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The copulation duration allometry in *Centrobolus* (Diplopoda: Spirobolida: Pachybolidae)

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Abstract

Of the determining factors of copulation duration across arthropods, I reviewed copulation duration variance in forest millipedes. The objective was to calculate the variance in copulation duration. The null hypothesis was mean copulation duration and copulation duration variance were independent of body mass. Copulation duration and standard deviation squared for 4 populations of millipedes were seen in the literature. Copulation duration correlated with it's variance (r=0.95, r^2=0.90, n=5, p=0.01). Durations ranged from *C. anulatus* (34.9 minutes) to *C. inscriptus* (303 minutes). Female mass was correlated to copulation duration variance (r=0.95, z-score=1.86, n=4, p=0.03). Millipedes were similar to some arachnids where the duration of copulation and variance in copulation duration correlated with intra-specific size variation. Female mass correlated to copulation duration (r=0.99, z-score=2.71, n=4, p<0.01). Sexual size dimorphism (SSD) was related to male mass (r=-0.97, z-score=-2.17, n=4, p=0.01). Prolonged copulation duration was interpreted to have correlated with the intensity of sperm competition and female control of copulation duration. Females are thought to control the duration of copulation based on mass.

Keywords: equal, female, male, mating, mass, sperm, variance

1. Introduction

Copulation duration is a response to sperm competition [1]. It determines insemination, fertilization, egg number/production, and paternity [2, 3]. There are many determining factors of copulation duration across arthropods, such as the timing of insemination varies with spermatophore size and male genital titillation when there is indirect sperm transfer [4]. Even heat stress in males can negatively affect copulation duration [5]. It was "proposed that prolonged copulations gain meaning in multiple mating situations and should play a role in sperm competition or other forms of sexual selection" [6].

Optimal copulation duration is dependent on male and female size [7]. Size-dependent copulation duration and mate guarding occur in the fly *Drosophila melanogaster* [8], the scorpionfly (*Panorpa cognata*) [9], spiders [10], the skeleton shrimp *Caprella penantis* [11], the carrion beetle *Necrophila americana* [12], orb-web spiders [13], the millipede *Centrobolus inscriptus* [7] and yellow dungflies [14]. This is not the case in the millipede *Nyssodesmus pythos* [15].

The aim here is to (1) quantify copulation duration variance. In millipedes, copulation is usually prolonged and differs between species and between populations [16]. Control is given for species with equal intraspecific variance in copulation duration. I also test for (2) size-related copulation duration in males and females. Here I calculate copulation duration and copulation duration variance in mate-guarding forest millipedes. I search the literature for calculations of variance in copulation duration of four populations of forest millipedes and perform interpopulation comparisons to test the null hypothesis that copulation and variance in copulation duration are independent.

2. Materials and Methods

Variance in copulation durations (means and standard deviation squared) for 4 populations of forest millipedes (Infraclass: Helminthomorpha Pocock, 1887) [31] were obtained from the literature [17, 18]. Male and female mass (g) was made available in 5 cases, including 4 species of the genus *Centrobolus* (Table 1). Mass was obtained using a Mettler AC 100 Auto balance. Copulation duration (minutes) and their standard deviation squares were taken and correlated at http://www.socscistatistics.com/tests/pearson/default2.aspx. Correlation coefficients were compared at https://www.medcalc.org/calc/comparison-of-correlations.php. Copulation duration was compared between species with equal variance, equal mass, and different variance and different mass using a MedCalc (Registered) comparison of means calculator (https://www.medcalc.org/calc/comparison_of_means.php). I controlled for copulation duration, copulation duration variance, mass, and SSD. Figures were plotted at http://www.gigacalculator.com/calculators/correlation-coefficient-calculator.php. Two events of *C. inscriptus* were recorded, in 1995 and 1998; both mass measurements were included here.

