Article

Year-round correlation between mass and copulation duration in forest millipedes

Mark Cooper
School of Animal, Plant & Environmental Sciences, University of the Witwatersrand, Johannesburg 2050, South Africa
E-mail: cm.i@aol.com

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Abstract
Correlates of diplopod size include diet, copulation duration, energy expense of copulation, oxygen consumption, precipitation, sex and temperature. Sexual Size Dimorphism (SSD) in the diplopod genus *Centrobolus* has a positive correlation with body size and copulation duration. Intraspecific variation in mass was calculated in forest millipedes and correlated with copulation duration (R^2=0.68, *d.f.*=7, p=0.01). Interspecific variation in mass was calculated in forest millipede species and correlated with copulation duration (R=0.6711, R^2=0.4504, p=0.144473, n= 3, 3).

Keywords copulation; Diplopoda; horizontal; lighter; mass.

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1 Introduction

The Darwinian viewpoint identifies two mechanisms of sexual selection. Intra-sexual (male-male) competition and intersexual (‘female choice') or epigamic selection (Darwin, 1871). Sexual selection is a corollary to natural selection which enables mating behaviours to be explained from a common evolutionary perspective (Ghiselin, 1969). Prolonged copulation and sperm competition imply that males compete for the fertilization of ova within the female reproductive tract (Parker, 1979). The intense form of intra-sexual competition may be coupled to ‘female choice' (Eberhard, 1985). The ability to mate multiply and delay fertilization predispose organisms to sperm competition (Birkhead and Moller, 1992; Dewsbury, 1988). With the possibility for individual events to be decoupled, and the time interval between them to be protracted, the timing of insemination becomes crucial (Barnett and Telford, 1994). The contribution of males to the next generation is often more variable than that of females (Bateman, 1948). The result of sexual selection may proceed as an evolutionary arms race between the sexes (Dawkins and Krebs, 1979). The outcome is more intricate than simply the classical conflict of interests between the sexes (Emlen and Oring, 1977; Parker, 1979; Arnquist, 1989).

Males and females are expected to maximize the mating quantity and quality respectively (Thornhill and Alcock, 1983; Halliday and Arnold, 1987). Females are able to maximize mate quality, while males maximize mate quantity (Dawkins and Krebs, 1979; Eberhard, 1997). Diplopoda is important environmental indicators and demonstrates polygynandrous mating systems (Barnett and Telford, 1994, 1996; Barnett et al., 1993, 1995; Telford and Dangerfield, 1990, 1993, 1994, 1996). Sexual Size Dimorphism (SSD) which is an effect of sexual selection where the two sexes of the same species exhibit different characteristics beyond the differences in their sexual organs, although common sexual differences are thought to occur in body mass, length, width and leg dimensions of over half the taxa studied (Dwarakanath, 1971; Enghoff, 1992; Hopkin and Read, 1992; Adolph and Geber, 1995; Cooper, 1995; David, 1995; Webb and Telford, 1995; Cooper, 1998; Nesrine and Enghoff, 2011; Echeverría et al., 2014; Cooper, 2015, 2016, 2017; Ilić, 2017; Cooper, 2018; Cooper, 2019; Javonovic, 2018). SSD in the diplopods does not follow the biological rule (Cooper, 2018). For example, in the forest genus *Centrobolus,* it has a positive correlation with body size (Cooper, 2018). *Centrobolus* resemble the majority of invertebrates in SSD is mostly reversed (Cooper, 2018). Heavier-shorter-wider females are under a type of fecundity selection (Cooper, 2016). Larger males have increased reproductive success through a female preference for a larger size if there is size assortative mating behaviour (Telford and Dangerfield, 1993).

2 Materials and Methods

Millipedes were collected between February and December 1996 where they inhabited indigenous coastal forest (Cooper, 1998). Live specimens of each sex were transported to the laboratory where conditions were kept under a constant regime of 25°C temperature; 70% relative humidity; 12: 12 hrs light-dark cycle. Food was provided in the form of fresh vegetable *ad libitu*m. Individuals had unknown mating histories. Unisex groups were housed in plastic containers containing moist vermiculite (±5cm deep) for 10 days before performing single and double mating experiments in *C. inscriptus*. Mass was obtained from all four *Centrobolus* species. These basic descriptive figures were statistically tested for intersexual differences using a parametric t-test for 2 independent means.

3 Results

In all species tests (Table 1) of male and female mass, males were lighter than females (Table 1). *C. digrammus* males differed from females in mean mass (t=3.16996; p=0.002217; n=6). *C. fulgidus* males differed from females in mean mass (t=-3.11615; p=0.00165; n=11). *C. ruber* males differed from females in mean mass (t=5.89992; p<0.00001; n=18). *C. inscriptus* two data sets were pooled and the mean's compared showing a difference between male and female mass (t=2.3162, n=273; p=0.020918). In males, body mass explained a significant percentage of body length (R^2=0.65, *d.f.*=54, p<0.005) and dorsal tergite width (R^2=0.09, *d.f.*=54, p<0.05). The same was true for female body length (R^2=0.79, *d.f.*=39, p=0.005) and dorsal tergite width (R^2=0.58, *d.f.*=39, p<0.005). The consistent dependency of the latter two parameters on body mass rendered body mass as the single-most informative factor.

