COPULATION DURATION IS RELATED TO EJACULATING VOLUME IN *CENTROBOLUS INSCRIPTUS* (ATTEMS, 1928)

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Abstract: **One species of *Centrobolus* was identified (*C. inscriptus*) based on morphology and confirmed using Scanning Electron Microscopy (SEM) of the gonopod structure. Copulation duration was recorded. Ejaculate volumes were measured in single and double matings. Copulation duration and ejaculate volumes were either negatively or positively related depending on the presence of a second mating. Copulation duration and ejaculate volumes were positively related (r=1.00, Z score=4.38, n=15, p<0.01) in first matings but not second matings (r=0.84, Z score=1.22, n=15, p=0.11). In double matings: first matings left spermathecal volume correlated with copulation duration (r=0.99, Z score=2.52, n=15, p<0.01) as did right spermathecal volume (r=0.97, Z score=2.07, n=15, p=0.02). In single matings copulation durations (n=12) were (negatively) correlated with the combination of left and right spermathecal volumes pooled with total ejaculate volumes (r=-0.82, Z score=-1.98, n=6, p=0.02). In single matings left ejaculate volumes pooled with total ejaculate volume was not significantly correlated (r=-0.74, Z score=-0.95, n=4, p=0.17) but right was (r=-0.96, Z score=-1.90, n=4, p=0.03). Variability in copulation duration was gaged. Variability in copulation duration and ejaculate volumes were not all negatively related. Variability in copulation duration and ejaculate volumes were negatively related (r=-1.00, Z score=-3.16, n=4, p<0.01) in first matings and in second matings (r=-0.96, Z score=-1.99, n=4, p=0.02). In double matings: first matings left spermathecal volume correlated with variability copulation duration (r=-0.98, Z score=-2.22, n=4, p=0.01) as did right spermathecal volume but marginally (r=-0.89, Z score=-1.42, n=4, p=0.08); second matings left ejaculate volume correlated with variability in copulation duration (r=-0.98, Z score=-2.41, n=4, p<0.01) and right spermathecal volume was marginally related (r=-0.89, Z score=-1.42, n=4, p=0.08). In single matings variability in copulation durations (n=12) was (positively) correlated with the combination of left and right spermathecal volumes pooled with total ejaculate volumes (r=0.82, Z score=1.98, n=4, p=0.02). Variability in copulation duration was not related to left ejaculate volumes pooled with total ejaculate volume (r=0.74, Z score=0.95, n=4, p=0.17) but was related to right ejaculate volumes pooled with total ejaculate volume (r=0.96, Z score=1.90, n=4, p=0.03). P_2 was determined as 54.06 and changed from 32.33 (approximately one-third) to 75.80 (approximately three-quarters) with a 24-hour re-mating interval as copulation duration was related to ejaculating volume.**

Keywords: **endurance, ejaculate, female, male, mating, spermatheca.**

I. INTRODUCTION

The red millipede genus *Centrobolus* is well known for studies on sexual size dimorphism (SSD) and displays prolonged copulation durations for pairs of individuals of the species [7-12]. *Centrobolus* is distributed in temperate southern Africa with northern limits on the east coast of southern Africa at -17° latitude South (S) and southern limits at -35° latitude S. It consists of taxonomically important species with 12 species considered threatened and includes nine vulnerable and three endangered species [27]. It occurs in all the forests of the coastal belt from the Cape Peninsula to Beira in Mocambique [26]. Spirobolida has two pairs of legs modified into gonopods on the eighth and ninth diplosegments [29]. In *Centrobolus* the coleopods are the anterior gonopods of leg-pair eight and can be classed as paragonopods or peltogonopods because they are fused into a single plate-like structure and play a subsidiary role as inseminating devices while leg-pair nine are sperm-transferring [1]. The sternites (or stigma-carrying plates [30]) prevent lateral shifting (stabilizer) and stretch the vulva sac in a medial plane [6]. They facilitate insemination during prolonged copulation durations [5].

