Australia with North and South America. *Ecology* 66: 1859–1866.

NEL, J.A.J. 1992. Fluctuations in small mammal populations in the Kalahari. Zoological Society of Southern Africa Symposium, Kimberley, South Africa.

NELSON, J.F. & CHEW, R.M. 1977. Factors affecting seed reserves in the soil of a Mojave desert ecosystem, Rock Valley, Nye Country, Nevada. *Am. Midl. Nat.* 97: 300–320.

PARMENTER, R.R., MACMAHON, J.A. & VAN DER WALT, S.B. 1984. The measurement of granivory by desert rodents, birds and ants: a comparison of an energetics approach and a seed dish technique. *J. Arid Env.* 7: 75–92.

PRICE, M.V. & JENKINS, S.H. 1986. Rodents as seed consumers and dispersers. In: Seed dispersal, (ed.) D.R. Murray. Academic Press, Australia.

SKINNER, J.D. & SMITHERS, R.H.N. 1990. The Mammals of the Southern African Subregion. University of Pretoria, Pretoria.

SOHOLT, L.F. 1973. Consumption of primary production by a population of kangaroo rats (*Dipodomys merriami*) in the Mojave Desert. *Ecol. Mono.* 43: 357–376.

SWANEPOEL, C.M. 1980. Some factors influencing the breeding season of *Praomys natalensis*. *S. Afr. J. Zool.* 15: 95–98.

TAYLOR, K.D. & GREEN, M.D. 1976. The influence of rainfall in diet and reproduction in four African rodent species. *J Zool. Lond.* 180: 367–389.

WATSON, C.R.B. 1987. The comparative ecology of two small mammal communities in the Kruger National Park. Unpub. M.Sc. thesis, University of Pretoria.

Males control the duration of copulation in the tropical millipede *Alloporus uncinatus* (Diplopoda: Julida)

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

Prolonged copulation in *Alloporus uncinatus* is a form of mate guarding against sperm competition. Here we show, using a simple experiment, that males control the duration of copulation, an often overlooked assumption regarding the adaptive significance of prolonged copulation. The sex-specific evolutionary benefits of prolonged copulation are discussed in relation to the role played by sperm competition in the evolution of the mating system of *A. uncinatus*.

Lang paringstye by *Alloporus uncinatus* beskerm paargenote teen spermkompetisie. Ons dui hier met behulp van 'n eenvoudige eksperiment aan dat mannetjies die duur van paring beheer. Dit het betrekking op 'n aanname wat dikwels oorgesien word ten opsigte van die aanpassingsbelang van lang paringstye. Die geslagspesifieke evolutionêre voordele van lang paringstye word bespreek met betrekking tot die rol wat spermkompetise in die ontwikkeling van die paringstelsel van *A. uncinatus* speel.

A controversy exists over whether or not prolonged copulation has evolved through more than one suite of selective pressures (Thornhill 1984) and benefits males (e.g. Parker 1970; Sillen Tullberg 1981; Dickinson 1986), females (e.g. Wilcox 1984) or both sexes (see Walker 1980).

Clark (1988) tested two alternative hypotheses to explain the adaptive significance of prolonged copulation in the water strider *Gerris remigis*. The data refuted a female foraging hypothesis where females prolong mating to avoid interference from other males, thereby improving their foraging efficiency; but supported a male mate-guarding hypothesis in which the mating period but not genital joining is prolonged. However, implicit in both potential explanations are assumptions concerning the roles of males and females in controlling mating time.

These experiments could not determine which sex controlled copulation duration (Clark 1988). This knowledge may have relevance in determining the sex-specific benefits of prolonged copulation. For example, if it is advantageous to males to guard females, physical control of female movement would be an efficient mechanism particularly if achieved with minimal energetic cost to the male. There may also be benefits for the female though more likely there will be an associated cost which could lead to a sexual conflict of interest with selection favouring discrimination and avoidance behaviour by females especially if already mated.

