

Mating behaviour and mate choice experiments in some tropical millipedes (Diplopoda: Spirostreptidae)

S.R. Telford *

Zoology Department, University of Pretoria, Pretoria, 0002 Republic of South Africa

J.M. Dangerfield

Department of Biology, University of Botswana, Private Bag 0022, Gaborone, Botswana

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Single and multiple choice mating experiments were conducted using individuals of six species of spirostreptid millipede collected from five separate localities in Zimbabwe. Mating behaviour and copulation duration were recorded. In three of the species between-population comparisons were made. The most common copulatory behaviour was highly physical with the male coiled tightly around the female. In one species (*Calostreptus* sp.) the sexes copulated in parallel with no overt physical manoeuvring by the male. This species also had the shortest copulation duration. In single choice experiments random mating was assumed when mating frequency was independent of male body mass. This occurred in both populations of *Calostreptus* sp., *Spinotarsus* sp. 1 and one of the populations of *Alloporus uncinatus*. In four cases there was a significant positive relationship between mating frequency and body mass. Only three populations mated randomly in the multiple choice experiments. In two populations mating was random in single choice and non-random in multiple choice experiments and the reverse occurred in one population of *Odontopyge* sp. 3. The implications of these results are discussed in relation to processes of male–male competition and female choice.

Enkelvoudige en meervoudige voorkeurparing-eksperimente is uitgevoer deur die gebruik van individue van ses spesies van spirostreptide millipede wat uit vyf verskillende streke in Zimbabwe versamel is. Paringsgedrag en die tydsduur van kopulasie is aangeteken. Tussen-populasie-vergelykings is in drie van die spesies uitgevoer. Die algemeenste paringsgedrag was hoogs fisies met die mannetjie styf om die wyfie gedraai. In een van die spesies (*Calostreptus* sp.) het die geslagte parallel aan mekaar gekopuleer met geen duidelike fisiese beweging deur die mannetjie nie. Hierdie spesie het ook die kortste kopulasieduur van al die spesies. In die enkelvoudige voorkeur-eksperimente is toevallige paring aangeneem mits die paringsfrekwensie onafhanklik was van die mannetjies se liggaamsmassa. Dit het voorgekom in beide populasies van *Calostreptus* sp., in *Spinotarsus* sp. 1 en in een van die populasies van *Alloporus uncinatus*. In vier van die gevalle was daar 'n betekenisvolle positiewe verhouding tussen paringsfrekwensie en liggaamsmassa. Net drie populasies het toevallige paringsgedrag getoon in die meervoudige voorkeur-eksperimente. In twee van die populasies was paring toevallig in enkelvoudige voorkeur- en nie-toevallig in meervoudige voorkeur-eksperimente. Die teenoorgestelde het voorgekom in een populasie van *Odontopyge* sp. 3. Die implikasies van die resultate word bespreek in die lig van prosesse van mannetjie–mannelike kompetisie en wyfie voorkeur.

* To whom correspondence should be addressed

Patterns of non-random mating based on behavioural or morphological criteria are assumed to be a consequence of some form of sexual competition. Typically these processes are competition between males for access to females or competition between males to be chosen by females (Darwin 1871; Partridge & Halliday 1984). Size-selective mating is a common mating pattern in mating systems where male body size correlates with competitive ability and males compete for access to females (Wells 1977). It can also occur in the absence of male–male competition if females display a general preference for larger males (Ryan 1983).

The direct and indirect effects of male–male competition responsible for observed deviations from random mating (e.g. Alexander, Hoogland, Howard, Noonan & Sherman 1979; Borgia 1979; Arak 1983; Gosling 1986) are difficult to separate from the effects of female choice. This has led to a controversy over whether or not female choice is selected for in adaptive or non-adaptive ways (Boake 1986; Kirkpatrick 1982).

