus* were calculated from previously published data in Telford and Dangerfield [39].

2. Materials and Methods

Up to three factors were measured from the sample of 2 infraclasses (Helminthomorpha and Pentazonia), 3 orders (Sphaerotheriida, Spirobolida, Spirostreptida), 4 families (Odontopygids, sphaerotheriids, spirostreptids, trigoniulids), 6 genera, and 36 species: (1) body length (mm) in placing individuals alongside a plastic rule (calibrated in mm); (2) width (mm) with Vernier calipers; and (3) mass (accurate to 0.01 g) data was extracted from published data [36-40]. Savanna helminthomorphs *Calostreptus* sp. (Hwange), *Calostreptus* sp. (Sengwe), *Doratogonus* (= *Alloporus*) *uncinatus* (Hwange), *D. uncinatus* (Mazowe), *Odontopyge* sp.2 (Marondera), *Odontopyge* sp.3 (Marondera), *Odontopyge* sp.3 (Vic. Falls) and *Spinotarsus* sp.1 (Marondera) were collected in Zimbabwe (February 1989).

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Forest helminthomorphs *Centrobolus fulgidus* (Richards' Bay Minerals), *C. inscriptus* (Mtunzini) and *C. ruber* (Anerley, Port Shepstone) were collected in South Africa (February 1996). Helminthomorph size was calculated as shape volume based on the formula for a cylinder ($l \cdot \pi \cdot r^2$) where l was body length and r half of the width *i. e.* radius. Forest pentazonian body width (mm) was extracted from Attems [40] data on *Sphaerotherium* and size calculated as volume based on the formula for a sphere ($4/3 \cdot \pi \cdot r^3$) where r was the radius. In both helminthomorph and pentazonians, SSD was estimated as the mean female volume divided at mean male volume and converted into a SSD index by subtracting 1 [41]. Allometry for SSD was based on a general allometric model where male size = α (female size) ^{β} [42-45].

2.1 Statistical Analysis

SSD were calculated using Microsoft Office Excel mathematical and statistical formula. Male and female widths were either halved, cubed and multiplied at pi using a combination of mental arithmetic, power and product functions (pill millipedes) or halved, squared and multiplied at pi and length using the same approach (worm-like millipedes). Once calculated, species body size measurements were treated as the independent x-variable or factor and measurements of SSD derived from ratios of female volumes divided at male volumes were treated as the dependent y-variables and were inserted into: Spearman's Rho online calculator (<http://www.socscistatistics.com/tests/spearman/Default2.aspx>). Similarly for the linear regression mass, volume and SSD were inserted into the online calculator (<http://www.socscistatistics.com/tests/regression/Default.aspx>).

Calculations were performed for (1) a Spirobolida data set which included *Centrobolus* volumes and SSD on taxa collected as Cooper [36], (2) a Sphaerotheriida data set which included *Sphaerotherium* volumes and SSD on taxa collected by Attems [40], and (3) a Spirostreptida data set which included the four savanna genera collected in Telford and Dangerfield [42]. A second correlation analysis was performed on all 3 groups using Pearson's correlation coefficient analysis to test for negative correlations between size and SSD. Additional analysis included (4) Helminthomorphs (forest and savanna together) and (5) forest taxa (*Centrobolus* and *Sphaerotherium*).

3. Results

The allometric equation for *Centrobolus* was (1) $\hat{y} = 0.00051X - 0.01071$. SSD ranged from 0.63 – 2.89 (1.55 ± 0.63 ; $n \geq 18$) and was not negatively correlated ($R = 0.70485$; $P = 0.00109$; $n = 18$ spp.) with volume ranging from 284 – 2683 mm³ (1097.89 ± 638.06 ; 18) (Table 1). The allometric equation for *Sphaerotherium* was (2) $\hat{y} = 0.00045X + 1.38384$. SSD ranged from 1.49 – 5.36 (2.96 ± 1.40 ; $n \geq 7$) and was not negatively correlated ($R = 0.46429$; $P = 0.29393$; $n = 7$ spp.) with volume ranging from 224 – 2877 mm³ (1299.43 ± 1127.84 ; 7) (Table 2). The allometric equation for the mixed sample of savanna and forest helminthomorphs was (3) $\hat{y} = -0.03795X + 1.34816$. In the sample of savanna and forest worm-like diplopods SSD ranged from 0.88 - 1.62 (Mean \pm SD = 1.26 ± 0.23 ; $n = 1233$) and no significant negative correlations ($R = -0.230594$; $P = 0.49513$; $n = 11$ spp.) were found with mass ranging from 0.75 – 8.30 g (2.42 ± 2.57 ; 1233) (Table 3)

Table 1: Body size, sexual size dimorphism (SSD) and SSD index for *Centrobolus* Cook.