The copulation duration and copulation duration variability were recorded in one *Centrobolus* species [4]. These are worm-like millipedes that have female-biased SSD [7-12, 15-21, 24]. From the results, correlations between copulation duration, copulation duration variability, and ejaculate volume were checked.

II. MATERIALS AND METHODS

One species of *Centrobolus* was identified based on morphology and confirmed using Scanning Electron Microscopy (SEM) of gonopod structure

(*C. inscriptus*). The copulation durations were recorded in single and double matings accurate to minutes. Copulation duration and ejaculate or spermathecal volumes in Disintegrations per minute (D. p. m.) (left, right, and total) were correlated here using a Pearson Correlation Coefficient (https://www.gigacalculator.com/calculators/correlation-coefficient-calculator.php).

A. Animal collection and maintenance

Millipedes were hand collected from the indigenous coastal forest at Twin Streams Farm, Mtunzini, South Africa (28°55'S, 31 °45'E). Live specimens of each sex were transported to Cape Town and kept at 25°C temperature; 70% relative humidity; 12:12 hours light-dark cycle. Food was provided in the form of fresh vegetable *ad libitum*. Unisex groups were housed in plastic containers containing moist vermiculite (± 5cm deep) before the mating experiments commenced.

B. Male radioisotope labeling, female spermathecae removal, and ejaculate detection

Ejaculate priority patterns were quantified by calculating P_2 as a volumetric indicator of the proportion of offspring sired by the second male to mate with a twice-mated female [3]. The reason for selecting this measure was because *C. inscriptus* would not oviposit under laboratory conditions and so offspring counts could not be made. The experimental protocol was based on a strict *a priori* approach with the ejaculate being the unit for consideration [24]. The radioisotope labeling technique allowed two types of ejaculates to be discerned [28]; for its application in millipedes see [2]), A Hamilton syringe was used to inject 50 microliter aliquots of tritiated [*methyl*-^{3}H] thymidine (85 Ci/mmol, Amersham, UK) between the tergites of the 10th and 11th diplosegments of individual males (L). The second class of males did not receive the treatment and were left unlabelled males (UL). Females were killed in ethyl-acetate jars after their last copulation and the paired sperm storage organs were dissected under a magnifying lens (5X). Left and right spermathecae were placed in separate 7ml scintillation vials and vortexed for the 30s with 0.1 ml concentrated HCl to promote rapid tissue homogenization [1]. Acid was neutralized with 0.1ml 5M NaOH before adding 3.5 ml scintillation fluid (Scintillator 299, Packford). The volume of labeled ejaculate present in the female spermathecae was quantified in disintegrations per minute (Dpm) of radioisotope using a 1600 scintillation counter (low count reject= 0; Dpm multiplier= 1). Thus Dpm values were used as volumetric indications of the labeled ejaculate present in the female spermathecae. The weakness of this method was that it did not take into account variation in sperm production, sperm quality, sperm motility within the female, intercellular sperm-egg interactions, and intra-cellular sperm-egg interactions.

C. Mating experiments

Before being placed into mating arenas (glass aquaria 30 X 22 X 22 cm), individual animals were marked on the posterior segments with colored correction fluid. This allowed every individual's mating history to be followed. Approximately five minutes after they had established a copula position, pairs were removed from the mating arena and placed into plastic beakers (13cm diameter) where the copulation duration was recorded. This removal was necessary to eliminate the effects of male-male competition on intersexual conflict. Radiolabelled males were used in artificially-terminated matings to elucidate the timing of insemination (*sensu. D. uncinatus* [1]). Copula pairs were separated after different time intervals within the first 30 minutes of the copula. Double mating sequences were performed to test for mating order and interval effects. Mating order was controlled by mating a female first with a labeled male followed by an unlabelled male, and then vice versa (L-UL versus UL-L). Females were given the opportunity for a second mating either immediately after the first (0-hour delay) or approximately 24 hours later (24-hour delay). As controls, females that had single matings with labeled males were dissected immediately or after 24 hours (L(0) versus L(24)). Females that had single matings with unlabelled

males were dissected similarly to control for background radiation.

