

Article

A review on studies of behavioural ecology of *Centrobolus* (Diplopoda, Spirobolida, Pachybolidae) in southern Africa

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Abstract

Forty-two studies on fire millipedes are 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 to female mating strategies and sperm usage were included.

Keywords competition; conflict; cryptic.

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1 Introduction

Originally, selection was conceived as operating in two distinct processes of male-male competition and female choice (Darwin, 1871). The distinction between the two processes became modified into male-male competition and epigamic selection because all selection was considered between sexes (Huxley, 1938). 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 (Bateman, 1948). Sperm competition was the manifestation of male-male competition wherein rival males competed for fertilizations rather than mating *per se* (Parker, 1970). Cryptic female choice involved selection for courtship, elaborate male genitalia, and post-copulation products (Eberhard, 1996). 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 (Smith, 1984). Different forms of sperm storage, and the sperm storage organs themselves, determine the use of the remaining rivals' sperm in fertilization (Eberhard, 1996).

42 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.

2 Materials and Methods

42 studies of the behavioural ecology of millipedes in southern Africa were reviewed and referenced (Cooper, 2014a, b, 2015a, b, 2016, 2016a, b, c, d, e, f, g, h, i, j, k, l, m, n, o, p, q, r, 2017, 2017a, b, c, d, e, f, g, 2018a, b, c, d, e, f, g, h, i, j, k). 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

42 studies of the behavioural ecology of millipedes in southern Africa were reviewed (Cooper, 1998, 2014a, b, 2015a, b, 2016, 2016a, b, c, d, e, f, g, h, i, j, k, l, m, n, o, p, q, r, 2017, 2017a, b, c, d, e, f, g, 2018a, b, c, d, e, f, g, h, i, j, k).

Table 1 Conclusions from 25 of 42 studies in the genus *Centrobolus* Cook.

Conclusion	References
Ideally, an experiment needs to experimentally manipulate the sex ratios <i>in situ</i> . 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 MI. Sex ratios, mating frequencies and relative abundance of sympatric millipedes in the genus <i>Chersastus</i> . <i>Arthropods</i> . 2014; 3(4):174-176. https://doi.org/ct6r
Evidence exists for all 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 M. Post-insemination associations between males and females in Diplopoda. <i>Journal of Entomology and Zoology Studies</i> . 2016; 4(2):283-285. https://doi.org/cn6v
Four species of <i>Centrobolus</i> were confirmed in gonopod ultrastructure.	Cooper MI. Confirmation of four species of <i>Centrobolus</i> Cook based on gonopod ultrastructure. <i>International Journal of Entomology Research</i> . 2016; 1(3):7-9. https://doi.org/cn6w
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 MI. Do females control the duration of copulation in the aposematic millipede <i>Centrobolus inscriptus</i> ? <i>Journal of Entomology and Zoology Studies</i> . 2016; 4(6):623-625. https://doi.org/cn62
The reduced copulation durations in hetero-specific crosses may be explained in the female sooner norm (\hat{a}°).	Cooper MI. Fire millipedes obey the female sooner norm in cross mating <i>Centrobolus</i> Cook. <i>Journal of Entomology and Zoology Studies</i> . 2016; 4(1):173-174. https://doi.org/cn63
<i>Centrobolus</i> gonopods possess structures with functions in sperm displacement.	Cooper MI. Gonopod mechanics in <i>Centrobolus</i> Cook. <i>Journal of Entomology and Zoology Studies</i> . 2016; 4(2):152-154. https://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	Cooper MI. Heavier-shorter-wider females in the millipede <i>Centrobolus inscriptus</i> (Attems). <i>Journal of Entomology and Zoology Studies</i> . 2016; 4(2):509-510. https://doi.org/cn65

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.	
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.	Cooper MI. Instantaneous insemination in the millipede <i>Centrobolus inscriptus</i> (Attems) determined by artificially terminated mating. Journal of Entomology and Zoology Studies. 2016; 4(1):487-490. https://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 MI. Sexual bimaturism in the millipede <i>Centrobolus inscriptus</i> (Attems). Journal of Entomology and Zoology Studies. 2016; 4(3):86-87. https://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 MI. Sexual conflict over the duration of copulation in <i>Centrobolus inscriptus</i> (Attems). Journal of Entomology and Zoology Studies. 2016; 4(6):852-854. https://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 MI. Sperm dumping in <i>Centrobolus inscriptus</i> (Attems). Journal of Entomology and Zoology Studies. 2016; 4(4):394-395. https://doi.org/cn69
Symmetry in ejaculate volumes was consistent with the mechanism of sperm displacement <i>i. e.</i> mixing-self-sperm displacement.	Cooper MI. Symmetry in ejaculate volumes of <i>Centrobolus inscriptus</i> (Attems). Journal of Entomology and Zoology Studies. 2016; 4(1):386-387. https://doi.org/cn7f
Mate-guarding was affected in predation in the millipede <i>C. inscriptus</i> .	Cooper MI. Syncopulatory mate-guarding affected by predation in the aposematic millipede <i>Centrobolus inscriptus</i> in a swamp forest. Journal of Entomology and Zoology Studies. 2016; 4(6):483-484. https://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 MI. Tarsal pads of <i>Centrobolus</i> Cook. Journal of Entomology and Zoology Studies. 2016; 4(3):385-386. https://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 MI. The influence of male body mass on copulation duration in <i>Centrobolus inscriptus</i> (Attems). Journal of Entomology and Zoology Studies. 2016; 4(6):804-805. https://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 MI. The relative sexual size dimorphism of <i>Centrobolus inscriptus</i> (Attems) compared to 18 congeners. Journal of Entomology and Zoology Studies. 2016; 4(6):504-505. https://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 M. Re-assessment of Rensch's rule in <i>Centrobolus</i> . Journal of Entomology and Zoology Studies. 2017; 5(6), 2408-2410. https://doi.org/cn7n
Body mass in southern African worm-like millipedes positively relates to copulation duration.	Cooper MI. Allometry of copulation in worm-like millipedes. Journal of Entomology and Zoology Studies. 2017; 5(3), 1720-1722. https://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	Cooper MI. Copulation and sexual size dimorphism in worm-like millipedes. Journal of Entomology and Zoology Studies. 2017; 5(3):1264-1266. https://doi.org/cn7p

for longer.

