

Sperm Competition of
Macrocheles muscaedomesticae (Scopoli)
(Acarina : Mesostigmata : Macrochelidae), with Special Reference to
Precopulatory Mate Guarding Behavior*

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Abstract – The adult males of the manure-inhabiting predatory mite, *Macrocheles muscaedomesticae*, mounted on the backs of pharate female deutonymphs and guarded them from other males for several hours until female emergence and ensuing copulation. I assumed that an adaptive significance of such characteristic precopulatory mate guarding behavior was closely related to inter-male sperm competition. An existence of 2 sexually compatible strains having different esterase isozyme patterns were found through polyacrylamidegel electrophoresis. A double copulation experiment utilizing these patterns as genetic markers was conducted. In 410 F_1 progeny from doubly copulated mothers examined, 409 daughters were fathered by the first males, and only 1 was fathered by the second male (F_1 males were eliminated because of the arrhenotokous sex determination system). These results seem to indicate that males of *M. muscaedomesticae* guard the immature females in order to secure virgin individuals to mate with.

Macrocheles muscaedomesticae (Scopoli) is a free-living predatory mite inhabiting domestic animal manure, where it preys on eggs and larvae of flies, nematodes and other small animals (Fig. 1a). It is well known as a natural enemy of the house fly (*Musca domestica* L.) and has long been studied for utilization as a biological control agent (Wade & Rodriguez 1961; Axtell 1969; Ito 1978). However, we have insufficient knowledge on its behavioral habits, especially regarding reproductive behavior.

I observed that the adult male continued his mount on the back of pharate female deutonymphs to guard them from other males for several hours until their emergence, after which the pair copulated. This precopulatory mate guarding behavior has been known in some phytophagous mites, crustaceans and insects (Ridley 1983). On the other hand, postcopulatory mate guarding behavior is well known in the males of many insect species such as damselflies, dragonflies and dung flies. In these cases the male guards the female after copulation to prevent other males' remating with her until she completes oviposition (Parker 1970; Alcock 1982).

Mate guarding is understandable in the context of male mating strategies (Thornhill & Alcock

1983). The adaptive significance of postcopulatory mate guarding has generally been explained from the sperm competition hypothesis, because the last male in copulation fertilizes eggs with his own sperm, replacing whatever sperm of previous males is in the spermathecae (Thornhill & Alcock 1983; Gwynne 1984). Some close relationships between precopulatory mate guarding and sperm competition seem to exist, but experimental evidence is scarce (Birkhead & Pringle 1986).

In *M. muscaedomesticae*, I assumed that a male's sperm precedence (priority in fertilization over other males) was greatly influenced by the order of his mating in multiple copulation. To investigate sperm precedence in this species, an observation of mating behavior and double copulation experiments were conducted with 2 sexually compatible strains having different esterase isozyme patterns.

Materials and Methods

(1) The Mites

Two colonies of *M. muscaedomesticae* were

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collected; from a poultry house at the Experimental Farm of Kyoto Prefectural University, Shimogamo, Kyoto, in June 1986, and at the National Grassland Research Institute, Nishi-Nasuno, Nasu, Tochigi Pref., in September 1987. In the Nasu colony, there was a strain having an esterase isozyme pattern different from that of the Kyoto colony. The Kyoto colony and the inbred strain from Nasu colony are hereafter referred to as "Kyoto strain" and "Nasu strain".

The mites were reared for successive generations on an artificial medium, which consisted of moistened wheat bran and rice husks, in a plastic container (12.5 cm in diameter, 5 cm in depth and the cover with a window, 4 × 5 cm, screened with polyester mesh), and kept in an incubator under conditions of 10L:14D photoperiod and $27 \pm 1^\circ\text{C}$. The free-living saprophagous nematode, *Diplogasteroides spengelii* de Man (Rhabditida: Diplogasteridae) was allowed to reproduce in this medium as prey of the mites.

