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Five factors affecting copulation duration in the breeding season in forest millipedes *Centrobolus* Cook, 1897

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Abstract
The objectives of this study were to determine what happened when copulation duration varied with five factors in *Centrobolus.* The mean copulation duration was correlated with female width, male width, the month with the highest number of days with precipitation, moments of inertia, and precipitation of the forest millipede genus *Centrobolus*. There was a linear relationship between copulation duration and female width (r = 0.97, Z score = 2.97, n = 5, p = 0.001), male width (r = 0.90, Z score = 2.05, n = 5, p = 0.02), moments of inertia (r = 0.67, Z score = 1.81, n = 8, p = 0.03), and precipitation (r = 0.85, Z score = 1.77, n = 5, p = 0.04). There was a marginal linear relationship between copulation duration and the month with the highest number of days with precipitation (r = 0.77, Z score = 1.46, n = 5, p = 0.07). Variance in the polygynandrous reproductive systems of *Centrobolus* occurred with longer copulations at higher precipitation with wider females having greater moments of inertia and wider males having lower moments of inertia during the height of the rainy season.

Keywords: copulation, duration, millimeter, moments, precipitation, width

Introduction

Females that choose to resolve intersexual conflicts over copulation duration will suffer less from lost time and obtain the chance to accrue benefits by pursuing other activities. The role of sequential female mate choice in species with polygynandrous mating systems that foster sperm competition with males providing no material benefits to the female can be used to answer many questions. Three especially important questions that have been addressed are why females mate multiply, what rules do they follow in making a successive choice, and what different criteria are used in the choice [8]. Females can engage in either a pre-copulatory mate choice or a relative postcopulatory mate choice.

Millipedes have highly polygynandrous mating systems that are very complex because males and females can mate multiply and prolong copulations to different degrees. The dynamics of mating and maintained genital contact have been thoroughly investigated [3]. Males control the duration of copulation and maintain genital contact with their females with the intensity of sperm competition. This supports the adaptive mate-guarding hypothesis, yet the (passive) role of the female that endures copulation is vague. The possible role of the female that endures and controls copulation duration, which ultimately is a limiting factor for males, has been neglected for a long time despite the possession of a sperm-storage organ being a primary predisposition to high variance in sperm competition [12, 13, 15].

In *Centrobolus* millipedes mate choice is determined through prolonged copulation and five factors can be identified as correlates of copulation duration: female width, male width, moments of inertia, the month with the highest number of days with precipitation, and mean annual precipitation is correlated with the copulation duration in the pachybolid millipede genus *Centrobolus* [2, 3, 5]. The null hypothesis is that all five factors affect different copulation durations among species.

Materials and Methods

Four species from the genus *Centrobolus* Cook, 1897 were identified and compared. The average copulation durations were obtained from the "Mating dynamics of South African forest millipedes *Centrobolus* (Diplopoda: Pachybolidae)"; for *C. anulatus, C. fulgidus, C. inscriptus* (n=2X), and *C. ruber* [3]. The *C. inscriptus* duplicate was obtained from another thesis [5]. Body widths of species were measured using vernier calipers.

The month with the highest number of days with precipitation and mean annual precipitation values were obtained from https://en.climate-data.org/search/?q=. Female width, male width, the month with the highest number of days with precipitation, moments of inertia, and mean annual precipitation were checked for correlations with copulation duration among species using the Pearson Correlation.