3. Results

Copulation duration standard deviation squares (variance) were correlated with copulation durations of forest millipedes (Fig. 1. r=0.94351368, Z score=2.50192362, n=5, p= 0.00617604). *C. anulatus* was different from *C. fulgidus* (t=6.748, df=25, p<0.0001); both had equal variance (345.96). Male mass did not correlate to copulation duration (r=0.68342542, z-score=0.83551354, n=4, p=0.20171426). Female mass correlated to copulation duration (Fig. 2. r=0.99119869, z-score=2.71079571, n=4, p=0.0033615). Female mass correlated with copulation duration variance (Fig. 3. r=0.95223328, z-score=1.85520003, n=4, p=0.03178377). Male mass did not correlate with copulation duration variance (r=0.42352809, z-score=0.45198351, n=4, p=0.32564045). There was no difference between the correlation coefficients of male and female mass with copulation durations (z-statistic=-1.3260, n=4, 4, p=0.1848). There was no difference between the correlation coefficients of male and female mass with copulation duration variances (z-statistic=-0.9922, n=4,4, p=0.3211). Copulation durations differed between *C. inscriptus* and *C. ruber* (t=-14.848, n=115, 32, p<0.0001); which had subequal mass. No difference between copulation durations occurred in *C. anulatus* versus *C. ruber* (t=0.864, df=38, p=0.3930). SSD did not relate to copulation duration variance (r=-0.21240220, z-score=-0.21568570, n=4, p=0.41461640). SSD did not relate to copulation duration (r=-0.50892625, z-score=-0.56127963, n=4, p=0.28730343). SSD was related to male mass (Fig. 4. r=-0.97428050, z-score=-2.17035484, n=4, p=0.01498993). SSD was not related to female mass (r=-0.49358253, z-score=-0.54078577, n=4, p=0.29432760). Copulation durations were neither related to latitude nor temperature.

Table 1: Mean copulation duration (minutes), mass (g), and copulation duration variance (S. D.^{2}) in forest millipedes (n=5). Samples sizes for copulation duration are in parentheses.

Species	Copulation duration	Variance (S.D.^{2})	Male mass (g)	Female mass (g)	SSD	Reference
Centrobolus anulatus	34.9 (8)	345.96				
Centrobolus inscriptus	170 (115)	2401	2.48	2.27	0.9153	[18]
Centrobolus inscriptus	303 (39)	13225	2.00	2.61	1.3050	[17]
C. fulgidus	66.4 (51)	345.96	1.29	1.97	1.5271	[18]
Centrobolus ruber	39.8 (32)	174.12	1.28	2.00	1.5625	[18]