The 80 000 extant species of millipede (Hoffman 1979;

Blower 1985) belonging to the arthropod phylum Uniramia (Manton 1977) comprise a major element of the soil fauna in both tropical and temperate ecosystems (Dangerfield 1990). However, compared to their close relatives, the Hexapoda, little is known about their reproductive biology and behaviour. In southern Africa surface activity is strongly seasonal and related to feeding and reproduction (Dangerfield & Telford 1991; Dangerfield, Milner & Matthews 1993). Population densities during periods of surface activity are high (Dangerfield & Telford 1989) and several species can coexist in a given habitat (Dangerfield & Telford 1993).

Here we adopt a comparative approach and observe the patterns of mate acquisition under controlled laboratory conditions for six species of spirostreptid millipede. Our experiments test for size-assortative and size-selective mating based on body mass. We include between-population comparisons for three of the species and use our results to predict the degree of diversity and plasticity in millipede

mating systems and the processes of sexual competition involved.

Methods

The species

Species and generic names used in the present study are after Auems (1928). However, because of the uncertain taxonomic status of many southern African species, particularly within the family Odontopygidae (R.L. Hoffman, pers. comm.), identification beyond genus level was not attempted for most species. The species were distinguished by careful observation of behavioural and morphological characters which included measurements of male gonopods (Telford & Dangerfield, unpublished data). Two members of the family Spirostreptidae (*Alloporus uncinatus* and *Calostreptus* sp.) and four members of the family Odontopygidae (*Odontopyge* sp. 2 and 3, *Spinotarsus* sp. 1 and 2) were used in the mating experiments.

Collection sites

Animals were collected from five separate geographic localities in Zimbabwe during February 1989. *Spinotarsus* sp. 1 and 2, *Odontopyge* sp. 2 and 3 were collected from the Grasslands Research Station, Marondera (18°10'S / 31°30'E). An additional collection of *Odontopyge* sp. 3 was made at a grassland site 30 km south-east of Victoria Falls (17°55'S / 25°50'E). *Alloporus uncinatus* was collected from a riparian forest site near Mazowe Dam (17°30'S / 30°57'E) and from *Burkea* bush in Hwange National Park (18°35'S / 26°20'E). *Calostreptus* sp. was collected from the same *Burkea* bush in Hwange and from mopane woodland in Sengwa Wildlife Research Area (18°22'S / 28°17'E). All animals were returned to the laboratory shortly after collection where they were separated by sex and kept in the laboratory at 22°C, 75% RH for two weeks.

Copulation duration

Matings were generated in a glass arena (30 cm × 20 cm) containing equal numbers of males and females. Pairs were transferred to separate plastic pots (12 cm × 10 cm diameter) immediately after pair formation and at separation the duration of copulation was recorded (minutes). This procedure was carried out at room temperature (25°C) and repeated for all species and populations.

Single choice mating experiments

Females of known mass were placed in 12 cm diameter × 15 cm deep plastic pots containing a shallow layer of moist sawdust. Males of known mass were randomly allocated to the females within the pots. The body masses of males and females are summarized in Table 1. Interactions between individuals were observed until the characteristic copula position was achieved, then males and females were separated. Once separated, females were left alone for a period of 5 min prior to the introduction of subsequent males. In total, males and females were offered a minimum of two and a maximum of eight mating opportunities. From this sequence of experiments, a pairing history of males and females was

Table 1 Mean body masses (g ± 1 S.D.) of male and female millipedes used in single choice mating experiments. Range in body mass and sample size are given in brackets

Family/species	Population	Females	Males
Spirostreptidae			
<i>Alloporus uncinatus</i>	Mazowe	6,6 ± 1,9 (2,8–15,2, 261)	6,7 ± 1,7 (3,2–17,9, 260)
	Hwange	8,5 ± 1,2 (5,7–11,1, 31)	7,9 ± 1,1 (5,9–9,6, 23)
<i>Calostreptus</i> sp.	Hwange	1,2 ± 0,2 (0,8–1,8, 41)	0,8 ± 0,1 (0,7–1,1, 29)
	Sengwa	0,9 ± 0,1 (0,7–1,1, 29)	0,6 ± 0,1 (0,5 ± 1,0, 29)
Odontopygidae			
<i>Odontopyge</i> sp.3	V. Falls	0,9 ± 0,1 (0,7–1,6, 37)	0,8 ± 0,1 (0,6–1,0, 36)
	Marondera	1,6 ± 0,3 (1,0–2,0, 18)	1,24 ± 0,14 (1,0–1,58, 26)
<i>Odontopyge</i> sp.2	Marondera	1,9 ± 0,5 (1,0–3,0, 41)	1,4 ± 0,3 (1,0–1,9, 20)
<i>Spinotarsus</i> sp.1	Marondera	0,7 ± 0,1 (0,4–0,9, 35)	0,8 ± 0,1 (0,6–1,0, 17)