D. Statistical analysis

Normally distributed data were analyzed with Pearson's correlation (r) and t-tests (t) while Spearman's rank-order correlation and two-tailed Mann-Whitney U-tests (Z) were selected as non-parametric analogs with Wilcoxon tests (T) used on any matched pairs. The Kruskal Wallis 1-way Anova (H) was used to test for differences in dpm data before running the Mann-Whitney U-tests (U).). I tested for an absolute difference between left and right ejaculate volumes using a P-value calculator selecting in means of absolute differences between mean dpm values with a Z-test on raw data.

III. RESULTS

A. Copulation duration and ejaculate volumes

Copulation duration and ejaculate volumes were positively related (Figure 1: r=0.99968814, Z score=4.382978, n=15, p=0.00000586) in first matings but not second matings (r=0.83846858, Z score=1.21599426, n=15, p=0.11199362). In double matings (Table 1): first matings left spermathecal volume correlated with copulation duration (Figure 2: r=0.98716160, Z score=2.52101086, n=15, p=0.00585093) as did right spermathecal volume (Figure 3: r=0.96857602, Z score=2.06874727, n=15, p=0.01928484). In single matings (Table 2) copulation durations (n=12) were (negatively) correlated with the combination of left and right spermathecal volumes pooled with total ejaculate volumes in double matings (Figure 4: r=0.70328457, Z score=2.62131034, n=12, p=0.00437966) and single matings (Figure 5: r=-0.81535143, Z score=-1.97937028, n=6, p=0.02388710). In single matings left ejaculate volumes pooled with total ejaculate volume was not significantly correlated (r=-0.73942273, Z score=-0.94920457, n=4, p=0.17125827) but right was (Figure 6: r=-0.95630291, Z score=-1.90076505, n=4, p=0.02866633). First copulation durations were not different in time to second copulation durations (Z=1.1687, U=12.5, n=4, 4, p=0.2425). Copulation durations were normally distributed (D=0.2608, n=8, p=0.1121) (D=0.1825, n=3, p=0.9579). P_2 was determined as being between 49% and 59.125000% (Mean=54.062500; n=4) and changed from 32.33% to 75.795000% after a 24-hour re-mating interval. Copulation duration with an interval (24 h) was not different to copulation duration without an interval (Z=1.607, U=14, n=4, 4, p=0.1081). Copulation durations in single mating experiments did not differ from copulation durations in double mating experiments (Z=1.1278, U=18, n=3, 8).

Table 1. Means (±1S.E.) of copulation duration and labeled ejaculate volume present in the spermathecae of females performing double matings.

Mating series	n	First copulation duration (min)	Second copulation duration (min)	Left ejaculate volume in spermathecae (dpm)	Right ejaculate volume in spermathecae (dpm)	Total ejaculate volume in spermathecae (dpm)	Surrogate P_2 (%)
L-UL (0)	1	347 (±0.00)	328 (±0.00)	542 (±0.00)	358 (±0.00)	901 (±0.00)	
UL-L(0)	7	324 (±33.87)	275 (±37.36)	358 (±143.83)	339 (±161.95)	698 (±221.09)	43.66
L-UL (24)	4	275 (±127.94)	233 (±73.75)	140 (±98.42)	92 (±59.36)	232 (±135.29)	
UL (24)	3	324 (±48.29)	248 (±20.03)	381 (±77.23)	300 (±38.83)	681 (±214.21)	74.59

Table 2. Means (±1S.E.) of copulation duration and labeled ejaculate volume present in the spermathecae of females performing single mating.

Mating series	n	copulation duration (min)	Ejaculate volume in spermathecae (dpm) Left	Right	Total

L (0)	*	185(±186.94)	655 (±0.00)	1467 (±0.00)	2121 (±0.00)
L (24)	8	256 (±121.65	172 (±60.93)	144 (±81.75)	316 (±97.92)
UL	17	319 (±95.35)			

*copulation duration n=4, ejaculate volume n=1.

