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A review of studies on the fire millipede genus *centrobolus* (diplopoda: trigoniulidae)

Mark Cooper**Abstract**

Studies on *Centrobolus* spp. were reviewed in which mechanisms of selection, sperm competition and cryptic female choice were studied. Approaches (1) quantify size dimorphism and find the selection pressures operating on the sexes, (2) determine the functional significance of male and female genitalia, (3) understand why there should be a conflict of sexual interests in prolonged copulations, and (4) resolve the mechanisms of sperm competition and cryptic female choice in comparing male mating strategies to female sperm usage were included.

Keywords: choice, competition, conflict, copulation, cryptic

1. Introduction

Originally, sexual selection was conceived as operating in two distinct processes of male-male competition and female choice [1]. The distinction between the two processes became modified into male-male competition and epigamic selection because all selections were considered between sexes [2]. Further major theoretical changes took place, one of which was to show how the strength of selection could be measured as offspring production relative to mating success [3]. Sperm competition was the manifestation of male-male competition whereby rival males competed for fertilizations rather than mating *per se* [4]. Cryptic female choice involved selection for courtship, elaborate male genitalia, and post-copulation products [5, 6]. The dynamics within a mating system may be an evolutionary stable balance between the two mechanisms or the outcome of a conflict of interests between the sexes [7]. Different forms of sperm storage, and the sperm storage organs themselves, determine the use of the remaining rivals' sperm in fertilization [6]. 34 studies on the *Centrobolus* genus were reviewed in which mechanisms of selection; sperm competition and cryptic female choice were studied. Approaches to: (1) quantify size dimorphism and find the selection pressures operating on the sexes, (2) determine the functional significance of male and female genitalia, (3) understand why there should be a conflict of sexual interests in prolonged copulations, and (4) resolve the mechanisms of sperm competition and cryptic female choice in comparing male mating strategies and sperm precedence to female mating strategies and sperm usage were included. The conclusions from 25 studies were moderated and tabulated here.

2. Materials and Methods

35 studies of the behavioural ecology of millipedes in southern Africa were reviewed and referenced. Short digital object identifier's were constructed for each publication at the site <http://shortdoi.org/>. The conclusions of the publications were tabulated (Table 1).

3. Results

35 studies of the behavioural ecology of millipedes in southern Africa were shown [8-43].

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Table 1. Conclusions from the 25 of 35 studies in the genus *Centrobolus* Cook.