(2) Observation

Mating behavior (precopulatory mate guarding, male-male combat and copulation) of the mites of Kyoto strain was observed in a special observation cell (a circular arena made with plaster-charcoal substratum, Fig. 2). During the observation, the cell was protected with a coverslip for microscopic slides to prevent the mites from escaping, and periodically watered to maintain moisture in the substratum. Observation was done under a binocular stereoscopic microscope ($\times 10 - \times 40$) with fluorescent illumination (1,600 lx).

(3) Electrophoretic Methods

Esterases of the 2 strains were analyzed by the slab polyacrylamide gel electrophoresis method. The adult mites were individually homogenized with 10–30 μl buffer containing 32% sucrose and 0.1% Triton X-100. The concentrations of

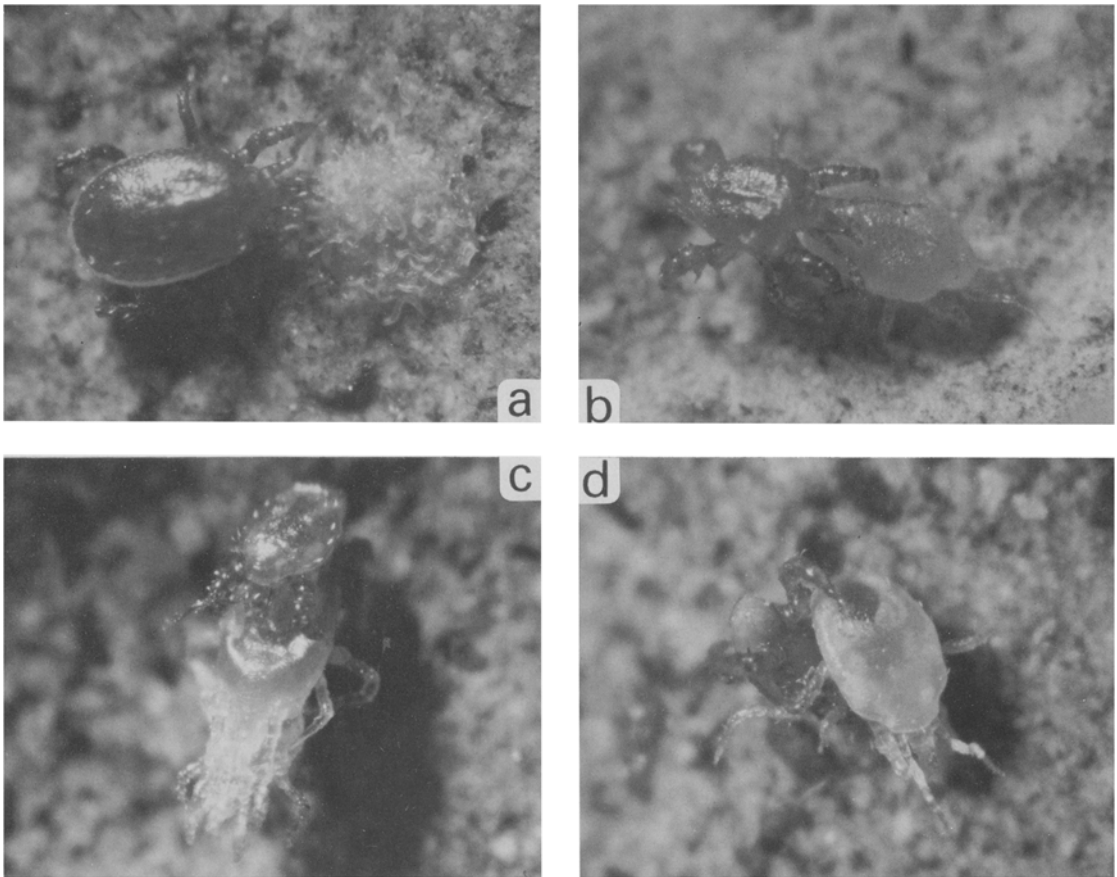


Fig. 1. Behavior of *Macrocheles muscaedomesticae* (Scopoli). a: An adult female (ca. 1 mm in body length) preying upon nematodes. b: An adult male guarding a pharate female deutonymph. c: A just molted female attended by a male. d: Copulation in venter-to-venter position.