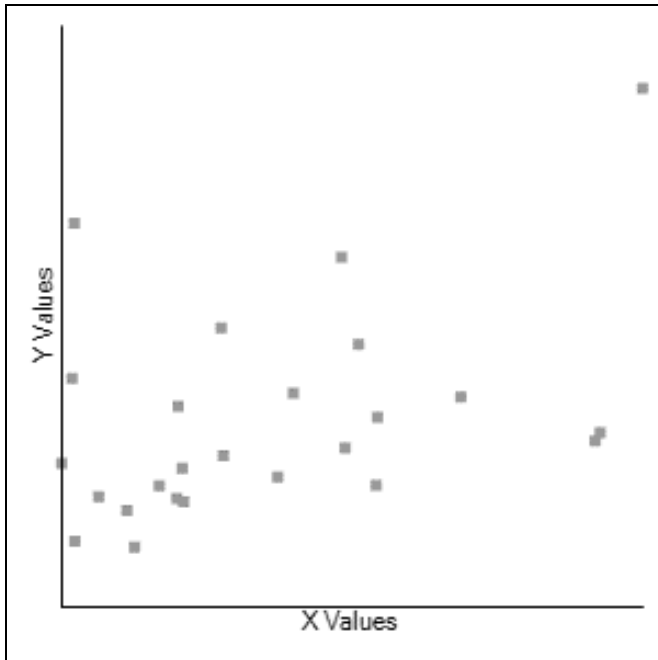
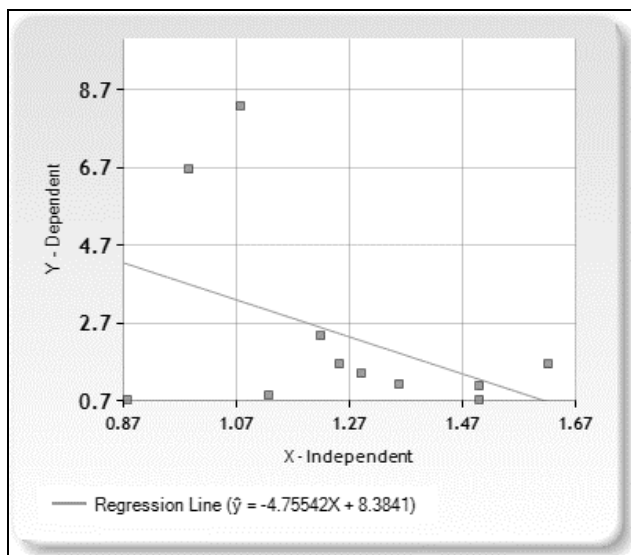
Species	Body size (mm ³)	SSD	SSD-1	Sample size (n)
<i>C. albitarsus</i>	952	2.89	1.89	1
<i>C. decoratus</i>	557	0.63	-0.37	1
<i>C. digrammus</i>	522	1.01	0.01	6
<i>C. dubius</i>	1210	1.35	0.35	1
<i>C. fulgidus</i>	1518	1.65	0.65	11
<i>C. fulgidus</i>	1.65 g	1.25	0.25	22
<i>C. immaculatus</i>	1580	2.72	1.72	1
<i>C. inscriptus</i>	2.38 g	1.22	0.22	176
<i>C. inyanganus</i>	775	1.44	0.44	1
<i>C. lawrencei</i>	962	1.57	0.57	1
<i>C. lugubris</i>	2046	2.18	1.18	1
<i>C. promontories</i>	284	0.69	-0.31	1
<i>C. pusillus</i>	756	2.08	1.08	1
<i>C. ruber</i>	1.64 g	1.62	0.62	36
<i>C. rugulosus</i>	1666	1.97	0.97	1
<i>C. sagatinus</i>	1659	1.27	0.27	1
<i>C. silvanus</i>	749	1.13	0.13	1
<i>C. titanophilus</i>	393	1.15	0.15	1
<i>C. transvaalicus</i>	669	1.26	0.26	1
<i>C. tricolor</i>	781	1.10	0.10	1
<i>C. vastus</i>	2683	1.81	0.81	1

Table 2: Body size, sexual size dimorphism (SSD) and SSD index in *Sphaerotherium* Brandt 1833.

Species	Body Size (mm ³)	SSD	SSD-1	Sample size (n)
<i>S. cinctellum</i>	2660	1.73	0.73	1
<i>S. commune</i>	281	3.97	2.97	1
<i>S. compressum</i>	1501	3.62	2.62	1
<i>S. punctulatum</i>	2877	5.36	4.36	1
<i>S. spinatum</i>	1282	2.21	1.22	1
<i>S. tenuitarse</i>	224	1.49	0.49	1
<i>S. tuberosum</i>	271	2.37	1.37	1

Table 3: Body size, SSD and SSD index for savanna worm-like millipedes (localities in parentheses).