Results

There was a linear relationship between the mean copulation duration and female width (Fig. 1: r = 0.97038723, Z score = 2.96827853, n = 5, *p* = 0.00149743). Female width was normally distributed (D = 0.272, n = 5, *p* = 0.77055). There was a linear relationship between the mean copulation duration and male width (Fig. 2: r = 0.89581750, Z score = 2.05150153, n = 5, *p* =0.020109). There was a linear relationship between mean copulation duration and moments of inertia (Fig. 3: r = 0.66852064, Z score = 1.80688507, n = 8, *p* = 0.03539005). Mean male moments of inertia were not related to copulation duration (r = 0.76230118, Z score = 1.00168565, n = 4, *p* = 0.15824772). Mean female moments of inertia were significantly related to copulation duration (Fig. 4: r = 0.99695037, Z score = 3.24217874, n = 4, *p* = 0.00059316). The least-squares regression line was y = 18.73838872x - 33.25420271 for the moments of inertia and mean copulation duration, and y = 37.16224410x - 297.27850677 for the female moments of inertia and mean copulation duration. Moments of inertia were normally distributed (D = 0.16846, n = 10, *p* = 0.89593). Moments of inertia were normally distributed in males (D = 0.23843, n = 5, *p* = 0.8754). Moments of inertia were normally distributed in females (D = 0.21196, n = 5, *p* = 0.94088). There was a marginal positive correlation between mean copulation duration and the month with the highest number of rainy days (Fig. 5: r = 0.77431277, Z score = 1.45806716, n = 5, p = 0.07241106). The least-squares regression line was y = 126.21147366x - 1714.67632531 for the month with the highest number of rainy days and mean copulation duration. The month with the highest number of rainy days was normally distributed (D = 0.25637, n = 5, *p* = 0.82435). There was a significant positive correlation between mean copulation duration and precipitation (Fig. 6: r = 0.84852388, Z score = 1.76897942, n = 5, *p* = 0.03844861). The least-squares regression line was y = 0.39115822x + 914.00590505 for the precipitation and mean copulation duration. Precipitation was normally distributed (D = 0.26904, n = 5, *p* = 0.78113). Mean copulation durations were normally distributed (D = 0.31348, n = 5, *p* = 0.61074).

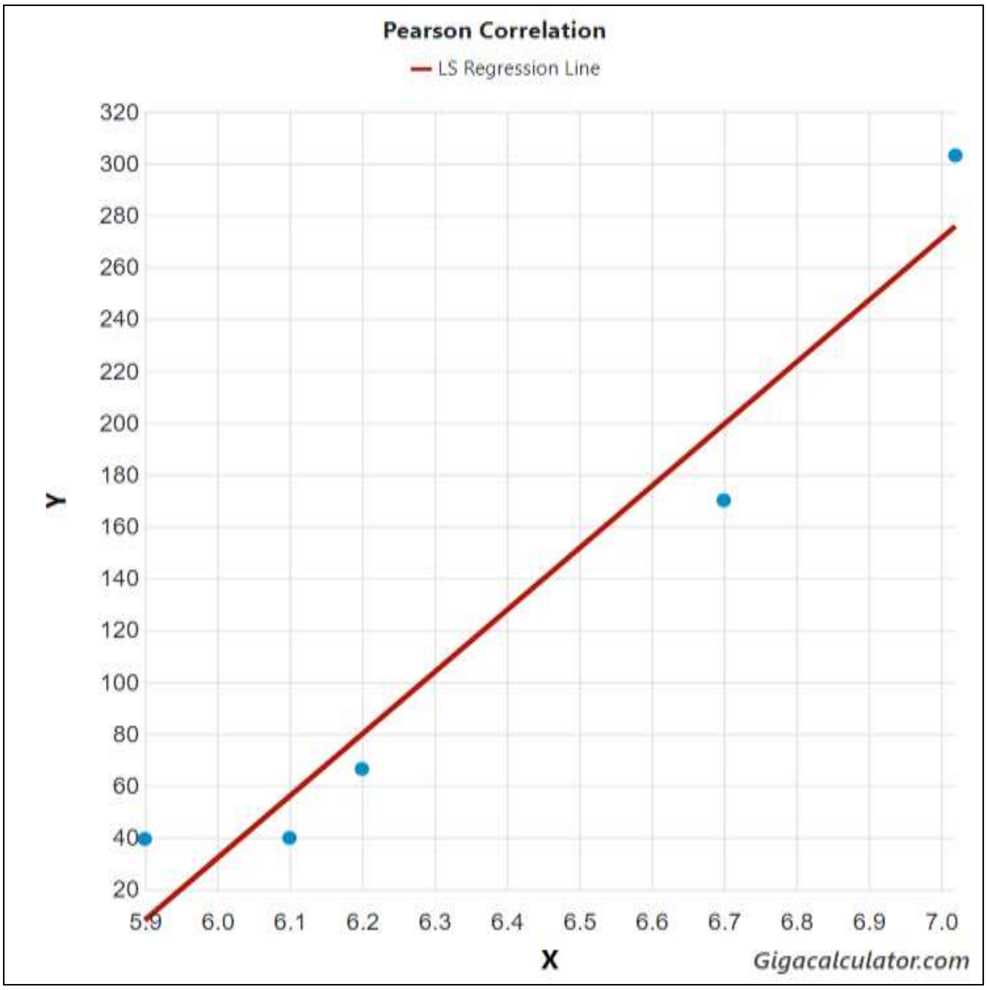

Fig 1: A linear relationship between female width (mm) and copulation duration (minutes) in five samples of forest millipedes (*Centrobolus*).