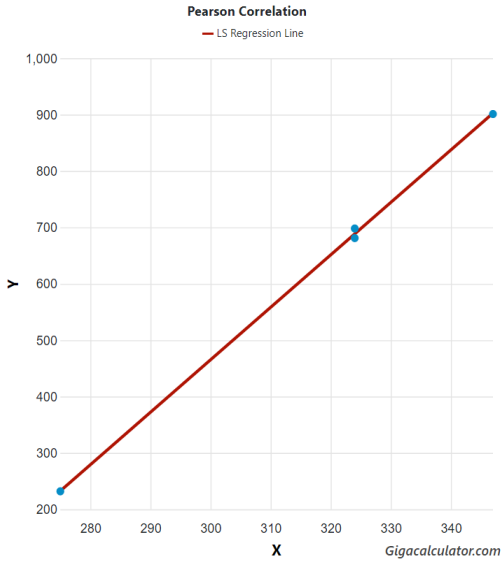

Figure 1. Relationship between copulation duration (x) and ejaculate volume (y) in first matings with a species of *Centrobolus* (*C. inscriptus*).

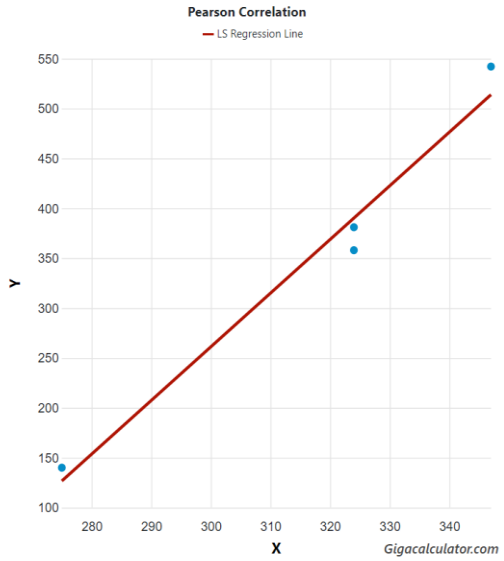

Figure 2. Relationship between copulation duration (x) and left spermathecal volume (y) in first matings with a species of *Centrobolus* (*C. inscriptus*).

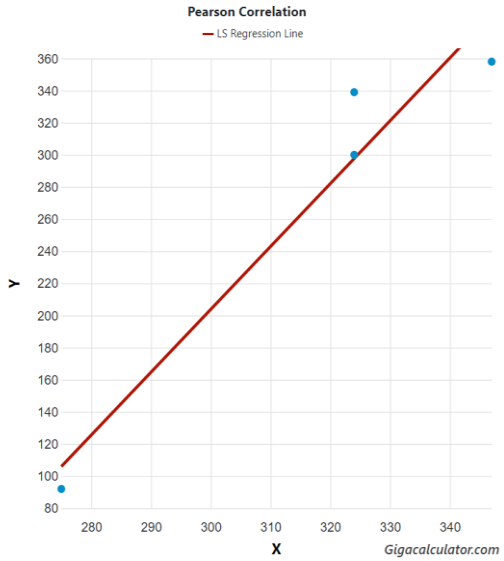

Figure 3. Relationship between copulation duration (x) and right spermathecal volume (y) in first matings with a species of *Centrobolus* (*C. inscriptus*).

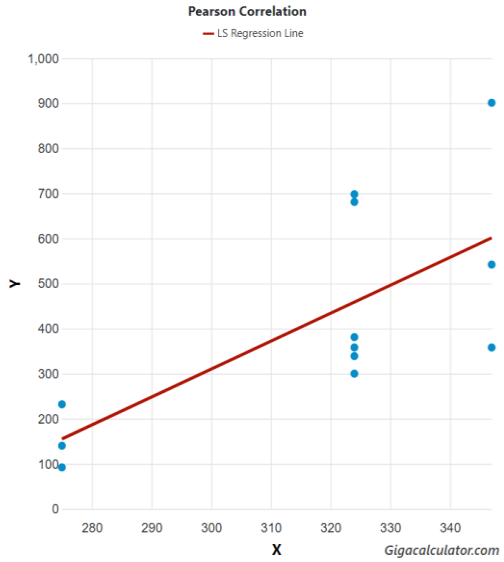

Figure 4. Positive correlation between copulation duration (x) and a combination of left and right spermathecal volumes pooled with total ejaculate volume (y) in the presence of a second mating.