Experiments that determine male and female effects on mating time may be difficult to design, and for many species observations alone are insufficient to make the distinction (but see Eberhard 1985). Consequently, most attempts to address this problem have been indirect, with a tendency to focus more on the predictions of the adaptive hypotheses for prolonged mating rather than the assumptions implicit in them (e.g. Clark 1988).

Previously we have shown that for the tropical millipede *Alloporus uncinatus*, copulation duration varies between populations (Telford & Dangerfield 1991a). This population difference allowed us to design a simple experiment to test the assumption that in *A. uncinatus* males control the duration of copulation. We predicted that if males control copulation then mating times for between population pairings should not differ significantly from mating times for the population from which the males originate. To test this prediction, we conducted experiments with pairings of males and females from the same populations as controls and between-population reciprocal crosses as treatments in a contingency design.

Samples of surface active animals were collected by hand from two widely separated geographic locations in Zimbabwe; riparian forest near Mazowe (17° 30' S, 30° 57' E) and *Burkea* scrub in Hwange National Park (18° 44' S, 26° 55' E). Collections were made and experiments conducted during February and March 1989. Individual males and females were placed together in plastic pots (12 cm diameter × 15 cm deep) containing a thin layer of moist soil. Courtship ensued followed rapidly by copulation. Copulation duration (minutes) was measured from the moment the pair assumed the characteristic copula position (see Telford & Dangerfield 1991b) to the time when the male and female separated.

The copulation durations generated from these mating combinations are summarized in Table 1. Within-population copulation durations showed that animals from Hwange mate for a significantly longer time than animals from Mazowe (Mann-Whitney *U* test, $U = 757,5$; $p < 0,001$; Table 1). The results of between population reciprocal crosses generated copulation durations consistent with durations characteristic of the population from which males originated (Table 1). Although females accepted males from both populations, the results of reciprocal crosses suggest that, in copula pairs of *A. uncinatus* males control the duration of copulation. These results lend support to the hypothesis that prolonged mating in *A. uncinatus* is a form of mate guarding against sperm competition.

In an earlier experiment we showed that mating time for *A. uncinatus* increases with increase in male bias in the operational sex ratio (OSR); a situation that mimics variation in the intensity of competition between males for access to females (Telford & Dangerfield 1991a) and we interpret this as a phenotypic response to local changes in the intensity of intrasexual competition. These results, the results of the present study, and behavioural observations suggest that sperm competition is the process responsible for selection favouring the evolution of this form of mate guarding. In *A. uncinatus* the exact nature of sperm competition is not known but the prerequisites exist: multiple mating, internal fertilization and sperm storage (Blower 1985; Telford & Dangerfield 1991a, b). Furthermore, during copulation male gonopods not only play a role in sperm transfer but also function in the displacement of sperm from previous matings (Barnett, Telford & de Villiers 1991, in press).

Table 1 Mean duration of copulation (minutes ± S.D.) in all combinations of matings. Sample sizes are given in brackets. Mann-Whitney *U* test pairwise comparisons are given at the ends of rows and columns

		MALES		
		Mazowe	Hwange	
FEMALES	Mazowe	122,7±49,4 (35)	183,1±65,1 (23)	756***
	Hwange	104,4±31,7 (23)	205,8±60,8 (25)	867***
		107^{ns}	676^{ns}	

***$p < 0,001$; ^{ns} not significant

Males achieve the copula position by coiling around the body of the female in a tight 'embrace' (see figure 1 in Telford & Dangerfield 1991b) and females rarely attempt to escape from a male once in copula. It is probably the unique nature of copulation in these animals which allows the male to exert some control over mating time. The reason why mating pairs from the two populations differ in copulation duration (in the absence of intrasexual competition) remains an interesting unanswered question. The Mazowe population breeds over a three-month period during summer under high population density conditions. Hwange animals breed over a shorter time and at a much lower population density. In the Mazowe population the OSR undergoes dynamic change (female biased to male biased, Telford & Dangerfield, in press) over the breeding season. OSR conditions for the Hwange population remain unknown. If selection had favoured an increase in mating time in response to population density, then on average, Mazowe animals should mate for longer than Hwange animals. Our results show the opposite. However, considering the degree of female bias in the OSR of the Mazowe population over most of the breeding season, then the benefits of prolonged mating may be outweighed by the costs in terms of lost additional mates encountered (Alcock, pers. comm.). This selection to reduce mating time may be responsible for the shorter duration matings in the high density Mazowe population, compared to the low density Hwange population.