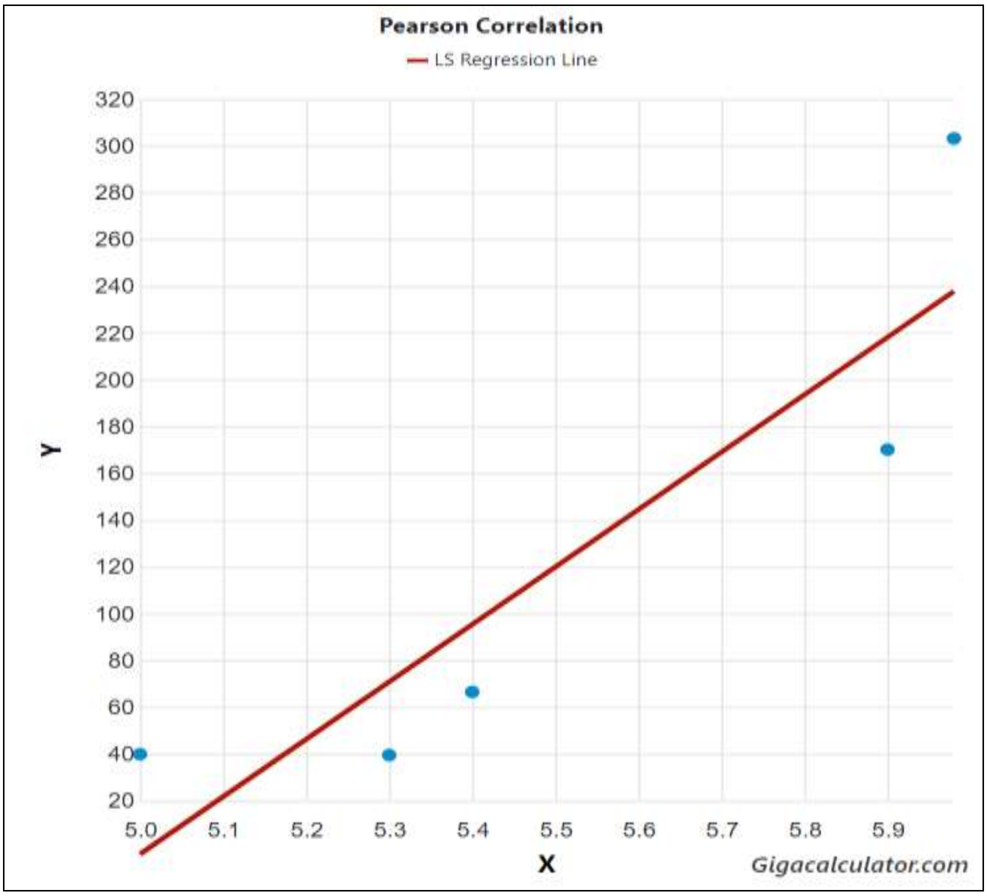

Fig 2: A linear relationship between male width (mm) and copulation duration (minutes) in five samples of forest millipedes (*Centrobolus*).