acrylamide and Triton X-100 in gels were 8.0% and 0.04%, respectively. Twenty samples were placed on each vertical gel slab ($4\ \mu\text{l}$ of homogenate of single mite per each sample). Electrophoresis was performed with Tris-glycine running buffer (pH 8.3) at a constant current of 3.2 mA/cm width (150–250 V) for 120–140 min. Bromophenol blue (BPB) was used as a marker dye. After electrical charging, the gel slab was soaked in 0.02% solution of 1-naphthylacetate in 0.1 M phosphate buffer, pH 6.0, for 30 min at 20°C . Then esterases in the gel slab were visualized by staining in 0.4% solution of Fast Blue BB salt for 10 min at 20°C .

(4) Crossing Experiments

A crossing experiment between the Kyoto and Nasu strains was conducted to determine inheritance of the isozyme patterns detected from the electrophoresis. A newly emerged adult virgin female and a vigorous adult male (ca. 2 days old after emergence) as a pair were placed in an observation cell. After mating, females were reared individually in a small plastic container (36 mm in diameter, 20 mm in depth and the cover with a window, 15 mm in diameter, screened with polyester mesh) containing the artificial medium, and were then allowed to lay eggs. They were transferred to a new container every other day until their deaths. Phenotypes of the adult F_1 progeny from the inter-strain cross and the adult B_1 from back cross were examined by electrophoresis to determine genotype.

(5) Double Copulation

M. muscaedomesticae has a male-haploid and female-diploid sex determination system (arrhenotoky; Axtell 1969). The mother produces uniparental sons. If a homozygous recessive genotype female is fertilized by a dominant genotype male, she will bear heterozygous daughters, while if she is fertilized by a recessive male, she will bear homozygous recessive daughters.

A double copulation experiment was carried out in the following process. An adult (within 24 h after emergence) homozygous, recessive genotype virgin female and a vigorous adult male of a particular genotype were mated in the observation cell. The male was replaced by another genotype male. After mating (second copulation), the doubly copulated female was allowed to oviposit. Rearing of her offspring was conducted by the same procedure mentioned in section (4). For statistical analysis, the number of adults developed from the eggs was counted instead of the number of newly deposited eggs, because it was very difficult to find and count the eggs laid within the medium. Examination of

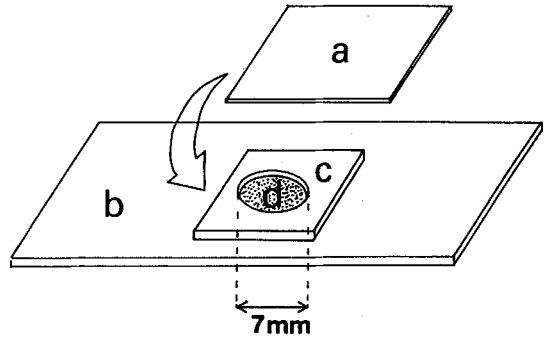


Fig. 2. The observation cell used in the present study. a: Coverslip for microscopic slide. b: Slide glass. c: Plastic plate (2 mm thickness). d: Circular arena (ca. $38\ \mu\text{l}$ capacity) with plaster-charcoal substratum.

phenotype of F_1 females by electrophoresis revealed the father's genotype. Thus, sperm precedence value (P_2 : proportion of offspring fathered by the second male, proposed by Boorman & Parker [1976]) was estimated.

