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Fire millipedes obey the female sooner norm in cross mating *Centrobolus* (Myriapoda)

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Abstract
Sexual mediation of copulation duration is reviewed in arthropods. Copulation duration and ejaculate volume were recorded in cross mating *Centrobolus* to test species' mediation differences. Conspecific *C. inscriptus* copulation durations were long (170.0 ± 49.3 min, n = 46), *C. annulatus* copulation durations were short (39.4 ± 18.6 min, n = 8), while mating between heterospecifics (*C. inscriptus* X *C. annulatus*) had the shortest copulation durations (12.4 ± 10.6 min, n = 6); when re-mating interval, sexual size dimorphism, sex ratio and ejaculate volume were controlled. âº (the female sooner norm) suggests size-assortative mating without a size based preference in these mate-guarding millipedes.

Keywords: control, copulation, cross, duration, female, male, mate-guarding

1. Introduction
Cross-mating experiments can test which sex mediates copulation [1-2]. Male mediation of copulation duration is known in the fruitflies *Drosophila melanogaster* [3-4] and *D. montana* [5], firefly *Photinus macdermotti* [6], millipede *Alloporus uncinatus* [7], mite *Macrocheles muscaedomesticae* [8], spiders *Hogna helluo* [9] and *Argiope keyserlingi* [10], praying mantid *Ciulfina*[2], and soldier fly *Merosargus cingulatus* [11]. Female mediation is known only in the millipede *Alloporus uncinatus* [12].
Numerous species of millipede can coexist in sympatry [13-17]. The inscribed red millipede *Centrobolus inscriptus* and the red ringed millipede *C. annulatus* exemplify this sympatry [17]. They have equal sexual size dimorphism [18], but differ in copulation duration [19] and genital structure [20].
A one-way cross experiment between *C. inscriptus* and *C. annulatus* was performed to find changes in mediation of copulation duration.

Materials and Methods
Data were collected during the rainy seasons (1996-1998) as millipede surface activity is seasonal and related to feeding and reproduction in southern Africa [17, 21-24]. *Centrobolus inscriptus* (Attems, 1928) and *C. annulatus* (Attems, 1934) were sampled in coastal forest belt at Twin Streams Farm, Mtunzini (28°55'S; 31°45'E). Live specimens were transported to the laboratory, where unisex groups were housed in plastic containers lined with moist vermiculite (5 mm deep) at 25 ˚C temperature; 70% relative humidity; 12:12 hour light-dark cycle. Fresh vegetables were provided *ad libitum*. Males and females of both species were placed in glass arenas (30 X 22 X 22 mm). Copulation durations were recorded by isolating mating pairs using plastic beakers (13 cm diameter). The radio isotope labelling technique was used to record and control ejaculate volume [12, 25].

Results
Mating pairs formed within 20 minutes of introducing the males to females. Conspecific *C. inscriptus* copulation durations were long (170.0 ± 49.3 min, n = 46) and *C. annulatus* copulation durations were short (39.4 ± 18.6 min, n = 8). Mating between heterospecifics (*C. inscriptus* X *C. annulatus*) had even shorter copulation durations (12.4 ± 10.6 min, n = 6). Differences in copulation duration were significant (Mann-Whitney U-test: Z = 2.56, n = 8, 6, P = 0.01). Differences in ejaculate volume were not significant (Mann-Whitney U-test: Z = 1.23, n = 8, 6, P = 0.22).

Discussion

Cross-mating in *Centrobolus* has not been observed in nature. Mating *C. inscriptus* males with *C. annulatus* females were created in the laboratory to show copulation duration changed with species when re-mating interval, size, sex ratio and ejaculate volume were controlled. Copulation may be female mediated in *C. inscriptus*.

The explanation for the reduced copulation duration in the hetero-specific crosses cannot be based on species sexual size preference [18], sex ratio [17] or sperm load [25] as these factors were controlled in the cross mating experiment. It is possible that variation in genital morphologies and loss of genital contact are responsible for the reduced copulation durations [26]. Female mediation or loss of female control is suggested as the explanation for reduced copulation durations in the hetero-specific cross. If female mediation is species-specific and based on genital contact, then the loss of genital contact following insemination may result in loss of mediation and shorter copulation duration. Further analysis of the variation in the timing of insemination is needed to test whether the genital contact is coupled with insemination and sperm displacement and exclude male control.

Conclusion

The reduced copulation durations in hetero-specific crosses may be explained by the female sooner norm (âº) [27].

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