Copulation duration of second males was significantly related to their body masses in *C. inscriptus* (R^2=0.68, *d.f.*=7, p=0.01). Similar relationships, between all combinations of copulation duration and male and female body masses, were absent from another double mating (R^2=0.42, *d.f.*=6, p>0.05). SSD correlated with a mass in *C. inscriptus* as the first copulation duration was not significantly dependent on the sexual size dimorphism within copulating pairs (r=0.2, n=46, p>0.05), but the second copulation durations was (r=0.41, n=46, p=0.004).

Table 1 Copulation durations and body mass in *Centrobolus*

Species	Duration	n	CV	Male mass	Female mass
C. inscriptus	170±49.3	115	29.0	2.0	2.61
C. fulgidus	66.4±418.6	51	28.0	1.29	1.97
C. ruber	39.8± 13.2	32	33.1	1.28	2.00

There was a positive correlation between copulation duration and body mass across species (Fig. 1: R=0.6711, R^2=0.4504, p=0.144473, n= 3, 3).

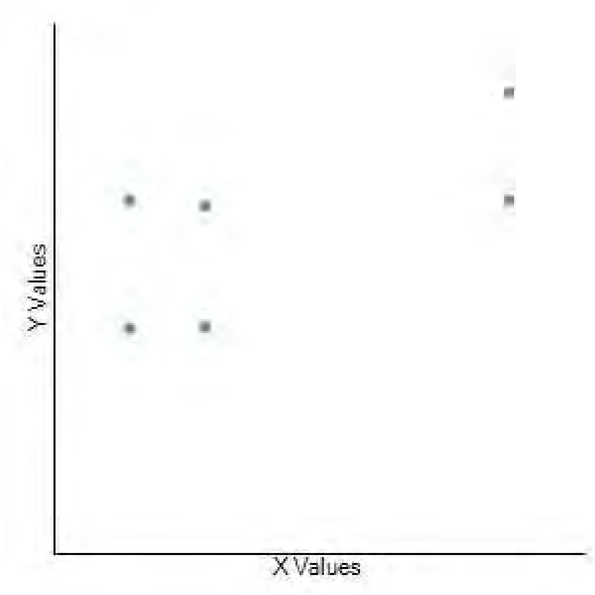

Fig. 1 Positive correlation between copulation duration and body mass across millipedes (R=0.6711, R^2=0.4504, p=0.144473, n= 3, 3).

4 Discussion

Correlates of diplopod size include diet, copulation duration, and energy expense of copulation, oxygen consumption, precipitation, sex and temperature (Dwarakanath, 1971; Penteado et al., 1991; Telford and Webb, 1998; Echeverría et al., 2014; Brygadyrenko and Ivanyshyn, 2015). In *C. inscriptus* SSD is positively related to body size, beyond the 7-9.5 range given for other species in this genus (Lawrence, 1987). Increased insemination efficiency via close apposition of male and female genitalia explain size-assortative mating (Licht, 1976). Morphometric trends suggest males are adapted for increased mobility and the ability to locate females (Ghiselin, 1969). Male bodies are more streamlined and possess longer legs so engaging in mate-searching behaviour and reducing the amount of time diverted from foraging to reproduction behaviours (Woolbright, 1983). The prolonged copulation durations in *C. inscriptus* assure paternity (Cooper, 2015). Female preference may impose directional selection upon a static character not correlated with male body size (Marquez, 1985). This is true for copulation duration where the ejaculate volumes produced were independent of a male's body size (Cooper, 1995, 1998). The lighter mass the males in all four species in *Centrobolus* extends on studies which shows the size of Juliformia "has two main components: body diameter and a number of" rings and provides new information on millipede mass (Enghoff, 1992). The idea of slenderness in juliform male millipedes is supported (Nesrine and Enghoff, 2011).

The abundance of lighter males shows millipedes maximize size through an increase in the body volume of the cylinder through both length and width. In situations of size-assortative mating, females show a preference for larger size (Telford and Dangerfield, 1993). *C. inscriptus* males have a greater body length and are slender and lighter than females and body mass which is positively related to copulation duration (Cooper, 1998). In single mating, males were also found to be lighter and in multiple mating showed heavier males ranked higher in the mating order in *Alloporus uncinatus* (Telford and Dangerfield, 1993). Selection on males has maximized size through increases in length which correlated to SSD, second copulation durations and mass (Cooper, 1998).

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