generated. These experiments were conducted with all species except *Spinotarsus* sp. 2.

Multiple choice mating experiments

Receptive females (those females that readily accepted males) were placed in separate 20 cm diameter × 30 cm deep pots. Three males were introduced to the pot and the interactions observed until the female achieved the copula position with one of the three males. In all experiments the males were ranked as first, second and third according to differences in body mass (Table 2). Individual males were identifiable from a temporary liquid paper mark (Tippex) on the body. Once the copula position was achieved, the pairs were separated and the experiment repeated. Three pairings were allowed using the same individuals.

Careful observations of mating behaviour and interactions between males were made during these experiments and the identity of successful males and their order of mating noted. These multiple choice mating experiments were conducted using individuals from all species and all populations.

These experiments were designed to quantify non-random mating based on male body size. The achievement of the copula position was used as an indicator of the acceptance of a male as a mating partner by the female.

In the subsequent sections we describe the experimental results in terms of mating frequency and mating patterns. Obviously the experimental protocol could not allow for copulation (*sensu* Sillen-Tullberg 1981) and, therefore, does not represent true mating. However, for the sake of clarity and to avoid the introduction of ambiguous terms, we chose to use 'mating' in preference to any more specific descriptions of our results.

Table 2 Mean body masses (g \pm 1 S.D.) of females and first, second, and third rank males used in multiple choice mating experiments. Range in body mass and sample size are given in brackets

Species/ population	Females	First rank male	Second rank male	Third rank male
<i>A. uncinatus</i>				
Mazowe	8,1 \pm 3,4 (3,0–17,8, 78)	9,5 \pm 1,4 (8,9–10,7, 78)	8,1 \pm 1,0 (6,9–8,8, 78)	7,0 \pm 1,2 (6,6–7,7, 78)
Hwange	8,7 \pm 1,3 (5,7–11,1, 30)	8,9 \pm 0,6 (7,2–9,6, 28)	8,1 \pm 0,6 (6,9–9,5, 28)	7,1 \pm 0,9 (5,9–8,5, 28)
<i>Calostreptus</i> sp.				
Hwange	1,2 \pm 0,2 (0,9–1,8, 14)	0,9 \pm 0,1 (0,7–1,1, 13)	0,8 \pm 0,1 (0,7–1,0, 13)	0,6 \pm 0,1 (0,7–0,9, 13)
Sengwa	0,9 \pm 0,1 (0,7–1,1, 13)	0,7 \pm 0,1 (0,6–0,9, 10)	0,6 \pm 0,1 (0,5–0,8, 10)	0,6 \pm 0,1 (0,5–0,7, 10)
<i>Odontopyge</i> sp.3				
V. Falls	0,9 \pm 0,1 (0,7–1,2, 13)	0,9 \pm 0,1 (0,9–1,0, 13)	0,8 \pm 0,1 (0,8–0,9, 13)	0,7 \pm 0,1 (0,6–0,8, 13)
Marondera	1,5 \pm 0,3 (1,0–2,0, 10)	1,2 \pm 0,2 (1,0–1,3, 10)	1,0 \pm 0,1 (0,9–1,0, 10)	0,8 \pm 0,1 (0,8–0,9, 10)
<i>Odontopyge</i> sp.2				
Marondera	2,2 \pm 0,4 (1,1–2,8, 18)	1,7 \pm 0,2 (1,4–1,9, 18)	1,5 \pm 0,2 (1,2–1,7, 18)	1,3 \pm 0,2 (1,0–1,7, 18)
<i>Spinotarsus</i> sp.1				
Marondera	0,7 \pm 0,2 (0,5–0,9, 10)	0,9 \pm 0,1 (0,8–1,0, 9)	0,9 \pm 0,1 (0,8–1,0, 9)	0,7 \pm 0,1 (0,6–0,9, 9)
<i>Spinotarsus</i> sp.2				
Marondera	0,1 \pm 0,02 (0,6–0,14, 13)	0,1 \pm 0,01 (0,9–0,1, 13)	0,1 \pm 0,01 (0,8–0,1, 13)	0,1 \pm 0,01 (0,7–0,1, 13)