Results

(1) Mating Behavior

Adult males walked vigorously in the observation cell. Pharate female deutonymphs were, however, relatively inactive for several hours before their final molts although it was not possible to observe a noticeable quiescent period. When a walking male contacted a female, he climbed up her back and continued the contact of his palps and legs II with her dorsal region (Fig. 1b). Legs I (as sensory organ) were raised above his body as insect antennae and waved in the air constantly. If another male encountered such a pair, male-male combat occurred. The guarder and the opposer attacked each other with their legs II and IV, which are armed with prominent spurs. After the fight, the loser retreated and the winner recovered his guarding posture on the female.

The guarder kept his position on or beside a molting female (Fig. 1c). He did not help her molting. When the female was still whitish and had a soft body after emergence, the male mated with her. The copulation occurred in the following sequence: first, the male climbed up the female's back; second, he crawled underneath the female through a space between her legs; third, in this venter-to-venter position, he firmly grasped one side of the female leg III with his leg II; fourth, he inserted his spermatodactyl (the organ for sperm transfer in chelicera of mouth parts) into 1 of her 2 sperm induction pores which open between coxae III and IV, and seminal

fluid was transferred (Fig. 1d). Leg II, with a femoral, thumb-like spur, appeared to be useful to fix the female's leg III. The female was usually passive throughout the process. After copulation was completed, males began to search for new mates. It was observed that 101 out of 127 (80%) males ejaculated through only 1 sperm induction pore, while the rest switched to the other pore in a series of consecutive mating episodes with each individual female.

If a male encountered a young adult female (virgin or non-virgin), he usually attempted to copulate with her. Multiple mating of young females was often observed in experimental conditions. Durations of copulation were significantly different between virgin females and non-virgin females ($P < 0.001$). Mean time of the former was 521 s ($n = 64$, $SE = 18.7$ s) and that of the latter 60 s ($n = 63$, $SE = 7.2$ s). In the latter case, males stopped copulation even if females did not reject them. In most cases, males had little interest in older females (aged more than about 6 days after emergence) as their mates.

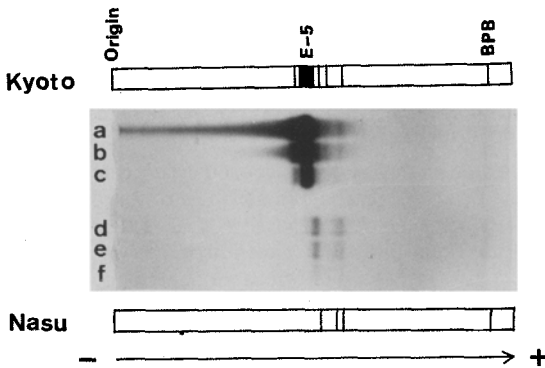


Fig. 3. Esterase isozyme patterns by electrophoresis method. a-c: The Kyoto strain. a: 1 female equivalent (FE). b: 2/3 FE. c: 1/3 FE. d-f: The Nasu strain. d: 1 FE. e: 2/3 FE. f: 1/3 FE.

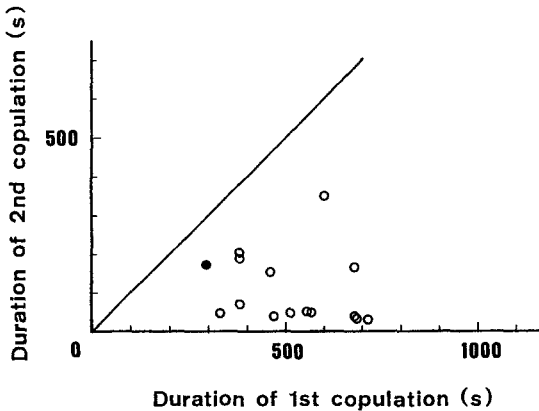


Fig. 4. A comparison of 1st and 2nd copula duration. ○: Second copulation was totally ineffective. ●: Only 1 daughter was fathered by the second male.

