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Sexual size dimorphism and corroboration of Rensch's rule in *Chersastus* millipedes (Diplopoda: Pachybolidae)

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Abstract

Sexual Size Dimorphism (SSD) was investigated in the millipede genus *Chersastus*. Mass, length and width were used to compare intraspecific variation in four species. Interspecific variation in volume was calculated in 18 species and an allometric coefficient of 0.85 found, which corroborates Rensch's rule in this genus.

Keywords: Allometry, hypoallometry, millipede, Rensch's rule.

1. Introduction

Millipedes are underrepresented in allometric analyses of Sexual Size Dimorphism (SSD) in invertebrates, although common sexual differences are known in body mass, length, width and leg dimensions of over half the taxa studied ^[1, 2]. They resemble the majority of invertebrates in that SSD is reversed ^[3-5].

In the present study, SSD in the genus *Chersastus* is investigated, Rensch's rule ^[4] tested, which predicts that SSD is negatively correlated with mean body size.

2. Material and Method

Three factors were measured from *Chersastus* species: (1) body length (mm) by placing individuals collected in South Africa (1996-1998) alongside a plastic rule (calibrated in mm); (2) width (mm) with Vernier calipers; and (3) mass (accurate to 0.01 g) was measured with a Mettler balance. *C. inscriptus* (Mtunzini), *C. fulgidus* (Richards' Bay Minerals), *C. ruber* (Anerley, Port Shepstone) and *C. digrammus* (Simon's Town waterfall) were collected in South Africa. These basic descriptive figures were statistically compared using Statistica (Mann-Whitney tests). Body length: width ratios were compared on arcsine transformed data. The mean values of length, width and number of segments was extracted from published data for 18 species ^[6, 7] and intersexual comparisons performed using Wilcoxon matched pairs tests.

Size was perceived as body volume and calculated based on the formula for a cylinder ($l \cdot \pi \cdot r^2$) where l is body length and r half of the width. SSD was estimated as the mean female volume divided by mean male volume and converted into a SSD index by subtracting 1 ^[8]. Allometry for SSD was based on a general allometric model where male size = α (female size) $^\beta$ ^[9].

3. Results

In 32 measurements (Table 1, n=16) of mass, length, width, and volume, females are more variable (n=14). Exceptions (n=2), where sexes are equal, were submitted to a variance ratio test ^[8]: in *C. inscriptus* ($F = 1.54$), indicating a lower female body mass, and where female body mass was lower, in *C. fulgidus* ($F = 3.72$), indicating no significant difference in body volume between sexes.

Although there is continuous SSD in mass, males are normally distributed and females are skewed towards larger mass. There are two peaks in the distribution of female mass which may represent a population disruption and directional selection for heavier females. Length is also continuous and the female distribution is skewed towards shorter individuals. Width is almost discontinuous and skewed towards wider females and intermediate males. The arcsine of length: width ratios indicates dimorphism similar to width alone.

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Chersastus millipedes range in width from *C. promontorius* to *C. vastus* (Table 2). Females are significantly greater in width (Wilcoxon: $T = 5.00$, $Z = 3.51$, $n = 18$, $P = 0.0005$), have more body rings ($T = 2.00$, $Z = 2.60$, $n = 18$, $P = 0.009$), but are no different in length ($T = 73.00$, $Z = 0.54$, $n = 18$, $P = 0.59$). Differences in width were consistent between the sexes of all species except for *C. promontorius* and *C. decoratus*. These measurements may have been recorded from lower stadia /sub-adult specimens?

Sexual dimorphism ratios (female: male) for length ranged from 0.72 - 1.28 (mean \pm SD = 0.99 ± 0.15) and width ranged from 0.92 - 1.50 (mean \pm SD = 1.22 ± 0.18), and

combined as length: width from 0.67 - 1.0 (mean \pm SD = 0.82 ± 0.11). There was a significant difference between the length: width ratios of males and females ($T = 0.00$, $Z = 3.52$, $n = 18$, $P = 0.0004$). Male and female lengths were significantly correlated ($r^2 = 0.82$, $n = 18$, $P < 0.05$), as was width ($r^2 = 0.85$, $n = 18$, $P < 0.05$). Male length correlated with male width ($r^2 = 0.26$, $n = 88$, $P = 0.02$) and female length correlated with female width ($r^2 = 0.32$, $n = 88$, $P = 0.00$). Mean volume ratios ranged from 0.63 - 2.72 (mean \pm SD = 1.49 ± 0.68). The regression of log male volume on log female volume was highly significant ($R = 0.85$, $F = 42.97$, $d. f. = 17$, $P < 0.0001$) with a positive slope less than 1 ($t = -5.21$, $d. f. = 16$, $p < 0.0005$)

Table 1: The measurements of sexual dimorphism in *Chersastus* spp. (n=4) showing mean, standard deviation (SD), and coefficient of variation (CV).