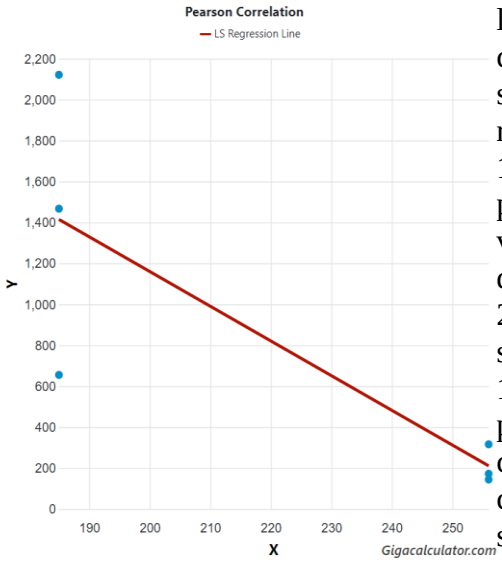

Figure 5. Negative correlation between copulation duration (x) and a combination of left and right spermathecal volumes pooled with total ejaculate volume (y) in the absence of a second mating.

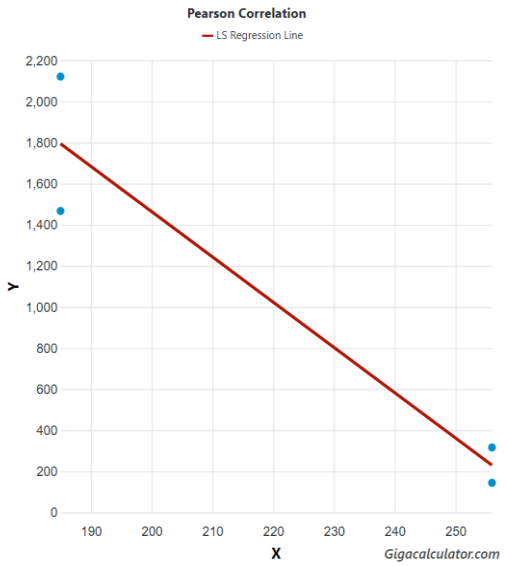

Figure 6. Relationship between copulation duration (x) and right and total ejaculate volume pooled (y) in *Centrobolus inscriptus.*

B. Variability in copulation duration and ejaculate volumes

Variability in copulation duration and total ejaculate volumes were negatively related in first matings (Figure 7: r=-0.99643204, Z score=-3.16356186, n=4, p=0.00077932) and in second matings (Figure 8: r=-0.96349477, Z score=-1.99251279, n=4, p=0.02315734). In double matings: first matings left spermathecal volume correlated with variability copulation duration (Figure 11: r=-0.97649247, Z score=-2.21587917, n=4, p=0.01334984) as did right spermathecal volume but margianlly (Figure 12: r=-0.89043331, Z score=-1.42401397, n=4, p=0.07722126); second matings left ejaculate volume correlated with variability in copulation duration (Figure 9: r=-0.98386852, Z score=-2.40601559, n=4, p=0.00806378) and right spermathecal volumewas marginally related (Figure 10: r=-0.89043331, Z score=-1.42401397, n=4, p=0.07722126). In single matings variability in copulation durations (n=12) were (positively) correlated with the combination of left and right spermathecal volumes pooled with left, right and total ejaculate volumes (Figure 13: r=0.81535143, Z score=1.97937028, n=6, p=0.02388710). Variability in copulation duration was not related to left ejaculate volumes pooled with total ejaculate volume (r=0.73942273, Z score=0.94920457, n=4, p=0.17125827) but was related to right ejaculate volumes pooled with total ejaculate volume (Figure 14: r=0.95630291, Z score=1.90076505, n=4, p=0.02866633). First copulation durations were not different in time to second copulation durations (Z=1.1687, U=12.5, n=4, 4, p=0.2425). Variability in first copulation durations were normally distributed (D=0.2811, n=4, p=0.3203) and in second copulation durations (D=0.1919, n=4, p=0.8688); combined (D=0.197, n=8, p=0.478). Variability in single mating copulation durations were normal (D=0.2752, n=3, p=0.4926). Variability in copulation duration with an interval (24 h) was not different to copulation duration without an interval (Z=-1.5972, U=2, n=4, 4, p=0.1102). Left and right ejaculate volumes were not different in single matings (Z score=0.556729, n=4, p=0.288856). Left and right ejaculate volumes were not different in double matings without an interval (Z score=-1.097426, n=4, p=0.136228). Left and right ejaculate volumes were not different with a 24 h interval (Z score=-0.405218, n=4, p=0.342659). Variability in copulation duration did not differ between single and double mating (Z=-1.9436, U=2, n=3, 8, p=0.05194).