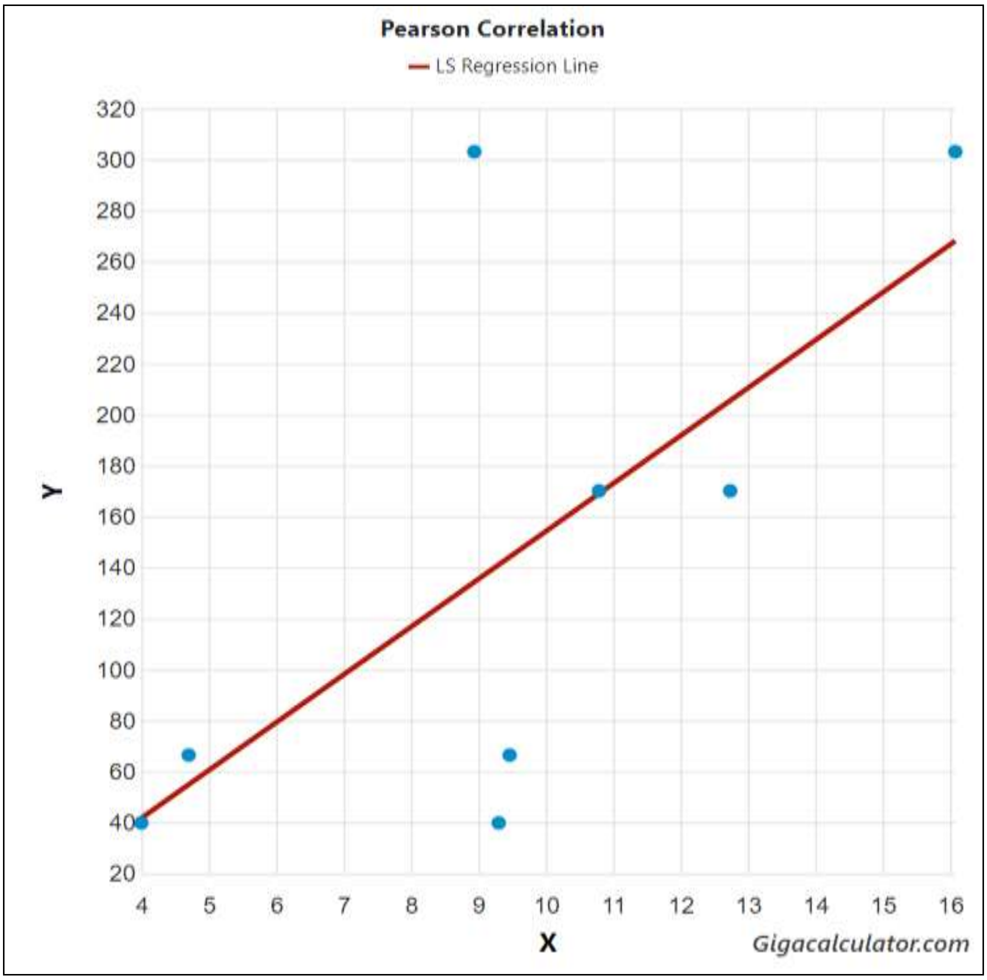

Fig 3: A linear relationship between male and female moments of inertia (x) and copulation duration (y) in forest millipedes (*Centrobolus*).

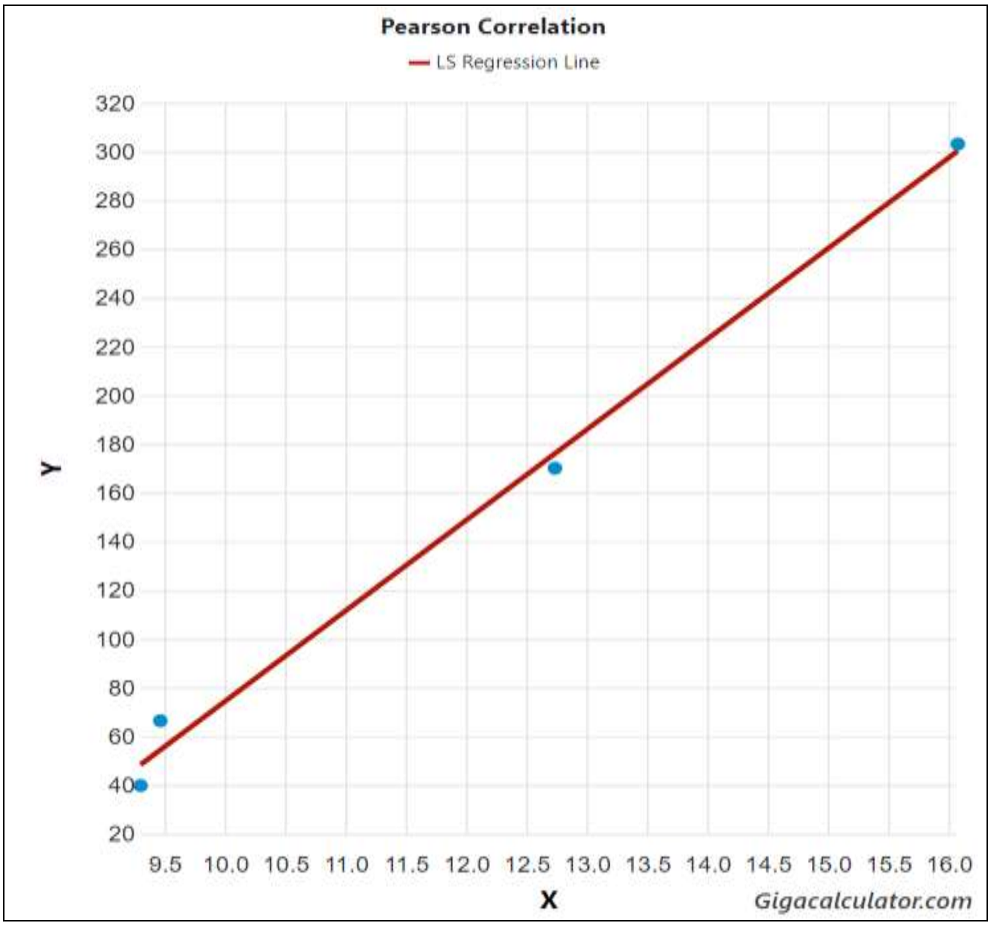

Fig 4: A linear relationship between female moments of inertia (x) and copulation duration (y) in forest millipedes (*Centrobolus*).