Species and measurement	Male Mean \pm SD	CV	Female Mean \pm SD	CV	Mann-Whitney U	n	Species Size
<i>Chersastus inscriptus</i>							
Mass (g)	2.48 \pm 0.57	23.0	2.27 \pm 0.28	12.3	-6.81***	88	2043
Length (mm)	67.4 \pm 2.9	4.0	63.0 \pm 3.6	5.7	7.13***	88	
Width (mm)	5.9 \pm 0.2	3.4	6.7 \pm 0.3	4.5	-11.11***	88	
Length: Width	11.50		9.06		-11.19***	88	
Volume (mm ³)	1841 \pm 175	9.5	2245 \pm 226	10.1	-9.8***	88	
<i>C. fulgidus</i>							
Mass (g)	1.29 \pm 0.14	10.9	1.97 \pm 0.42	21.3	-3.84**	11	2251
Length (mm)	56.2 \pm 2.5	4.4	63.5 \pm 5.2	8.2	1.23	11	
Width (mm)	5.4 \pm 0.2	3.7	6.2 \pm 0.4	6.5	-3.97***	11	
Length: Width	10.87		9.29		-3.97***	11	
Volume (mm ³)	2000 \pm 224	11.2	2501 \pm 197	7.8	-4.57***	11	
<i>C. ruber</i>							
Mass (g)	1.28 \pm 0.12	9.4 4.5	2.00 \pm 0.48	24.0	4.68***	18	1496
Length (mm)	57.8 \pm 2.6	4.0	62.3 \pm 6.3	10.1	1.34***	18	
Width (mm)	5.0 \pm 0.2		6.1 \pm 0.4	6.6	5.13***	18	
Length: Width	11.46		10.18		4.07***	18	
Volume (mm ³)	1141 \pm 104	9.1	1850 \pm 421	22.8	4.79***	18	
<i>C. digrammus</i>							
Mass (g)	0.68 \pm 0.05	7.4 4.2	1.02 \pm 0.23	22.5	-2.44	6	801
Length (mm)	49.9 \pm 2.1		54.5 \pm 5.4	9.9	-2.29	6	
Width (mm)	4.0 \pm 0.1	2.5	4.8 \pm 0.3	6.3	-3.32**	6	
Length: Width	12.53		11.43		-2.90*	6	
Volume (mm ³)	616 \pm 53	8.6	985 \pm 208	21.1	-3.28*	6	

Significance levels * $p < 0.01$, ** $p < 0.001$, *** $p < 0.0001$

Table 2: Male and female morphometric parameters recorded in *Chersastus* millipedes. All values are given as the mean measurements with sizes based on descriptions by Schubart (1966) and Lawrence (1967).

Species	Male Length (mm)	Width (mm)	Body rings	Female Length (mm)	Width (mm)	Body rings
<i>C. albitarsus</i>	39	4.0	42	50	6.0	42
<i>C. decoratus</i>	43	4.5	42	31	4.2	42
<i>C. digrammus</i>	41	4.0	45	34	4.4	45
<i>C. dubius</i>	52	5.0	45	51	5.9	45
<i>C. fulgidus</i>	54	5.2	43	52	6.8	44
<i>C. immaculatus</i>	49	4.7	39	60	7.0	40
<i>C. inyanganus</i>	40	4.5	39	43	5.2	42
<i>C. lawrencei</i>	43	4.7	43	43	5.9	43
<i>C. lugubris</i>	53	6.2	45	63	8.4	46
<i>C. promontorius</i>	33	3.6	45	27	3.3	45

<i>C. pusillus</i>	39	4.0	38	40	5.7	38
<i>C. rugulosus</i>	49	5.4	42	50	7.5	42
<i>C. sagatinus</i>	49	6.2	45	48	7.0	44
<i>C. silvanus</i>	46	4.4	43	44	4.8	44
<i>C. titanophilus</i>	28	4.1	43	29	4.3	44
<i>C. transvaalicus</i>	39	4.4	42	38	5.0	43
<i>C. tricolor</i>	45	4.5	43	37	5.2	43
<i>C. vastus</i>	65	6.0	43	63	8.2	44

Table 3: Body length: width ratios and mean body volume calculations for male and female *Chersastus* millipedes.

Species	Male		Female		Ratio (Female/Male)		Species size
	Length: width	Volume (mm ³)	Length: width	Volume (mm ³)	Length: width	Volume (mm ³)	Volume (mm ³)
<i>C. albitarsus</i>	9	490	8	1414	0.89	2.89	952
<i>C. decoratus</i>	9	684	7	429	0.78	0.63	557
<i>C. digrammus</i>	10	520	7	523	0.7	1.01	522
<i>C. dubius</i>	10	1030	8	1389	0.8	1.35	1210
<i>C. fulgidus</i>	10	1147	7	1888	0.7	1.65	1518
<i>C. immaculatus</i>	10	850	8	2309	0.8	2.72	1580
<i>C. inyanganus</i>	8	636	8	913	1.0	1.44	775
<i>C. lawrencei</i>	9	748	7	1176	0.78	1.57	962
<i>C. lugubris</i>	8	1600	7	3491	0.88	2.18	2046
<i>C. promontories</i>	9	336	8	231	0.89	0.69	284
<i>C. pusillus</i>	9	490	7	1021	0.78	2.08	756
<i>C. rugulosus</i>	9	1122	6	2209	0.67	1.97	1666
<i>C. sagatinus</i>	7	1464	6	1855	0.86	1.27	1659
<i>C. silvanus</i>	10	704	9	793	0.9	1.13	749
<i>C. titanophilus</i>	6	365	6	421	1.0	1.15	393
<i>C. transvaalicus</i>	8	593	7	746	0.88	1.26	669
<i>C. tricolor</i>	10	716	7	786	0.7	1.10	781
<i>C. vastus</i>	10	1838	7	3327	0.7	1.81	2683

4. Discussion

The significant difference between length: width ratios of males and females, and the differences in width but not length, indicate selection for larger female size but does not exclude selection for male length. The species where females had a greater number of segments, but were similar to males in length, indicates that they have shorter more squat individual segments compared to males. This could be useful in assessing the contraction versus elongation hypotheses for the evolution of the millipede form ^[2].

Mean volume ratios in *Chersastus* suggest a relatively high variance of SSD in the genus. The regression of male volume on female volume indicates that the size ratio increases with body size, *i. e.* hypo-allometrically, corroborating Rensch's rule in *Chersastus*.

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