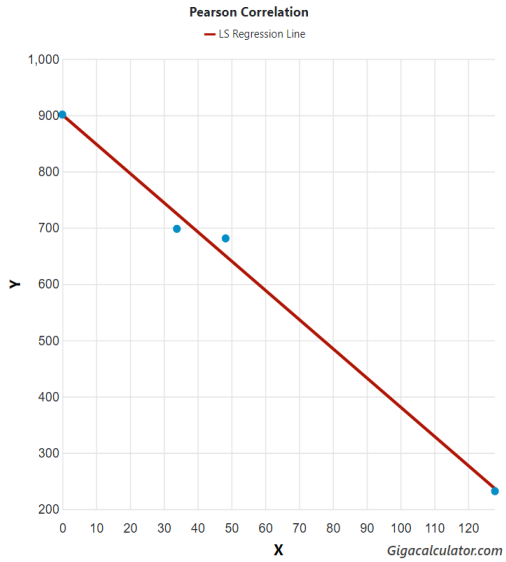

Figure 7. Relationship between variability in copulation duration (x) and ejaculate volume (y) in first matings with a species of *Centrobolus* (*C. inscriptus*).

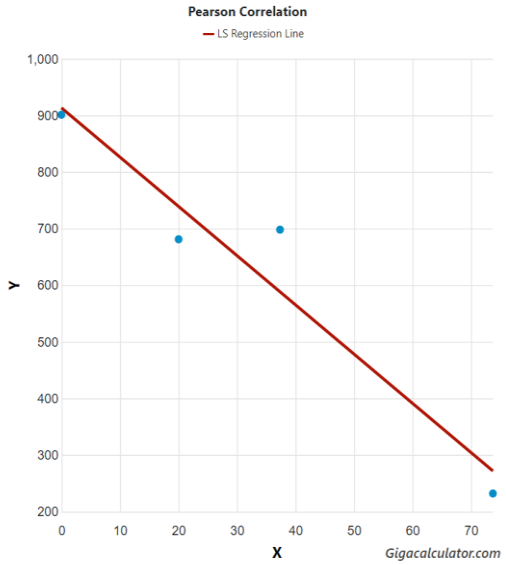

Figure 8. Relationship between variability in copulation duration (x) and total spermathecal volume (y) in second matings with a species of *Centrobolus* (*C. inscriptus*).

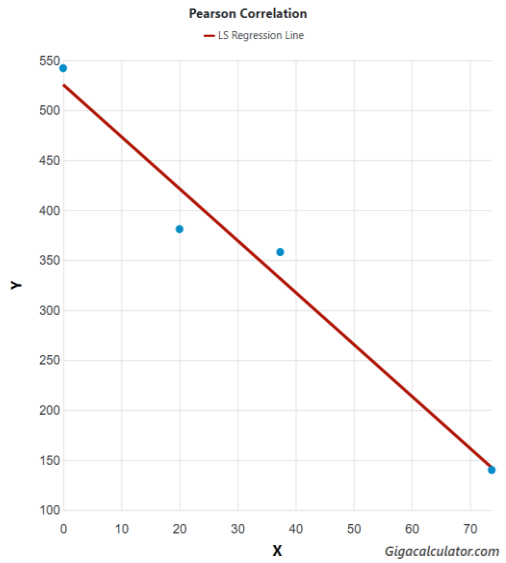

Figure 9. Relationship between variability in copulation duration (x) and left spermathecal volume (y) in second matings with a species of *Centrobolus* (*C. inscriptus*).