Species	Body Size (g)	SSD	SSD-1 SSD-1	Sample size (n)
<i>Calostreptus</i> sp. (Hwange)	1.10	1.50	0.50	70
<i>Calostreptus</i> sp. (Sengwe)	0.75	1.50	0.50	58
<i>Doratogonus uncinatus</i> (Hwange)	8.30	1.08	0.08	54
<i>D. uncinatus</i> (Mazowe)	6.65	0.99	-0.01	521
<i>Odontopyge</i> sp.2 (Marondera)	1.14	1.36	0.36	117
<i>Odontopyge</i> sp.3 (Marondera)	1.40	1.29	0.29	44
<i>Odontopyge</i> sp.3 (Victoria Falls)	0.85	1.13	0.13	83
<i>Spinotarsus</i> sp.1 (Marondera)	0.75	0.88	-0.13	52

**Fig 1:** Scatterplot showing the positive correlation between sexual size dimorphism (SSD) and body sizes for forest diplopods including *Centrobolus* and *Sphaerotherium*.**Fig 2:** Scatterplot showing the negative correlation between sexual size dimorphism (SSD) and body sizes for savanna diplopods including *Calostreptus*, *Doratogonus*, *Odontopyge* and *Spinotarsus* sp.1

4. Discussion

Allometric equations for (1) *Centrobolus* was positively correlated but not negatively; (2) *Sphaerotherium* was positively correlated but not significant; and (3) the mixed sample of savanna and forest helminthomorphs show body sizes and SSD was negatively correlated but not significantly.

Also, further analysis of (4) helminthomorphs, and (5) forest taxa showed no significant negative correlations. All 3 equations of relationships between SSD and body mass from the sample of 36 species of diplopods showed there was no significant negative correlations between SSD and body sizes. Rensch's rule was re-assessed in *Centrobolus* forest diplopods and no supporting evidence produced. However, mass and volume do not provide equal measures of SSD. In the case where both mass and volume were measured (*C. fulgidus*) this was evident [46]. In order to obtain more accurate results, the analysis for (1) and (2) included only volume (Fig. 1) while the analysis for (3) included solely mass measurements (Fig. 2). In the savanna millipedes the genus *Spinotarsus* showed male-biased sexual dimorphism. Three mass measurements of *Centrobolus* were included in the worm-like analysis. So, regressions between body sizes and SSD calculated here for 3 types of diplopods indicated no evidence for Rensch's rule.

Sexual size dimorphism appears to be higher for forest millipedes than the savanna millipedes. However, this Eco morphology is probably due to the greater variation of the forest millipedes which has evolved through climate change as is the case of refugial speciation with the forest *Sphaerotherium* representing the palaeotaxa [47]. Forest taxa illustrate differences in morphology and species composition [48]. Tree-climbing behaviour in several species suggests interspecific competition drives SSD [49].

Numerous studies are finding animal taxa having female biased SSD mostly disobey Rensch's rule including many of the invertebrates and frogs as well as a plethora of animal taxa [50-73]. A recent study on the European millipede *Pachyiulus hungaricus* shows "[s]ize and/or shape of the morphological traits (except the shape of male walking legs) used in our study were not subject to pre-copulatory sexual selection." [74] The absence of any relationships between size and mating was documented for the tropical millipede *Nyssodesmus pythos* [13]. My evidence for sexual selection on dimorphism is based on the relative size dimorphism in *Centrobolus* which shows size is important in determining the outcome of mating [47, 73, 76-77]. The mechanism is based on a conflict of interests [77]. In the millipede *Doratogonus uncinatus* female choice for mating partners is "size selective" [78]. The cross-mating experiments in *Centrobolus* suggest a combination of size assortative mating without a size based preference operates [79].

Further studies of diplopod sexual dimorphism may include more taxa and make use of the length and width measurements to calculate volumes using the geometric morphometric approach shown here for finding causal relationships of dimorphism. The sexual dimorphism calculated here may be converted into alternative indices of sexual dimorphism in order to update its relevance, e. g. M I index [80, 81]. It is worth noting sexual dimorphism and the selection pressures may be decoupled in time e. g. ostracodes [82]. Geometric morphometrics is useful for converting the

shape into size^[83]. Future goal is to compile the allometry for SSD for the diplopod fauna from South African savanna and forest biomes where a diversity of species has been documented to exist^[84, 85].

5. Conclusion

Sphaerotheriida, Spirobolida and Spirostreptida SSD does not negatively regress with body sizes but break Rensch's rule. Intersexual competition is believed to drive SSD in diplopods with forest taxa containing the diversity of species and sizes. A geometric morphometric approach successfully determined the shape and size of millipedes which enabled us to see a relationship, or lack thereof, between shape as size and SSD. The inverse of Rensch's rule was found in *Centrobolus* based on the relationship between SSD and body size.

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