(2) Isozyme Patterns by Electrophoresis

Fig. 3 shows characteristic esterase patterns of 2 strains of *M. muscaedomesticae*. Esterases were separated into several bands by the electrophoresis method. An E-5 band with a *Rm* (relative mobility to BPB) value of 0.50 was detected only in the Kyoto strain. The activity of the E-5 band was remarkably higher than the other bands seen in both strains.

(3) Inheritance of Isozyme Patterns

I assumed 2 alleles were in a locus; E_5^+ was a simple dominant allele bringing forth the E-5 band and E_5^- was a simple recessive alternative counterpart. On this assumption, genotypes of the Kyoto and Nasu strains would be represented as $E_5^+E_5^+$ and $E_5^-E_5^-$ in females and E_5^+ and E_5^- in males, respectively. Hybrid F_1 females ($E_5^+E_5^-$) would thus be expected to exhibit the E-5 band. The result of crosses between the 2 strains, support this assumption (Table 1). Male offspring always received only their mothers' genes. There seems no doubt that the E-5 band was reliable as a genetic marker to investigate sperm precedence.

(4) Double Copulation

Table 2 shows the results of the double copulation experiment. First and second copulations occurred within 10 min intervals. In both mating sequences of ($E_5^-E_5^- \text{♀} \times E_5^+ \text{♂}$) \times $E_5^- \text{♂}$ and ($E_5^-E_5^- \text{♀} \times E_5^+ \text{♂}$) (i.e. [$\text{♀} \times 1\text{st } \text{♂}$] \times 2nd ♂), almost all of F_1 female progeny were fathered by the first males which copulated with their mothers. In a total of 410 daughters, only 1 female was fathered by the second male in the latter sequence (namely $P_2 = 0.002$). In this exceptional case, the mother had borne 57 males, and also 32 females fathered by the first male, in the first 6-day period after copulation. She had also borne 13 males and no females in the next 4-day period, and then 2 males and the female in question in

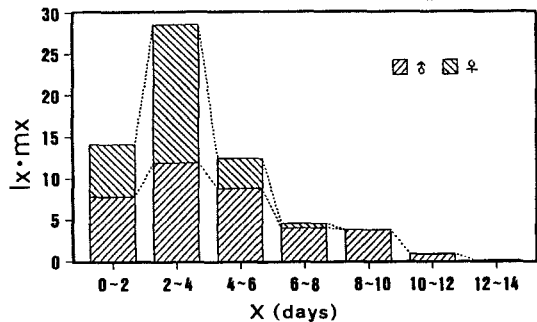


Fig. 5. The average numbers of age-specific F_1 progeny in 15 doubly copulated mothers. x: Age of mothers after emergence. lx: Age-specific survival rate of mothers. mx: Number of F_1 adults (including males) produced/mother/2 days.

Table 1. Inheritance of esterase isozyme pattern found in 2 different strains.

Parent(s) (genotypes)	Number of mothers	Number of progeny examined	Ratio of segregation (expected value) ^a			
			♀		♂	
			$E_s^+E_s^+$	$E_s^+E_s^-$	$E_s^-E_s^-$	E_s^+
Intra-strain cross						
Kyoto ♀ ($E_s^+E_s^+$) × Kyoto ♂ (E_s^+)	13	60 ♀ 60 ♂	60 (60)	0 (0)	60 (60)	0 (0)
Nasu ♀ ($E_s^-E_s^-$) × Nasu ♂ (E_s^-)	13	60 ♀ 60 ♂	0 (0)	60 (60)	0 (0)	60 (60)
Parthenogenesis						
Kyoto ♀ ($E_s^+E_s^+$)	13	60 ♂	—	—	60 (60)	0 (0)
Nasu ♀ ($E_s^-E_s^-$)	13	60 ♂	—	—	0 (0)	60 (60)
Inter-strain cross						
Kyoto ♀ ($E_s^+E_s^+$) × Nasu ♂ (E_s^-)	13	60 ♀ 60 ♂	60 (60)	0 (0)	60 (60)	0 (0)
Nasu ♀ ($E_s^-E_s^-$) × Kyoto ♂ (E_s^+)	13	60 ♀ 60 ♂	60 (60)	0 (0)	0 (0)	60 (60)
Back cross						
F ₁ ♀ ($E_s^+E_s^-$) × Kyoto ♂ (E_s^+)	13	60 ♀	60 (60)	0 (0)	—	—
F ₁ ♀ ($E_s^+E_s^-$) × Nasu ♂ (E_s^-)	13	60 ♀	33 (30)	27 (30) ^b	—	—