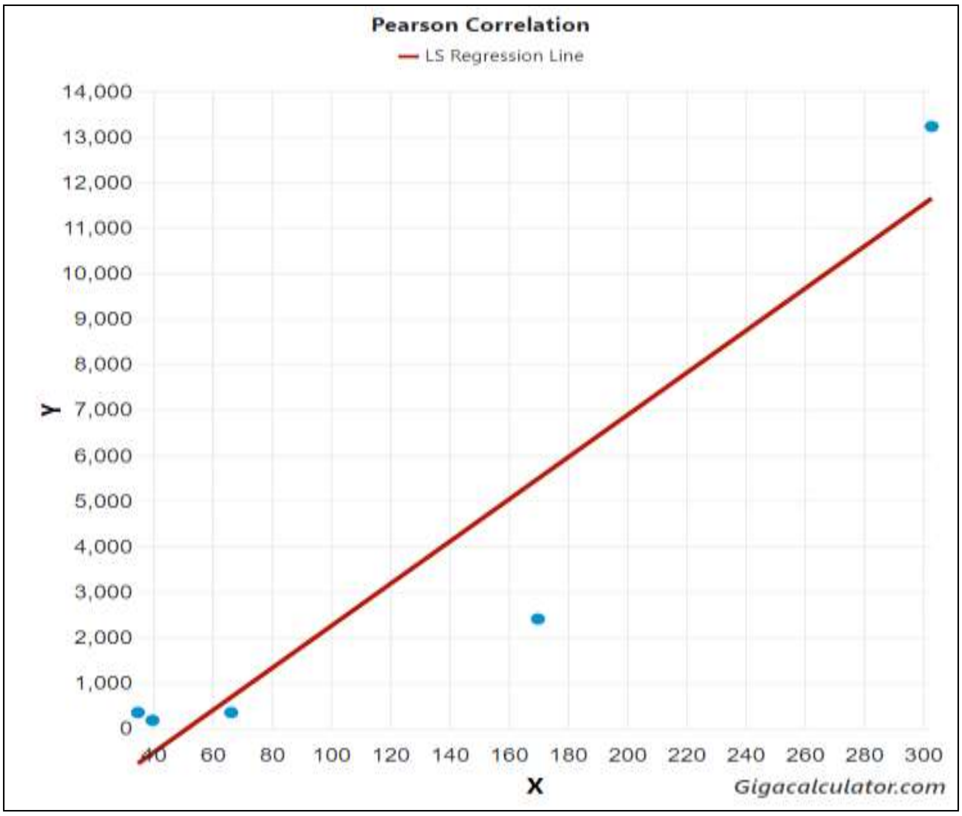

Fig 1: Regression of copulation duration variance (y-axis: minutes) on copulation duration (x-axis: minutes) in southern African forest millipedes *Centrobolus.*

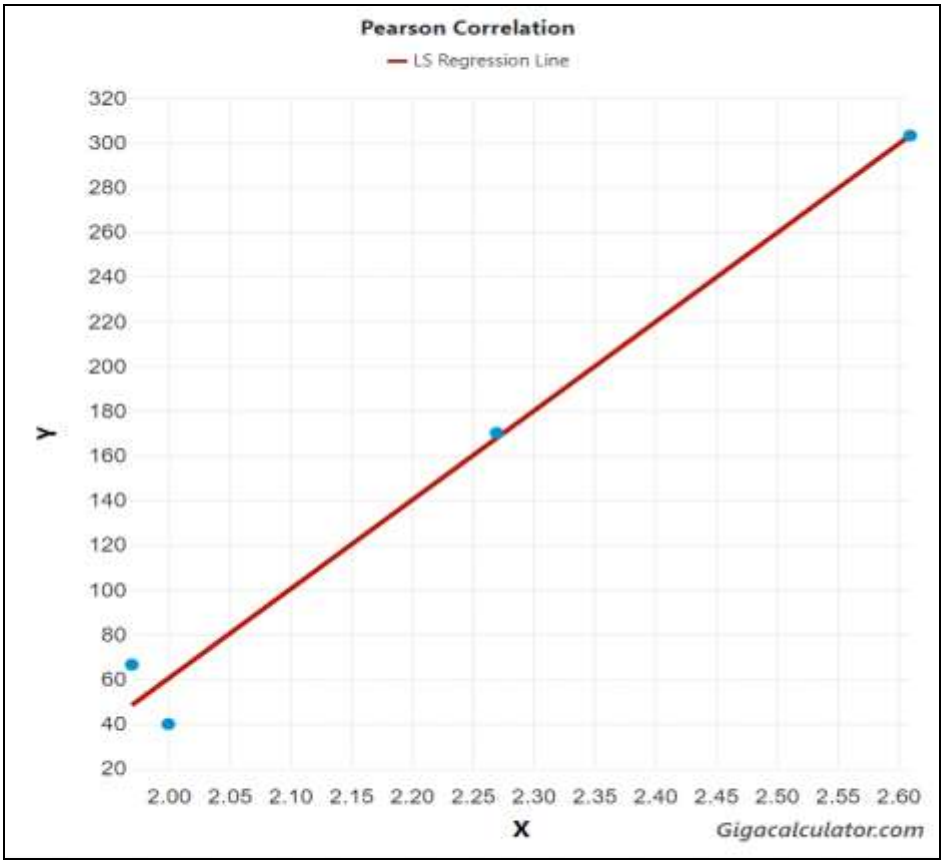

Fig 2: Correlation between female mass (x: grams) and copulation duration (y: minutes) in forest millipedes *Centrobolus*.