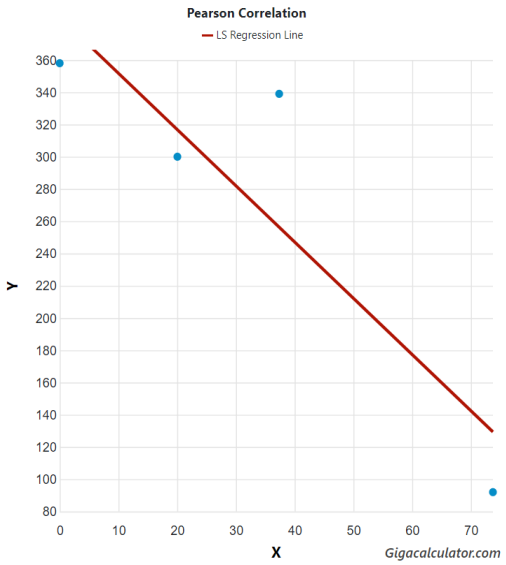

Figure 10. Relationship between variability in copulation duration (x) and a right spermathecal volume (y) in the presence of a second mating.

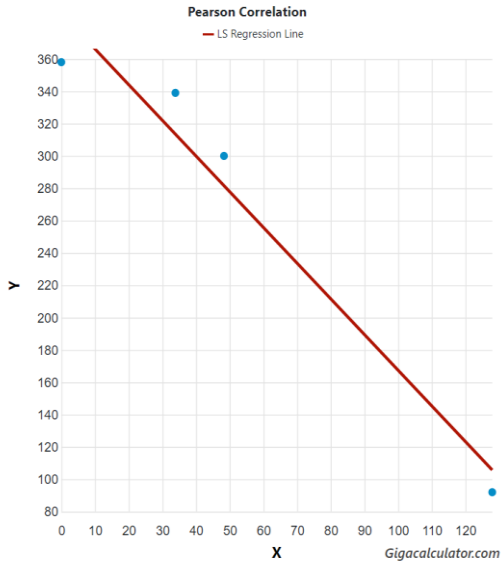

Figure 11. Negative correlation between variability in copulation duration (x) and left spermathecal volume (y) in first of double mating.

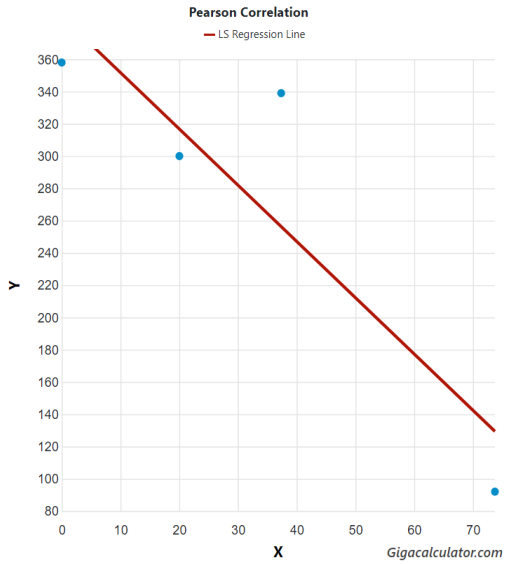

Figure 12. Negative correlation between variability in copulation duration (x) and right spermathecal volume (y) in first of double mating.