Results

Courtship and copulation

Preliminary courtship and final copulation was similar for all species except *Calostreptus* sp. A male approached a female from behind and moved towards the head along the dorsal surface. On reaching the head the male rapidly coiled around the female and pushed her head backwards. This allowed access to her genitalia located on the second abdominal segment. Copulation involved the transfer of sperm using secondary genitalia (gonopods) located on the seventh abdominal segment of the male.

The speed and vigour with which males achieved the copula position varied between species. Movements to attain the copula position by male *Alloporus uncinatus* were deliberate but slow, and avoidance behaviour by the female often resulted in an aborted attempt at copulation. Male odontopygids were more persistent in courtship, rapidly attained the copula position and copulation appeared to be more physical. Female odontopygids were able to reject courtship attempts by turning onto their dorsal surfaces and performing a series of brisk lateral undulations.

Copulation in *Calostreptus* sp. was characterized by the absence of any overt physical manoeuvring by the male. Preliminary courtship involved movement along the dorsal surface of the female but final copulation did not result in the male coiling his body round the female. The sexes

Table 3 Copulation duration in minutes (mean \pm 1 s.d.) for eight populations of spirostreptid millipede. Sample size is the number of completed copulations

Family/Species	Population	Copulation duration	Sample size
<i>Spirostreptidae</i>			
<i>Alloporus uncinatus</i>	Mazowe	122,7 \pm 49,4	35
	Hwange	205,8 \pm 60,8	25
<i>Calostreptus</i> sp.	Hwange	60,3 \pm 25,6	22
	Sengwa	33,8 \pm 22,9	25
<i>Odontopygidae</i>			
<i>Odontopyge</i> sp.3	V. Falls	80,2 \pm 25,3	20
	Marondera	85,6 \pm 16,6	19
<i>Odontopyge</i> sp.2	Marondera	66,0 \pm 11,2	28
<i>Spinotarsus</i> sp.1	Marondera	92,3 \pm 18,6	19

copulated in parallel with ventral surfaces contiguous.

Copulation duration

There was considerable variation and overlap in the duration of copulation both between species and between populations of the same species (Table 3). The two populations of *Calostreptus* sp., which copulate in parallel, had shorter mean copulation durations. There was significant variation in copulation duration between species within families (Spirostreptidae, ANOVA, $F_{3,106} = 75,3$; $p < 0,001$; Odontopygidae $F_{3,85} = 9,17$; $p < 0,001$) and where males coiled around the female ($F_{8,145} = 45,7$; $p < 0,001$). The two populations of *A. uncinatus* differed significantly in their mean copulation durations (Mann-Whitney U test, $U = 421$; $p < 0,001$) as did the two populations of *Calostreptus* sp. ($U = 437$; $p < 0,001$) but there was no significant difference in copulation duration between the two populations of *Odontopyge* sp. 3 ($U = 416$; $p > 0,1$).

Single choice mating experiments

A total of 493 females and 451 males belonging to six species were used in these experiments. We assigned males of each species to seven classes according to the frequency with which males achieved the copula position (0–6). The number of mating opportunities did not vary significantly between frequency classes ($F = 1,03$ to $2,90$; $p > 0,1$; $n > 16$).