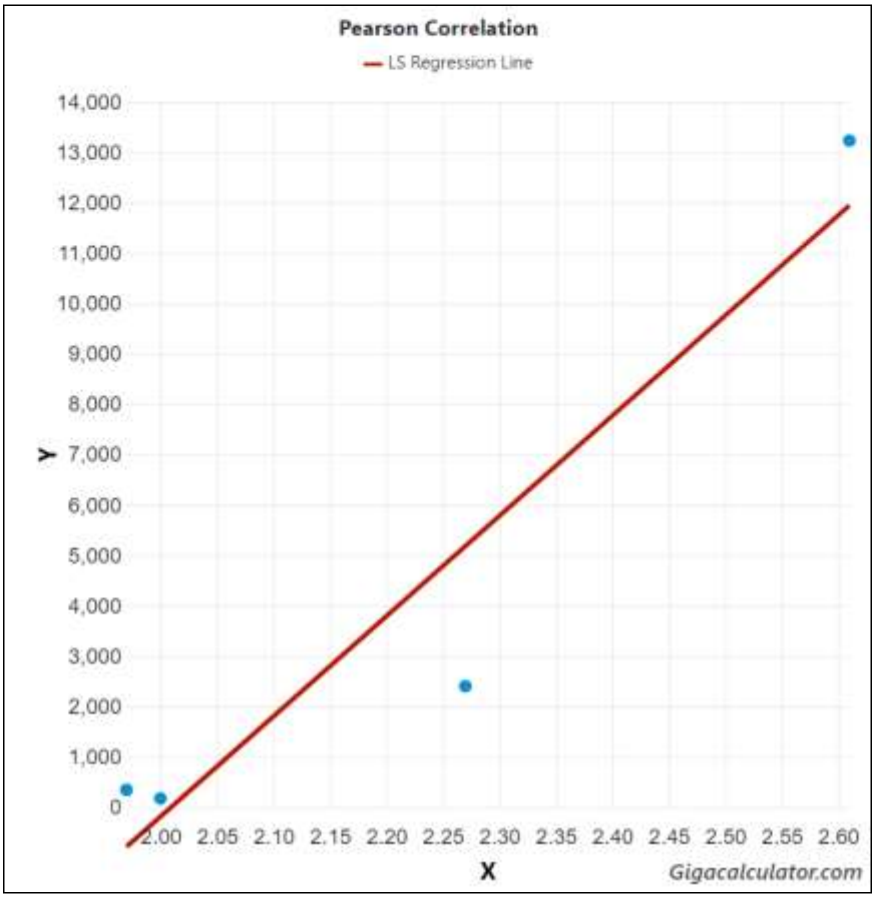

Fig 3: Correlation between female mass (x: grams) and copulation duration variance (y: minutes) in forest millipedes *Centrobolus*.

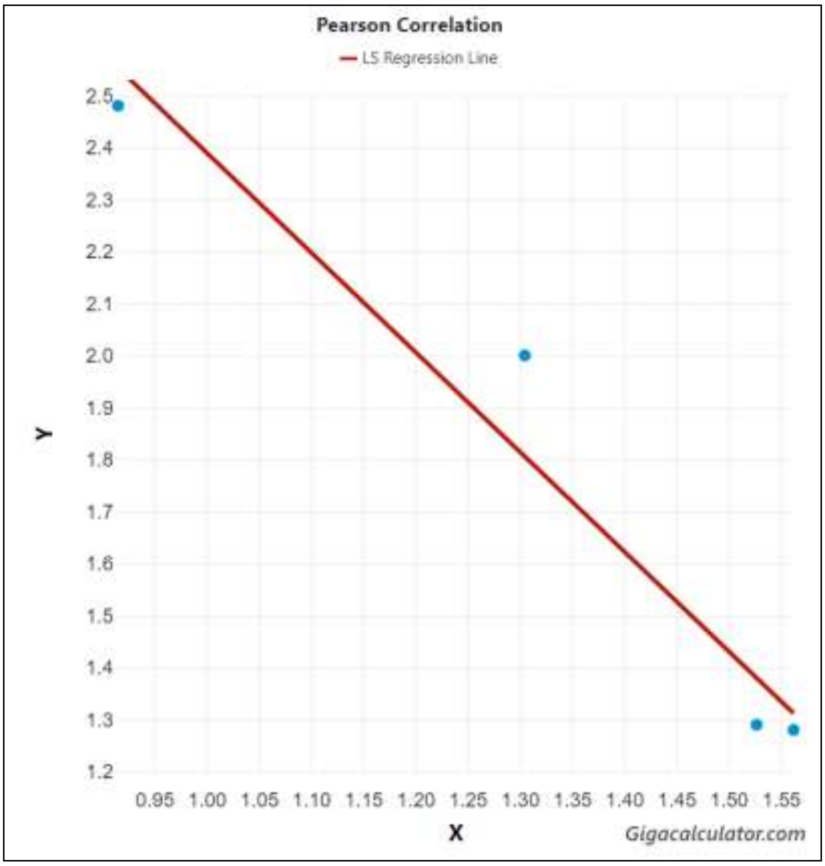

Fig 4: Relationship between Sexual Size Dimorphism (x: female to male) and male mass (y: grams) in *Centrobolus***.**