This study does not attempt to test the hypothesis that prolonged mating in *A. uncinatus* has evolved to reduce sperm competition. It does, however, test the assumption implicit in this hypothesis that males may control copulation duration. Selection may favour this ability because of the evolutionary benefits a male derives from prolonged mating under conditions of intense intrasexual competition. However, males and/or females can benefit from extended mating. Consequently, to fully understand the adaptive significance of prolonged copulation necessitates investigation of which sex controls its duration.

Acknowledgements

Tarombera Mwabvu, Busani Ndlela and Charity Mckiyi helped with the collection of animals and execution of experiments. Financial support was provided by the University of Zimbabwe and logistical support by the Tropical Soil Biology and Fertility programme. John Alcock and Peter Adler provided useful comments on an earlier version of the manuscript.

References

BARNETT, M., TELFORD, S.R. & DE VILLIERS, C.J. 1991. Gonopod morphology of the millipede *Orthoporus pyrhocephalus* a possible mechanism of sperm displacement. *Proc. Electron Micros. Soc. S.A.* 21: 179–180.

BARNETT, M., TELFORD, S.R. & DE VILLIERS, C.J. In press. Morphological evidence for sperm displacement in the millipede *Orthoporus pyrhocephalus. J. Zool. Lond.*

BLOWER, J.G. 1985. Millipedes. In: Synopses of the British fauna, (eds) D.M. Kermack & R.S.K. Barnes. E.J. Brill, London, 242 pp.

CLARK, S.J. 1988. The effects of operational sex ratio and food deprivation on copulation duration in the water strider (*Gerris remigis* Say). *Behav. Ecol. Sociobiol.* 23: 317–322.

DICKENSON, J.L. 1986. Prolonged mating in the milk-weed leaf beetle *Labidomera clivicollis* (Coleoptera: Chrysomelidae): a test of the 'sperm-loading' hypothesis. *Behav. Ecol. Sociobiol.* 18: 331–338.

EBERHARD, W.G. 1985. Sexual Selection and Animal Genitalia. Harvard University Press, Massachusetts.

PARKER, G.A. 1970. Sperm competition and its evolutionary consequences in the insects. *Biol. Rev.* 45: 525–567.

SILLEN-TULLBERG, B. 1981. Prolonged copulation: a male 'postcopulatory' strategy in a promiscuous species, *Lygaeus equestris* (Heteroptera: Lygaedae). *Behav. Ecol. Sociobiol.* 9: 283–289.

TELFORD, S.R. & DANGERFIELD, J.M. 1991a. Manipulation of the sex ratio and duration of copulation in the tropical millipede *Alloporus uncinatus*: a test of the copulatory guarding hypothesis. *Anim. Behav.* 40: 984–986.

TELFORD, S.R. & DANGERFIELD, J.M. 1991b. Sex in millipedes: laboratory studies on sexual selection. *J. Biol. Ed.* 199: 233–238.

TELFORD, S.R. & DANGERFIELD, J.M. In press. Mating tactics in a tropical population of the millipede *Alloporus uncinatus. Behaviour.*

THORNHILL, R. 1984. Alternative hypotheses for traits believed to have evolved by sperm competition. In: Sperm Competition and the Evolution of Animal Mating Systems. (ed.) R.L. Smith. Academic Press, Orlando, pp. 151–178.

WALKER, W.F. 1980. Sperm utilization strategies in non-social insects. *Am. Nat.* 115: 780–799.

WILCOX, R.S. 1984. Male copulatory guarding enhances female foraging in a water strider. *Behav. Ecol. Sociobiol.* 15: 171–174.