Conclusion	Reference
Mate avoidance and mating hotspots are not mutually exclusive hypotheses and both need testing. Additional knowledge on millipede reproductive systems can be useful in forest regeneration plans.	Cooper 2014a
Evidence exists for all of the predictions of mate-guarding except for showing (1) mate guarding is energetically costly, and (2) as the time between copulation and ovule position protracts it becomes less likely for males to remain with their partners.	Cooper 2016 http://doi.org/cn6v
Four species of <i>Centrobolus</i> were confirmed in gonopod ultrastructure.	Cooper 2016a, b http://doi.org/cn6w , http://doi.org/cn6x
There was no evidence for male control of copulation duration in <i>Centrobolus</i> . Evidence from the literature suggests female control of copulation duration in <i>C. inscriptus</i> .	Cooper 2016c http://doi.org/cn62
The reduced copulation durations in hetero-specific crosses may be explained as the female sooner norm (\hat{a}°).	Cooper 2016d http://doi.org/cn63
<i>Centrobolus</i> gonopods possess structures with functions in sperm displacement.	Cooper 2016e http://doi.org/cn64
The sexual differences between male and female body plans which is observable in millipedes may be biologically significant. The variance in the female form, together with the distributions of the measurements taken for <i>C. inscriptus</i> , illustrated most dimorphism was continuous and there is directional selection for heavier-shorter-wider females.	Cooper 2016f http://doi.org/cn65
Instantaneous insemination was demonstrated using artificially terminated mating in <i>C. inscriptus</i> in showing no relationship between ejaculate volume and copulation duration except for high and low volumes at the beginning of mating when the male loads and seats the gonopods before adaptive mate-guarding as prolonged copulation.	Cooper 2016g http://doi.org/cn66
Differences in the number of male and female stadia in <i>C. inscriptus</i> provide preliminary evidence for sexual bimaturism in arthropods.	Cooper 2016h http://doi.org/cn67
Larger females prolong copulation duration according to their body size in <i>C. inscriptus</i> but a conflict over terminating copulations was suggested due to the correlation between SSD and copula duration.	Cooper 2016i http://doi.org/cn68
During the 24h post-mating ejaculate volumes in <i>C. inscriptus</i> consistently decline and this was due to sperm dumping.	Cooper 2016j http://doi.org/cn69
Symmetry in ejaculate volumes was consistent with the mechanism of sperm displacement <i>i. e.</i> mixing-self-sperm displacement.	Cooper 2016m, n http://doi.org/cn7d , http://doi.org/cn7f
Mate-guarding was affected by predation in the millipede <i>C. inscriptus</i> .	Cooper 2016o http://doi.org/cn7g
Elaborate tarsal pads of the <i>Centrobolus</i> males appear not to be an adaptation for supporting the body column but sexually selected.	Cooper 2016p http://doi.org/cn7h
Copulations of second males were significantly related to male body mass in the presence of sexual size dimorphism in double mating experiments of <i>C. inscriptus</i> .	Cooper 2016q http://doi.org/cn7j
<i>C. inscriptus</i> was a large member of the genus with relatively large males and smaller females compared to 18 <i>Centrobolus</i> species for which data is available.	Cooper 2016r http://doi.org/cn7k
The inverse of Rensch's rule was found in <i>Centrobolus</i> based on the positive relationship between SSD and body size.	Cooper 2017 http://doi.org/cn7n
Body mass in southern African worm-like millipedes positively relates to copulation duration.	Cooper 2017a http://doi.org/cn7m
Sexual size dimorphism in southern African worm-like millipedes inversely relates to copulation duration because larger males copulate for shorter and larger females copulate for longer.	Cooper 2017b http://doi.org/cn7p
<i>C. digrammus</i> was unlike <i>C. inscriptus</i> with ordinarily small males and larger females which are similar compared to 18 <i>Centrobolus</i> species for which data is available.	Cooper 2017c http://doi.org/cn7r
<i>C. fulgidus</i> was similar to <i>C. inscriptus</i> with small males and larger females compared to 18 <i>Centrobolus</i> species for which data is available.	Cooper 2017d http://doi.org/cn7s
<i>C. ruber</i> males and females followed the trend for SSD and (break) Rensch's rule in <i>Centrobolus</i> .	Cooper 2017e http://doi.org/cn7t
Copulation duration related to male length in double mating <i>C. inscriptus</i> . Second mating intra-pair SSD is under female control and affects ejaculate precedence.	Cooper 2017f http://doi.org/cn7q
Copulations of females were significantly related to female body width in the presence of sexual size dimorphism in double mating experiments of <i>C. inscriptus</i> .	Cooper 2017g http://doi.org/cn7v
Diplopoda SSD does not negatively regress with body sizes but break Rensch's rule. Intersexual competition was believed to drive SSD in diplopods with forest taxa containing the diversity of species and sizes. A geometric morphometric approach successfully determined the shape and size of millipedes which enabled us to see a relationship, or lack hereof, between shape as size and SSD. The inverse of Rensch's rule was found in <i>Centrobolus</i> based on the relationship between SSD and body size.	Cooper 2018a, b, c http://doi.org/cn7x , http://doi.org/cn7z , http://doi.org/cn72

4. Discussion

35 publications included data from *Centrobolus*. Mate avoidance and mating hotspots are not mutually exclusive hypotheses and both needed testing [7]. Evidence exists for all of the predictions of mate-guarding except for showing (1) mate guarding is energetically costly in *Centrobolus*, and (2) as the time between copulation and ovule position protracts it becomes less likely for males to remain with their partners [11].