^a Phenotype: E-5 band appears in $E_s^+E_s^+$, $E_s^+E_s^-$ and E_s^+ , not appear in $E_s^-E_s^-$ and E_s^- .

^b The difference is not significant between observed and expected value (χ^2 -test, $P > 0.05$).

Table 2. Results of double copulation involving males of 2 different genotypes.

Parents' genotypes				Number of mothers	Number of each genotype in F ₁ progeny (mean ± SE)				Sex ratio (♀/♀ + ♂)
					♀		♂		
♀	1st ♂	2nd ♂	♂	$E_s^+E_s^-$	$E_s^-E_s^-$	Total	E_s^-		
$E_s^-E_s^-$	E_s^+	E_s^-	8	210	0	210	296	506	41.5 %
						(26.25 ± 2.92)	(37.00 ± 11.15)	(63.25 ± 12.50)	
$E_s^-E_s^-$	E_s^-	E_s^+	7	1	199	200	260	460	43.5 %
						(28.57 ± 5.71)	(37.14 ± 9.48)	(65.71 ± 12.19)	
Total				15		410	556	966	42.4 %
						(27.33 ± 3.10)	(37.07 ± 7.41)	(64.40 ± 8.77)	

the third 2-day period. Two days after the last oviposition, she died. Duration of her first copulation was relatively short (296 s) whereas that of the second was rather long (175 s), as compared with the means observed in the present study (514.8 ± 35.2 s for the first copulation and 110.3 ± 23.1 s for the second, Fig. 4).

The differences of mean productivity and sex ratio (= fertilization rate) of F₁ progeny between these 2 mating sequences were not significant (Table 2: Mann-Whitney's U test and χ^2 -test,

$P > 0.05$).

Fig. 5 shows the average numbers of age-specific F₁ progeny in the 15 doubly copulated females. The female adults began to lay eggs within 24 h after their emergence and the oviposition continued for an average of 8 days. Sixty-six percent of the total eggs were laid in the first 4-day period and most of the fertilized eggs (female progeny) were laid in the first 6-day period. The parent females died 9.47 (4–18) days after emergence.

Discussion

Precopulatory mate guarding behavior has been reported often in Tetranychidae (especially in the two-spotted spider mite, *Tetranychus urticae* Koch), Phytoseiidae and other plant-inhabiting mite groups (e.g. Hoy & Smilanick 1979; Potter 1979). This behavior has also been known in some macrochelid mites, e.g. *Macrocheles robustulus* (Berlese) and *M. saceri* Costa (Costa 1966, 1967); *M. boudreauxi* Krantz (Kinn & Witcosky 1977), but none of those authors have discussed its adaptive significance.

Sperm competition phenomenon of the Acari has been investigated only in *T. urticae* by using the sexually compatible colonies of albino and wild types as genetic markers (Helle 1967; Potter & Wrensch 1978). Authors reported that the first copulated males of *T. urticae* fertilized almost all eggs whereas the second copulations were generally ineffective. The markers based on isozyme polymorphism, such as E_5^+ and E_5^- in this study, are considered one of the best methods, as they are applicable to many animal species in which such visible mutation is unknown. Both Kyoto and Nasu strains were sexually compatible with each other because the fertility and the sex ratio of F_1 progeny observed (Table 2) did not differ significantly between the 2 mating sequences. The markers E_5^+ and E_5^- , therefore, will be very useful for other genetic studies of *M. muscaedomesticae*.