<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 MI. Relative sexual size dimorphism in <i>Centrobolus digrammus</i> (Pocock) compared to 18 congenics. Journal of Entomology and Zoology Studies 2017; 5(2):1558-1560. https://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 MI. Relative sexual size dimorphism in <i>Centrobolus fulgidus</i> (Lawrence) compared to 18 congenics. Journal of Entomology and Zoology Studies 2017; 5(3):77-79. https://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 MI. Relative sexual size dimorphism <i>Centrobolus ruber</i> (Attems) compared to 18 congenics. Journal of Entomology and Zoology Studies 2017; 5(3):180-182. https://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 MI. Size matters in myriapod copulation. Journal of Entomology and Zoology Studies. 2017; 5(2), 207-208. https://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 MI. The affect of female body width on copulation duration in <i>Centrobolus inscriptus</i> (Attems). Journal of Entomology and Zoology Studies 2017; 5(1), 732-733. https://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.	Cooper MI. Allometry for sexual dimorphism in millipedes (Diplopoda), Journal of Entomology and Zoology Studies. 2018; 6(1):91-96. https://doi.org/cn7x , http://doi.org/ctq2 ; http://doi.org/ctqz , http://doi.org/10.20431/2454-941X.0403003 , http://doi.org/ct36 , http://doi.org/ctqv , http://doi.org/cn7z , http://doi.org/cn72 , http://doi.org/ctqx , http://doi.org/ctqw

4 Discussion

In total of 42 publications included data from *Centrobolus*. Ideally, an experiment shows to experimentally manipulate sex ratios *in situ* (Cooper, 2014a); mate avoidance and mating hotspots are not mutually exclusive hypotheses and both need testing. 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). Four species of *Centrobolus* were confirmed in gonopod ultrastructure (Cooper, 2016a, b). 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* (Cooper, 2016c). The reduced copulation durations in hetero-specific crosses may be explained as the female sooner norm (\hat{a}°) (Cooper, 2016d). *Centrobolus* gonopods possess structures with functions in sperm displacement (Cooper, 2016e). The sexual differences between male and female body plans which was observable in millipedes may be biologically significant (Cooper, 2016f). 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 (Cooper, 2016f). 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 in prolonged copulation (Cooper, 2016g). Differences in the number of male and female stadia in *C. inscriptus* provided preliminary evidence for sexual bimaturism in arthropods (Cooper, 2016h). 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 (Cooper, 2016i).

During the 24h post-mating, ejaculate volumes in *C. inscriptus* consistently declined and this was due to sperm dumping (Cooper, 2016j). Symmetry in ejaculate volumes was consistent with the mechanism of sperm displacement *i. e.* mixing-self-sperm displacement (Cooper, 2016m, n). Mate-guarding was affected in predation on the millipede *C. inscriptus* (Cooper, 2016o). Elaborate tarsal pads of the *Centrobolus* males appeared not to be an adaptation for supporting the body column but sexually selected (Cooper, 2016p). 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* (Cooper, 2016q).

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 (Cooper, 2016r). The inverse of Rensch's rule was found in *Centrobolus* based on the positive relationship between SSD and body size (Cooper, 2017). Body mass in southern African worm-like millipedes positively related to copulation duration (Cooper, 2017a). 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 (Cooper, 2017b). *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 (Cooper, 2017c). *C. fulgidus* was similar to *C. inscriptus* with small males and larger females compared to 18 *Centrobolus* species for which data was available (Cooper, 2017d). *C. ruber* males and females followed the trend for SSD and (break) Rensch's rule in *Centrobolus* (Cooper, 2017e) 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 (Cooper, 2017f). Copulations of females were significantly related to female body width in the presence of sexual size dimorphism in double mating experiments of *C. inscriptus* (Cooper, 2017g). Diplopoda SSD does not negatively regress with body sizes but break Rensch's rule (Cooper, 2018a). Intersexual competition was believed to drive SSD in diplopods with forest taxa containing the diversity of species and sizes (Cooper, 2018g, h). In millipedes there was a trend for instantaneous insemination accompanied in sperm displacement and mixing of males during an adaptive mate guarding phase (Cooper 2016h). This was coupled with female mediation of ejaculate retention after copulation (Cooper 2016k).

Dynamic mating behaviours which evolved through male-male competition and choice were observed. Tarsal pads were considered as a taxonomic character and now examined as a secondary sexual character in males. Investigation into genital complexities and their functional roles in sperm competition and female choice are useful in millipedes (Cooper 1998, 2014a, b, 2015a, b, 2016, 2016a, b, c, d, e, f, g, h, i, j, k, l, m, n, o, p, q, r, 2017, 2017a, b, c, d, e, f, g, 2018a, b, c, d, e, f, g, h, i, j, k).

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