Random mating was assumed where mating frequency was independent of body mass in males. This occurred in *Calostreptus* sp., *Spinotarsus* sp. 1 and *A. uncinatus* from Hwange (Table 4). Males mated non-randomly in both populations of *Odontopyge* sp. 3, the Mazowe population of *A. uncinatus* and *Odontopyge* sp. 2. In all cases there was a significant correlation between frequency of mating and male body mass (Table 4).

Multiple choice mating experiments

A total of 224 multiple choice mating experiments were conducted: a minimum of 10 and a maximum of 78 for any one species, when given a choice of three potential mating

Table 4 Regression statistics for the relationship between frequency of acceptance and male body mass (g) for males in single choice mating experiments

Species	Population	Sample size	Regression statistics		
			intercept	slope	r
<i>A. uncinatus</i>	Mazowe	245	-6,10	0,77	0,503***
	Hwange	22	-0,43	0,49	0,212 ^{ns}
<i>Calostreptus</i> sp.	Hwange	28	2,50	0,78	0,054 ^{ns}
	Sengwa	39	1,93	1,48	0,095 ^{ns}
<i>Odontopyge</i> sp.3	V. Falls	35	-5,54	8,60	0,500**
	Marondera	25	-5,43	5,14	0,677***
<i>Odontopyge</i> sp.2	Marondera	19	-8,77	8,77	0,583**
<i>Spinotarsus</i> sp.1	Marondera	16	2,06	0,42	0,001 ^{ns}

Table 5 Acceptance by females of first, second and third rank males as first and second mating partners and the proportion of females that accepted a second male (PA)

Species	Population		1st	2nd	3rd	X ²	PA
			rank males	rank males	rank males		
<i>A. uncinatus</i>	Mazowe	1st	15	7	3	7,85*	0
		2nd	0	0	0	na	
	Hwange	1st	4	10	11	3,38 ^{ns}	48
		2nd	6	2	4	2,00 ^{ns}	
<i>Calostreptus</i> sp.	Hwange	1st	2	5	3	1,40 ^{ns}	40
		2nd	2	0	2	2,00 ^{ns}	
	Sengwa	1st	4	1	8	5,60*	46
		2nd	2	1	3	1,00 ^{ns}	
<i>Odontopyge</i> sp.3	V. Falls	1st	6	4	3	1,08 ^{ns}	0
		2nd	0	0	0	na	
	Marondera	1st	7	2	1	6,19*	0
		2nd	0	0	0	na	
<i>Odontopyge</i> sp.2	Marondera	1st	11	3	4	6,37*	50
		2nd	4	1	5	2,48 ^{ns}	
<i>Spinotarsus</i> sp.1	Marondera	1st	7	1	1	8,00**	33
		2nd	1	2	0	1,00 ^{ns}	
<i>Spinotarsus</i> sp.2	Marondera	1st	9	4	0	9,39**	0
		2nd	0	0	0	na	

partners that differed in body mass (Table 2), the Hwange populations of *Calostreptus* sp. and *A. uncinatus*, and the Victoria Falls population of *Odontopyge* sp. 3 showed random mating (Table 5). Non-random mating was recorded in the remaining species. With the exception of the Sengwa population of *Calostreptus* sp. in which the third ranked males (smallest) were most successful (Table 5), larger high ranking males most frequently achieved matings.

In five populations, between 33 and 50% of females accepted a second male whereas in the remaining populations the females accepted only one male (Table 5). In some replicates, females accepted the same male consecutively whereas in others the female accepted different males. How-

ever, the mating pattern for second males was random according to rank for all species and populations regardless of whether or not the female randomly or non-randomly accepted the first male (Table 5). Interestingly, females from the Mazowe population of *A. uncinatus* were unreceptive to second male mating attempts whereas 48% of females in the Hwange population accepted a second male.

Discussion

Random and non-random mating patterns were observed in these experiments. In the single choice experiments, we controlled for the effects of direct competition between males for access to females. Nevertheless, in four populations size-selective mating occurred. In these single choice experiments the presence of non-random mating patterns may be best explained by female mate choice; however, the choice criteria remain unknown.