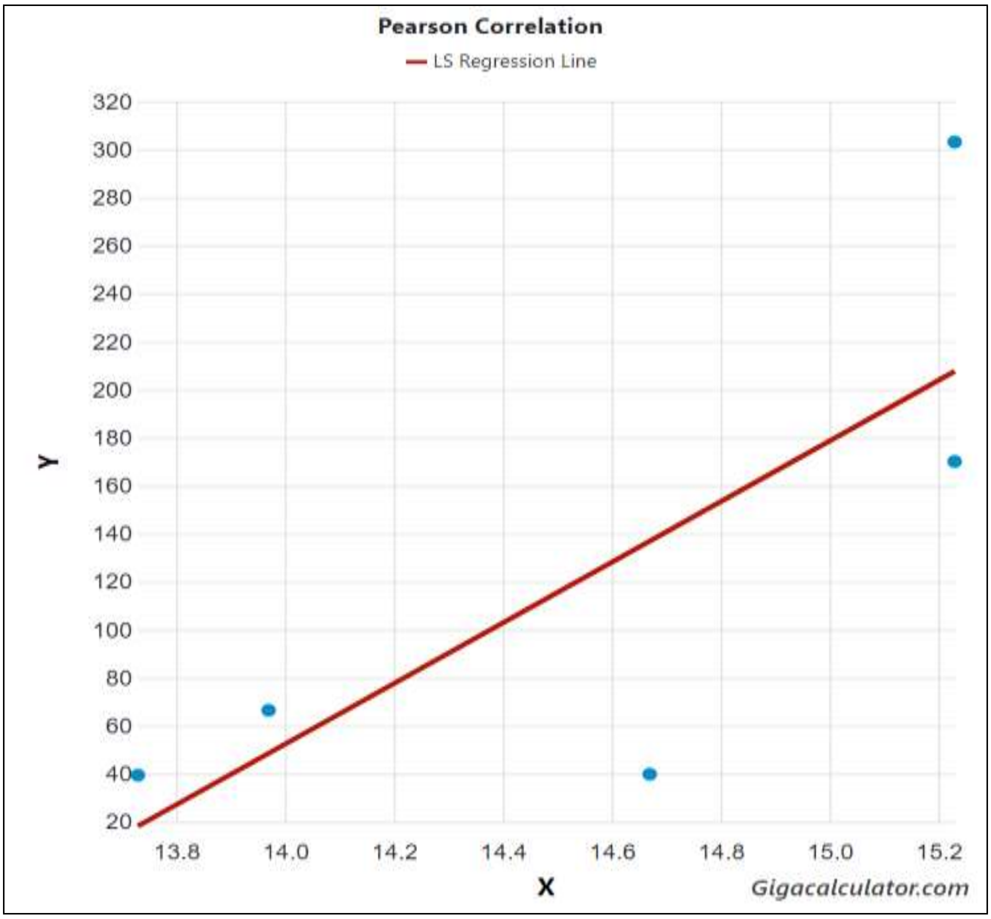

Fig 5: A linear relationship between the month with the highest number of days with precipitation (x) and copulation duration (y) in forest millipedes (*Centrobolus*).