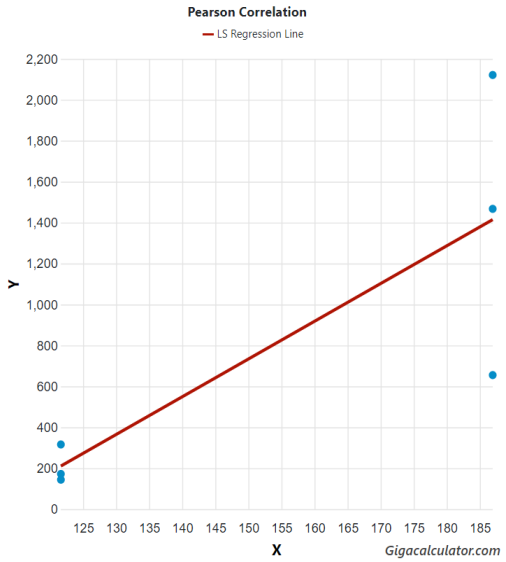

Figure 13. Relationship between variability in copulation duration (x) and left, right, and total ejaculate volume (y) in single matings.

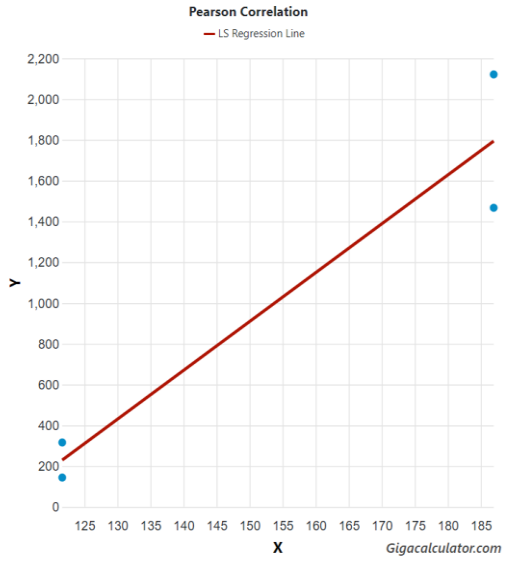

Figure 14. Relationship between variability in copulation duration (x) and right, and total ejaculate volume (y) in single matings.

IV. DISCUSSION

The copulation durations and copulation duration variabilities were recorded in one *Centrobolus* species [4]. A direct relationship between copulation duration and ejaculate volume is shown. All negative relationships between variability in copulation duration and ejaculate volume are found except in single matings where variability in copulation duration is positively

related to ejaculate volume. This may support the function of the copulation duration in sperm competition [13, 31]. A relationship between this behavioral trait is present across this species in single and double matings suggesting adaptation to insemination. The relationship between copulation duration and (right) ejaculate volume changes from negative in single matings to positive in the first of double matings illustrating that the ejaculate volume increased with copulation duration in the first of a double mating in the presence of competition. The relationship between copulation duration variability and ejaculate volume is positive in single matings and negative in both double matings illustrating that the ejaculate volume increased with variability in copulation duration only in the single matings and not double matings or in the presence of competition. The copulation duration in *Centrobolus* millipedes predicts a functional significance in assuring paternity for the one male depending on the presence or absence of a second mating. P_2 was determined as 54.062500 and changed from 32.33 (approximately one-third) to 75.795000 (approximately three-quarters) after a 24-hour re-mating interval. The copulation duration is not impacted by the re-mating interval in certain experiments. The variability in copulation duration is not impacted by the re-mating interval in double experiments. Variability in copulation duration related to (right and total) ejaculating volume. Variability in ejaculate volume is related to neither copulation duration nor variability in copulation duration (i. e. controlled).

V. CONCLUSION

Several new relationships between copulation duration and ejaculate volumes in *Centrobolus* millipedes support the function of the prolonged copulation through assuring paternity with a reduction of sperm competition. Prolonged copulation is related to both higher and lower ejaculate volumes depending on the presence of a second mating. P_2 is determined as 54.062500 and changed from 32.33 (approximately one-third) to 75.795000 (approximately three-quarters) after a 24-hour re-mating interval if copulation duration is related to ejaculating volume. Several new relationships were also found between variability in copulation duration and ejaculate volumes in *Centrobolus* millipedes to support the function of the prolonged copulation in assuring paternity with a reduction of sperm competition. Variability in the prolonged copulation is related to both higher and lower ejaculate volumes depending on the presence of a second mating.

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