4. Discussion

The shortest copulation durations were recorded for species that show less vigorous copulation; as is the case in other juliform millipedes, where differences in the duration of copulation are thought to reflect the intensity of sperm competition between species [11, 32, 35]. Prolonged copulation is a form of mate guarding whereby the male attempts to assure paternity by controlling the duration of copulation [19, 29]. In odonate species, long copulations (minutes-hours) are associated with sperm removal and short copulations (seconds) are associated with sperm repositioning [20]. Intense sperm competition was illustrated in significantly prolonged copulation in *C. inscriptus*, unlike *C. anulatus* and *C. fulgidus*; both had equal variance. *C. fulgidus* is predicted to have greater sperm competition than *C. anulatus*.

The different patterns of copulation duration displayed in the worm-like millipedes and in particular, the *Centrobolus* species indicate how more prolonged copulation and higher levels of sperm competition could have evolved. Initially, a population is under stabilizing selection, then the pressure for prolonging copulation as a paternity assurance in females produces directional selection for larger females, before a conflict of interests between the sexes may result. The mean copulation duration for a species at any one instant in time should also represent the outcome of a sexual conflict over insemination, depending on the relative ability of males and females to exert their interests over one another [21].

Female size correlates with copulation duration and standard deviation squares in copulation duration when there is variability in sperm competition [33, 34]. Furthermore, variance in copulation duration correlates with the cryptic female choice or female control in populations. I found species-specific mean copulation durations in *Centrobolus* and variation in copulation duration was different between forest species. This emphasizes a species-specific difference in the variance of copulation duration [7]. Copulation duration in millipedes extends beyond the time necessary to transfer sperm (insemination) [22]. As there is variance at the intraspecific level "[M]ating durations exceeding female optima serve males as a form of 'extended mate guarding': by inducing mating refractoriness in the female, a male extends the time over which its sperm is exclusively used to sire progeny and reduces the likelihood of the female being inseminated by a competitor" [8, 30]. There is an inverse relationship between body size and copulation duration without variance at the interspecific leveln. Significant correlations between copulation duration, variation in copulation duration, and size were found in both forest and savanna millipedes with an inverse relationship between the surface area to volume ratios and copulation duration in forest millipedes [23].

Copulation duration and its variance were directly correlated and increased with female body size across species suggesting copulation duration depends on body size [24]. The relationship between female body size and copulation duration changes with variance [24]. Relationships between copulation duration and body size were found in *Drosophila melanogaster* [12]. Millipedes were similar to spiders where the duration of copulation correlates with intra-specific size variation, also found in a scorpionfly (*Panorpa cognata*) where males in good condition copulate longer [9]. However, this study showed there was also a trend interspecifically for copulation duration to negatively correlate with body size in and across millipedes with equal variance in copulation duration. This emphasizes the importance of body size on mate guarding, as was the case in the skeleton shrimp *Caprella penantis* where male body size was the most important factor affecting competition for a receptive female [6]. The success of guarding males in millipedes is similar to the carrion beetle (*Necrophila americana*) which depends on size relative to males and the operational sex ratio [1]. Results from removal experiments in orb-web spiders show that larger males have a clear advantage in monopolizing females [25]. This was not always the case in forest millipedes, where female size is of primary importance and male size secondary to female choice for longer males which dependes on mating order [28] (Cooper, in press).

The size of females in each species is significant in predicting copulation duration [26, 27, 24]. Together, copulation duration and female size contribute to calculating optimal copulation durations of each population [2]. *C. inscriptus* males and *C. ruber* females have equal mass yet differ in copulation durations, copulation duration variances, and sexual size dimorphism; there is higher copulation duration variance in *C. inscriptus*, illustrating the more variability in sperm competition. This suggests females control the duration of copulation when they are larger which is usually the case in second copulations (Cooper, in press).

5. Conclusion

Copulation duration and its variance were directly correlated and increased with female body size across species suggesting copulation duration depends on body size. This suggests females control the duration of copulation when they are larger which is usually the case in second copulations.

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