The first prediction was confirmed and inferred from evidence in the millipede *Alloporus (=Doratogonus) uncinatus* which shows copulations are energetically costly [12]. Four species of *Centrobolus* were confirmed by gonopod ultrastructure [13-14], leaving the second prediction to be tested. There was no evidence for male control of copulation duration in *Centrobolus*; evidence from the literature suggests female control of copulation duration in *C. inscriptus* [15]. The

reduced copulation durations in hetero-specific crosses may be explained by the female sooner norm (\hat{a}°)^[16]. *Centrobolus* gonopods possess structures with functions in sperm displacement^[17]. The sexual differences between male and female body plans which was observable in millipedes may be biologically significant^[18]. The variance in the female form, together with the distributions of the measurements taken for *C. inscriptus*, illustrated most dimorphism was continuous and there was directional selection for heavier-shorter-wider females^[18]. Instantaneous insemination was demonstrated using artificially terminated mating in *C. inscriptus* in showing no relationship between ejaculate volume and copulation duration except for high and low volumes at the beginning of mating when the male loads and seats the gonopods before adaptive mate-guarding by prolonged copulation^[19]. Differences in the number of male and female stadia in *C. inscriptus* provided preliminary evidence for sexual bimaturism in arthropods^[20]. Larger females prolonged copulation duration according to their body size in *C. inscriptus* but a conflict over terminating copulations was suggested due to the correlation between SSD and copulation duration in double mating^[21]. During the 24h post-mating, ejaculate volumes in *C. inscriptus* consistently declined and this was due to sperm dumping^[22]. Symmetry in ejaculate volumes was consistent with the mechanism of sperm displacement *i. e.* mixing-self-sperm displacement^[25-26]. Mate-guarding was affected with predation in the millipede *C. inscriptus*^[27]. Elaborate tarsal pads of the *Centrobolus* males appeared not to be an adaptation for supporting the body column but sexually selected^[28]. Copulations of second males were significantly related to male body mass in the presence of sexual size dimorphism in double mating experiments of *C. inscriptus*^[29]. Copulations of second males were significantly related to male body mass in the presence of sexual size dimorphism in double mating experiments of *C. inscriptus*; a large member of the genus with relatively large males and smaller females compared to 18 *Centrobolus* species for which data was available^[30]. The inverse of Rensch's rule was found in *Centrobolus* based on the positive relationship between SSD and body size^[31]. Body mass in southern African worm-like millipedes positively related to copulation duration^[32]. Sexual size dimorphism in southern African worm-like millipedes inversely related to copulation duration because larger males copulate for shorter and larger females copulate for longer^[33]. *C. digrammus* was unlike *C. inscriptus* with ordinarily small males and larger females which are similar compared to 18 *Centrobolus* species for which data was available^[34]. *C. fulgidus* was similar to *C. inscriptus* with small males and larger females compared to 18 *Centrobolus* species for which data was available^[35]. *C. ruber* males and females followed the trend for SSD and (break) Rensch's rule in *Centrobolus*^[36]. Copulation duration related to male length in double mating *C. inscriptus* and second mating intra-pair SSD was under female control and affected ejaculate precedence^[37]. Copulations of females were significantly related to the female body width in the presence of sexual size dimorphism in double mating experiments of *C. inscriptus*^[38]. Diplopoda SSD does not negatively regress with body sizes but break Rensch's rule^[39]. Intersexual competition was believed to drive SSD in diplopods with forest taxa containing the diversity of species and sizes^[40-41]. Sexual size dimorphism and the rejection of Rensch's rule in Diplopoda (Arthropoda) was based on Trigoniulids, Sphaerotheriids and Spirostreptids^[41-43].

5. Conclusion

In millipedes there were trends of instantaneous insemination and sperm displacement in males during the adaptive mate guarding phase. Dynamic behaviours which evolved through male-male competition and choice were observed.

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