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## Sexual conflict over the duration of copulation in *Centrobolus inscriptus* (Attems)

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### Abstract

*Centrobolus inscriptus* provides evidence of a conflict of interests over control of copulation duration. Copulation in *C. inscriptus* lasts for  $173 \pm 41$  min. The re-mating interval between double matings was not impacted by the first copulation duration but was negatively related to the second copulation duration, so that when a female endured a long interval the following copulation was shorter. Female girth was positively correlated to the second copulation duration. The first copulation duration was not significantly dependent on the sexual size dimorphism within copulating pairs, but the second copulation durations was. In these matters of physical combat, the relative sizes of the combatants are thought to be of primary importance.

**Keywords:** *Centrobolus inscriptus*, copulation duration, millipede, mating

### 1. Introduction

Recent studies on the sexually dimorphic aposematic millipede *Centrobolus inscriptus* are providing insight into mating behaviour and ecology [1-18]. Control of mate-guarding in the spirostreptid millipede *Doratogonus uncinatus* proved males control the duration of copulation [19]. Here I review studies on *C. inscriptus* and test the null hypothesis: there is no conflict of interests over the duration of copulation. Body size suggests males contract and females prolong the duration of copulation in *C. inscriptus*.

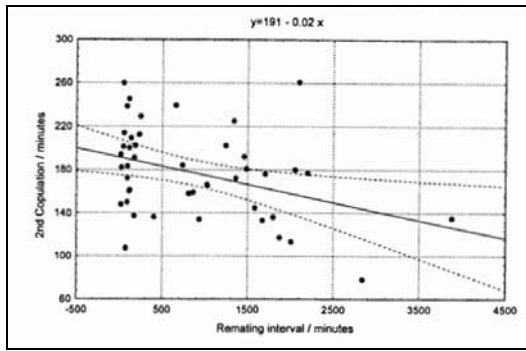
### 2. Materials and Methods

The literature was searched for all studies of *Centrobolus inscriptus*, both independent and dependent of copulation duration [1-18]. The author's own publication collection was consulted and relevant male *versus* female control was tabulated [3-10, 13-17, 20]. Correlates of copulation duration were examined [21-22].

### 3. Results

The copulations in *C. inscriptus* are highly prolonged and coiled (see Cooper, in press). Morphometrics Males and females differed significantly from each other in mass (Wilcoxon matched pairs test:  $T = 554$ ,  $n = 88$ ,  $P = 0.00$ ), length ( $T = 485$ ,  $n = 88$ ,  $P = 0.00$ ), and width ( $T = 2.5$ ,  $n = 88$ ,  $P = 0.00$ ). The pairing of individuals within the mating arenas seemed to be random, therefore no relationships between the relative sizes of males and females within mating pairs was expected. Copulation in *C. inscriptus* lasts for  $173 \pm 41$  min (Mean  $\pm$  SD,  $n = 46$ ). First ( $174 \pm 35$  min) and second ( $173 \pm 47$  min.) copulation durations of females were not significantly different ( $T = 507$ ,  $n = 46$ ,  $P = 0.91$ ) and were in no way related to each other ( $r_s = -0.06$ ,  $n = 46$ ,  $P = 0.69$ ). The remating interval was not impacted by the first copulation duration ( $r_s = 0.07$ ,  $n = 46$ ,  $P = 0.64$ ) but was negatively related to the second copulation duration ( $r_s = -0.31$ ,  $n = 46$ ,  $P = 0.04$ ), so that when a female endured a long interval the following copulation was shorter (Figure 1). This result can be represented another way to show the differences between the first and second copulation durations of each female (Figure 2). Although female girth was positively related to copulation duration [20], the absence of this relationship in the first copulation durations of double matings ( $r_s = 0.19$ ,  $n = 46$ ,  $P = 0.22$ ) is significant. Female girth was again positively correlated to the second copulation duration ( $r_s = 0.31$ ,  $n = 46$ ,  $P = 0.04$ ), suggesting that this is no artefact.

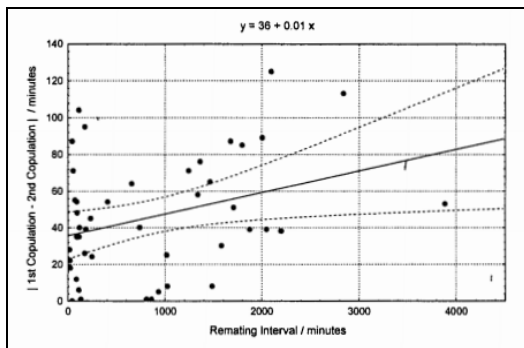
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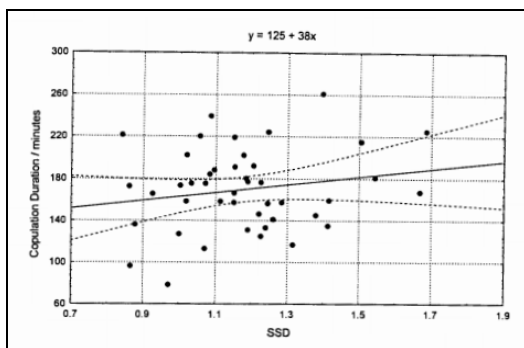
**Fig 1:** The change in the second copulation durations of female forest millipedes *Centrobolus inscriptus* (Attems) that mated after progressively longer intervals renders a slope possibly indicative of sexual control.  $r_s = -0.31$ ,  $n = 46$ ,  $P = 0.04$ .