I could prove from the results that the first copulated males of *M. muscaedomesticae* fertilized almost all eggs, whereas the second copulations were generally ineffective. It is evident that sperm displacement by the second male seldom occurs and that the first male has sperm precedence. Therefore, the male has to mate with virgin females for his reproductive success. In this context, it must be very effective for the male to perform precopulatory mate guarding because he can secure virgin females for his mates (all female deutonymphs are virgin as a matter of course). The adaptive significance of precopulatory mate guarding in *M. muscaedomesticae* can be understood from this process.

In respect to the evolution of precopulatory mate guarding, Ridley (1983) has argued that such behavior has evolved only in the species in which females are receptive to copulation only during very short and predictable periods. From my understanding, Ridley's hypothesis is summarized as follows: if the period during which the mating is possible is very short for some reason, the probability that mating occurs at each random meeting of both sexes will be very low; thus males performing precopulatory mate guarding will be able to meet acceptable females more frequently than other males. For example,

the female of the freshwater amphipod *Gammarus pulex* (L.) can be inseminated only during about 12 h after her molt in each breeding cycle (ca. 34 days) because of the physical and morphological restrictions of the hardening of her exoskeleton. As a result of precopulatory mate guarding for about 9 days, the male of this species can copulate immediately after her molt (Birkhead & Pringle 1986). In *M. muscaedomesticae*, about 100% ($n = 26$), 65% (20), 45% (20) and 15% (20) of virgin females copulated 24, 48, 72 and 96 h after emergence, respectively, when they were placed in an observation cell with males, and then began to deposit fertilized eggs (Yasui unpublished). The virgin females of *T. urticae* can copulate with their sons which have developed from their own unfertilized eggs deposited earlier, and then begin to produce daughters (Saitô 1987). In these 2 mite species, unlike *Gammarus*, adult females do not become physically and morphologically unreceptive within a brief period after their molt. Even if it is supposed that the receptive period of female *M. muscaedomesticae* is physically limited to a certain period (e.g. 24 h) after emergence, this period is enough to allow further copulation. If sperm displacement occurs in following copulations, the guarding males' fertilization advantage will be offset, unless the females copulate only once. When it is interpreted that a mean period from female's ecdysis to her first copulation corresponds to Ridley's "receptive period", the Ridley's hypothesis is applicable to the case of *M. muscaedomesticae*. In this case, it is considered that the female's short receptivity results not from any morphological restriction as in *Gammarus*, but from the first male's fertilization advantage in sperm competition. Therefore, the female's inability to remate or the first male's fertilization advantage in a multiple mating (in other words, the difficulty of sperm displacement by the later copulated male), as well as some physical and morphological restrictions, will be factors which shorten the female's receptive period. When future workers discuss the evolution of precopulatory mate guarding in certain animal species, it will be necessary to investigate sperm competition.

The mechanism by which first matings preclude later inseminations remains unknown. In most sperm displaceable insects, spermathecae are generally diverticula which open to the oviduct. Even when the later copulated male cannot remove the previous male's sperm in copulation, his sperm may be the first to reach the oviduct when the female oviposits (thereby attaining priority of fertilization), if he can position his sperm close to the entrance (= exit) of the spermatheca while he is pushing competitor's sperm distally (Thornhill & Alcock 1983). The track of sperm from the induction pore to ovary (through

the tubulus annulatus, ramus sacculus, sacculus foemineus and spermatheca) in the macrochelid mites is one-way and the structure necessary for sperm removal is not found in the male's spermatodactyl (Costa 1966; Young 1968; Thomas & Zeh 1984; Woolley 1988). Therefore, the first male may be able to have sperm precedence, if early induced sperm is in sufficient quantity to fertilize eggs—even when a second insemination occurs. Such a morphological difference of reproductive systems between sperm displaceable insects and *M. muscaedomesticae* may be one of the reasons why sperm displacement by second males hardly occurs in this species.

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