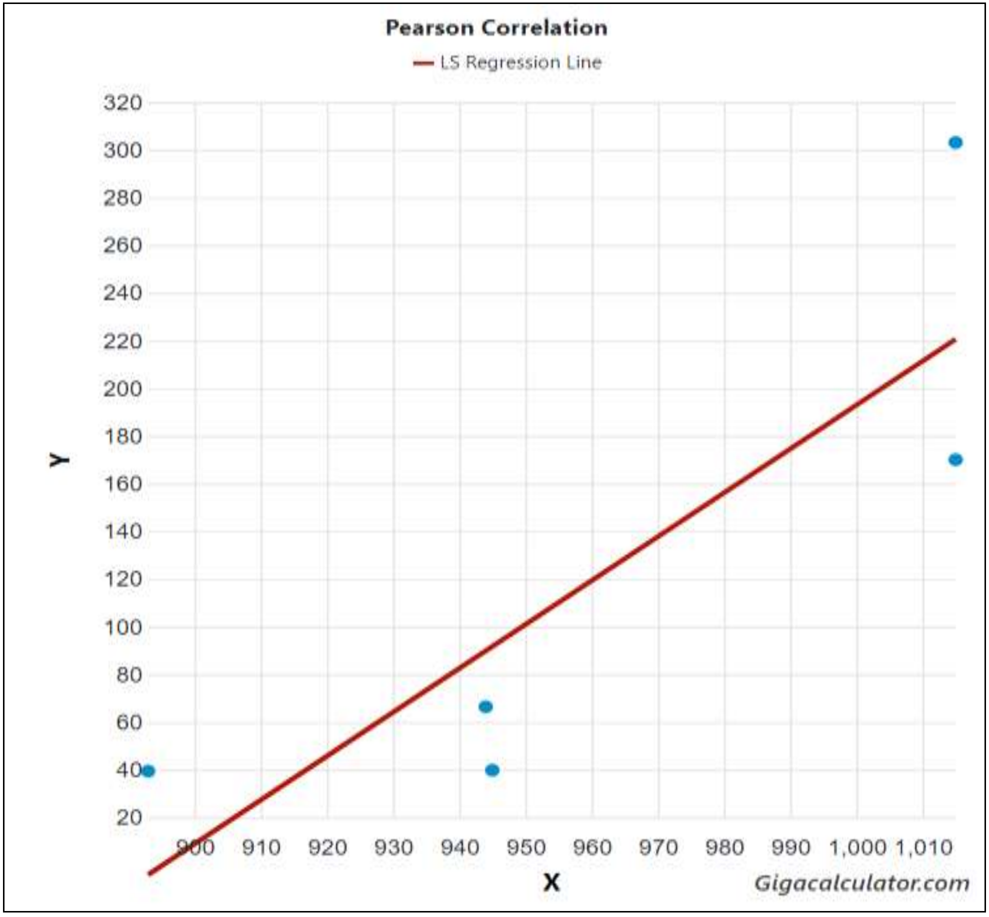

Fig 6: A linear relationship between precipitation (x) and copulation duration (y) in forest millipedes (*Centrobolus*).

Discussion

Positive linear relationships were found between mean copulation duration and female width, male width, moments of inertia, the month with the highest number of days with precipitation, and mean annual precipitation in *Centrobolus*. *C. inscriptus* had the longest mean copulation duration (303 minutes), the greatest female and male widths, highest moments of inertia, and occurred at the highest precipitation (1015 mm) while *C. anulatus* had the shortest copulation duration (39.4 minutes), low female and male widths, lowest moments of inertia, and occurred at the lowest precipitation (893 mm). This study supports female and male width, moments of inertia, and precipitation as predictors of the copulation duration in *Centrobolus*. Copulation duration increases with these four factors and marginally with the month with the most number of days with precipitation which supports the seasonality of copulation duration in these millipedes [3, 5]. These relationships with copulation duration are specific to this genus of millipedes and probably not found when comparing worm-like millipedes with them across the world.

The correlation between male and female widths and the correlation with each of them to copulation duration at the height of the breeding season (in this study) suggests positive size-assortative mating across species [6]. Size-assortative mating is also found in mud crabs *Scylla* [7]. Like fiddler, hermit crabs, and snow crabs, this is due to sexual selection [1, 9, 11]. When males have to overcome female resistance to mate, factors such as sexual size dimorphism - influenced by male and female width - can influence the outcome of the struggle [14].

Variation in copulation duration has been attributed to the sequence number of the copulation for the male on a day [10]. The variability in the interval between successive copulations, like that of the actual copulation duration, may have evolved through male or female-controlled processes. The prolonged remating intervals are unlikely to be the result of induced unreceptivity whereby the first male delays a female remating because the second male has the higher potential volumetric sperm priority after longer intervals. The operational sex ratio (OSR) is another factor responsible for natural variance in remating intervals.

On certain given days during the breeding season copulation duration and female width, male width, moments of inertia, the month with the highest number of days with precipitation, and mean annual precipitation predictably covary across four *Centrobolus* species.

Conclusion

Mean copulation duration increased with female width, male width, (female) moments of inertia, the month with the highest number of days with precipitation, and mean annual precipitation during the breeding season consistently across four *Centrobolus* species.

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