Eberhard (1985) has suggested that if the size of accessory genitalia scales positively with body size this would provide a potential mechanism for female choice. Such relationships between gonopod size and male body size exist in some spirostreptid millipedes (Telford & Dangerfield, unpublished data), hence this mechanism may be responsible for the size-selective mating observed in *Odontopyge* sp. 2, *A. uncinatus* and *Spinotarsus* sp. 2.

Interactions between males in multiple choice experiments both prior to and during copulation were minimal. Males rarely engaged in any form of physical contact and never appeared to compete directly for access to a female. Males would court and attempt to copulate with any individual they encountered regardless of sex. However, encounters between males tended to be resolved rapidly. In contrast, females were often seen to reject the courtship of certain males in favour of others. These male and female behaviours were typical of all species and do not support any obvious role for direct male-male competition in generating the observed mating patterns.

In the four populations that showed size-selective mating in the single choice experiments there were differing degrees of advantage accrued to larger males. Based on the regression equations given in Table 4, we calculated the predicted mating frequency for the interquartile range of male body mass distributions used in these experiments. Large males had between a three and six-fold advantage in mating frequency. Such a mating advantage based on body mass would result in high variance in male mating success within a natural population. Also, any variation in mating advantage should be paralleled by differences in the intensity of sexual competition between populations.

The duration of copulation is a measure of the period of genitalic contact between mating partners (Sillen-Tullberg 1981). This may not be the case for our measures, as previously we have shown for Mazowe *A. uncinatus* that copulation duration increases predictably with an increase of male bias in the operational sex ratio (Telford & Dangerfield 1991). Consequently, our measure of copulation duration may be a combination of true copulation and post-copulative contact guarding (*sensu* Parker 1974). In the current study, copulation duration was long and varied significantly between species. In *A. uncinatus* and *Calostreptus* sp. it also

varied between populations. Interestingly, copulation duration in populations showing a mating advantage to large males increased with an increase in the magnitude of the mating advantage ($r = 0,942$; $p = 0,058$). Such a result for only four populations should be treated with caution, nevertheless this result supports the idea that prolonged copulation is a form of mate guarding.

There were some inconsistencies between results from our two series of experiments. In *Spinotarsus* sp. 1 mating was random in single choice but size-selective in multiple choice experiments. In this species, males were very overt and persistent when attempting to copulate, such that females appeared to have little choice over mating partner. In *Odontopyge* sp. 3 from Victoria falls, mating was size-selective in single choice but random in multiple choice experiments, although the trend was for first rank males to be most successful. In *Calostreptus* sp. from Sengwa mating was random in single choice but size-selective for third rank males in the multiple choice experiments. This result may be due to the unique nature of copulation in this species but requires further investigation.

What is apparent from comparisons between populations of the same species is that copulation duration and mating pattern can be similar or significantly different. This result is not unexpected as mating systems are known to vary between and within species (Emlen & Oring 1977; Krebs & Davies 1987) and can also change within and between breeding seasons in a single population (Emlen & Oring 1977; Perril, Gerhardt & Daniel 1982; Arak 1983). This plasticity is believed to be a consequence of some combination of the effects of changes in environmental conditions, population density and adult sex ratio.

Environmental conditions were considered as an important factor in the determination of species assemblages in millipedes from southern Africa (Dangerfield & Telford 1993) and seasonal effects of environment are important in dictating activity patterns of four of the species used in this study (Dangerfield *et al.* 1993). The sex ratio of the Mazowe population of *A. uncinatus* also varies within a season (Telford & Dangerfield 1993). The conspicuous breeding activity and widespread distribution of tropical millipedes lends itself to further empirical studies of plasticity in mating systems.

The patterns of non-random mating seen here suggest that processes of sexual competition will occur in natural populations of millipedes. Female choice is possible through assessment of gonopod dimensions as an index of male quality. In addition, millipedes display the necessary morphological and behavioural prerequisites for sperm competition (Telford & Dangerfield 1991; Barnett, Telford & De Villiers 1991). Hence, indirect male-male competition is likely to complicate any benefits accrued to large males as a consequence of female choice.

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