### 3.1 Sexual size dimorphism

The first copulation duration was not significantly dependent on the sexual size dimorphism within copulating pairs (Figure 3:  $r = 0.2$ ,  $n = 46$ ,  $P > 0.05$ ), but the second copulation durations was (Figure 4:  $r = 0.41$ ,  $n = 46$ ,  $P = 0.004$ ). The absolute differences between first and second copulations (Figure 2), together with these results render slopes that are all potential indicators of the degree of sexual conflict.



**Fig 2:** The absolute difference in durations between successive copulations performed by individual female forest millipedes *Centrobolus inscriptus* (Attems) that had different re-mating intervals.  $r = 0.33$ ,  $n = 46$ ,  $P < 0.05$ .

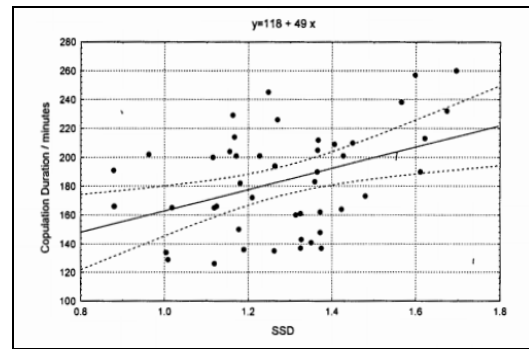


**Fig 3:** The first of two copulation durations by forest millipedes *Centrobolus inscriptus* (Attems) where mated pairs varied in sexual size dimorphism (SSD).  $r = 0.2$ ,  $n = 46$ ,  $P > 0.05$ .

Cooper (1995) found second male copulation duration correlated with body mass of second males ( $R^2 = 0.68$ ,  $d. f. = 7$ ,  $p = 0.01$ )<sup>[21]</sup>.

There were a minimum of 7 out of 15 cases for female control and another 8 out of these 15 cases include male control (Table 1). One study found copulation durations was

significantly positively correlated with female size and sexual size dimorphism but not male size<sup>[20]</sup>.



**Fig 4:** The second copulation durations of forest millipedes *Centrobolus inscriptus* where mated pairs had different degrees of sexual size dimorphism (SSD).  $r = 0.41$ ,  $n = 46$ ,  $P = 0.004$ .

**Table 1:** 15 Tabulated cases of potential male or female control in studies of *Centrobolus inscriptus* (Attems) independent of copulation duration.

Reference	Male control	Female control
3. Cooper 2015a	Yes	No
4. Cooper 2015b	Yes	No
Cooper 2016	No	No
5. Cooper 2016	Yes	Yes
6. Cooper 2016	Yes	No
7. Cooper 2016	No	Yes
8. Cooper 2016	No	No
9. Cooper 2016	Yes	No
10. Cooper 2016	Yes	Yes
13. Cooper 2016	Yes	No
14. Cooper 2016	No	No
15. Cooper 2016	No	Yes
16. Cooper 2016	No	Yes
17. Cooper 2016	No	Yes
20. Cooper & Telford 2000	Yes	Yes

Evidence exists for both male and female control independent of copulation duration in *C. inscriptus*<sup>[3-10, 13-17, 20]</sup>. In the absence of a preference there is size-assortative mating<sup>[6]</sup>. Sexual size dimorphism correlates positively with copulation duration<sup>[20]</sup>. This suggests either a conflict of interests over copulation duration or size-based control. Since *C. inscriptus* has relatively small females and large males<sup>[18]</sup> it would appear males have control. However this is only true in second of double matings and in cross-mating experiments between *C. inscriptus* X *C. annulatus* there was also size-based female control<sup>[6]</sup>. Female size relates to copulation duration<sup>[20]</sup>.

### 4. Discussion

14 cases out of 30 forms of evidence showed the presence for both male and female control independent of copulation duration in *C. inscriptus*<sup>[20]</sup>. When species specific patterns are analysed in *C. inscriptus* copulations are long and perhaps even costly for males<sup>[17]</sup>. Thus in 15 of 18 of the studies of *C. inscriptus* I found equal evidence for syncopulatory male control in prolonged copulations and struggles also under female control<sup>[1-18]</sup>. Females are thought to protract the time spent with each male and hence mediate sperm competition<sup>[23]</sup>. This also contracts the re-mating interval which is known to affect sperm competition and ultimately decides paternity<sup>[3]</sup>. The best predictors of female control of copulation duration are female size and sexual size dimorphism<sup>[20]</sup>.

How are sexual conflicts over copulation duration resolved? The larger animals are invariably the victors. The most important question is why are second copulations shorter than the first if larger females tend to endure longer copulations yet not retain significantly greater volumes of sperm? One answer could be that second copulations are male controlled and terminated earlier due to lower SSD. In mating pairs characterized by low SSD the male can assume more physical control over the female than in situations characterized by high SSD where the female is significantly larger. In matters of physical combat, the relative sizes of the combatants are of primary importance [24].

## 5. Conclusion

Larger females prolong copulation duration according to their body size in *C. inscriptus* but a conflict over terminating copulations is suggested due to the correlation between SSD and copulation duration in double matings.

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