Experimental and Applied Acarology (2005) 36: 187–197
DOI 10.1007/s10493-005-5303-7 

# Mating behavior of the predatory mite *Kampimodromus aberrans* (Acari: Phytoseiidae)

MARIA L. PAPPAS[1], GEORGE D. BROUFAS[2] and DIMITRIS S. KOVEOS[1,*]

*[1]Aristotle University of Thessaloniki, Faculty of Agriculture, Laboratory of Applied Zoology and Parasitology, 541 24 Thessaloniki, Greece; [2]Democritus University of Thrace, Department of Agricultural Development, Laboratory of Agricultural Entomology and Zoology, 68 200 Orestiada, Greece; *Author for correspondence (e-mail: koveos@agro.auth.gr; phone/fax: +30-231-0-998845)*

Received 27 August 2004; accepted in revised form 8 April 2005

**Key words:** Insemination mode, *Kampimodromus aberrans*, Mating behavior, Phytoseiidae

**Abstract.** The mating behavior of the predatory mite *Kampimodromus aberrans* was studied in the laboratory at a constant temperature of 25 ± 1 °C and a photoperiod of 16:8 (L:D). Forty pairs of newly emerged virgin females and unmated males, were maintained separately on leaf discs and their mating behavior, was observed continuously under a stereomicroscope. The mean time until first contact of female and male individuals was approximately 8.2 min. After the first contact the male moved to the top of the female's dorsum and subsequently underneath her in approximately 1.7 min and then the paired mites walked around on the leaf surface for approximately 7.5 min. Afterwards, the mites remained still in the mating position, i.e. the male beneath the female for an average period of 230.5 min. After mating, most of the females had one spermatophore in one of their spermathecae, whereas a few had one spermatophore in both spermathecae.

## Introduction

Predatory mites of the family Phytoseiidae are known to be important natural enemies of several spider mites and some species are able to maintain the populations of spider mites and eriophyoid mites at low levels (Sabelis 1985). Phytoseiids lay eggs only after copulation and some species require multiple matings in order to reach their maximum reproductive capacity (Hoy 1979; Schulten 1985). The venter-to-venter mating position is common among Phytoseiidae, with the male moving and remaining under the female. During the mating process sperm is transferred from the male's genital opening to his spermatodactyl and then to the female's sperm induction pores (Schulten 1985). The mating behavior has been studied in a few phytoseiid species e.g. *Phytoseiulus persimilis* Athias–Henriot (Amano and Chant 1978a), *Amblyseius andersoni* (Chant) (Amano and Chant 1978a; Overmeer et al. 1982), *Typhlodromus pyri* (Scheuten) (Overmeer et al. 1982), *Galendromus occidentalis* (Nesbitt) (Hoy and Cave 1985), *Euseius alstoniae* (Gupta) (Kumari and Sadana 1992), *Amblyseius colimensis* Aponte and McMurtry (Orlando and McMurty 1992) and *Neoseiulus womersleyi*

(Schicha) (Tsunoda 1994). Among these species considerable variation has been recorded in the sequence of behaviors from the first contact of male and female until the completion of mating, although eventually the male crawls under the female and remains in the venter-to-venter position during copulation.

The mating behavior of *P. persimilis* and *A. andersoni* has been studied extensively by Amano and Chant (1978a) who proposed two types of mating behavior in phytoseiids: the '*Amblyseius–Typhlodromus*' and the '*Phytoseiulus*' type. The main difference between the two is that in the '*Amblyseius–Typhlodromus*' type the male climbs first on the female's dorsum before moving under her, whereas in the '*Phytoseiulus*' type the male moves directly under the female without climbing on her. As described by Amano and Chant (1978a), the female and male remain in the venter-to-venter position, and spermatophoral material is transferred from the male's genital opening to his spermatodactyl and then into the spermathecae of the female through the sperm induction pores. Within minutes after the end of copulation the spermatheca becomes 'inflated' (i.e. expanded like a balloon without apparent spermatophoral material) (Amano and Chant 1978a). Following insemination spermatophoral material surrounded with a wall-like structure described as endospermatophore, is clearly visible within the spermatheca in microscopic slide preparations. In such cases the expanded spermatheca is described as inseminated (Amano and Chant 1978a). Considerable inter- and intra-specific variability has been recorded in the duration of copulation and the degree of spermatheca insemination in phytoseiids (Schulten 1985).

The predatory mite *Kampimodromus aberrans* Oudemans is widely distributed and has been recorded throughout Europe and North America (Duso and Vettorazzo 1999; Kreiter et al. 2002; Moraes et al. 2004). It has been considered an important natural enemy of certain spider mites and eriophyoid mites (Krantz 1973; McMurtry and Croft 1997). To our knowledge the mating behavior of *K. aberrans* has not been studied.

The present work, which is the first part of an ongoing project, provides a detailed description of the phases of mating behavior of *K. aberrans*, the time spent in each phase and the presence of sperm in the spermathecae after mating. Our aim is, to cast light on the reproductive biology of this mite, which could be of importance for further studies concerning its possible use in biological control programs.

## Materials and methods

### *Mite colony*

The laboratory colony of *K. aberrans* was established with approximately 650 adult mites collected from apple trees grown on the campus of the Aristotle University of Thessaloniki. The mites of the laboratory colony were main-

tained on detached bean leaves (*Phaseolus vulgaris* L.) which were kept in contact with water-soaked cotton wool which prevents escape of mites in a similar way as described by Overmeer (1985). On the leaf surface, a sufficient quantity of *Typha* sp. pollen was offered as food for the mites and a few cotton threads were placed as shelter and oviposition site. In each rearing unit 40–50 adult mites were maintained.

Every other day the eggs laid on the cotton threads were collected and transferred to new rearing units. To avoid inbreeding each new rearing unit was established with eggs collected from 4 to 5 randomly selected rearing units. Furthermore, every second week the old leaves were changed and mites randomly selected from different rearing units were transferred with the help of a fine camel hairbrush on a fresh bean leaf. The mite colony was maintained in a laboratory room at $T = 25 \pm 1$ °C, RH = 60–70% and a 16:8 (L:D) photoperiod.

### *Experimental mites*

Sixty gravid females, 10–15 days old, were randomly collected from colony rearing units (5–8 individuals from each unit) and were transferred onto a detached bean leaf. On the leaf surface *Typha* sp. pollen and a few cotton threads as oviposition site were added. Eggs laid by the females within 24 h were collected and transferred onto other detached bean leaves. The leaves with the eggs were inspected under a stereomicroscope every 8 h and newly hatched larvae were transferred individually to bean leaf discs 20 mm diameter on wet cotton wool inside cylindrical cells of a polystyrene multiwell tissue culture plate (Corning®, NY). On each leaf disc some pollen was added as food for the mites. Every 12 h the leaf discs were observed under a stereomicroscope and the developmental stage of each individual was recorded. After emergence 40 virgin females and an equal number of unmated males were maintained in the units for 1 day before use in the experiments.

### *Mating behavior and duration of copulation*

To describe the mating behavior, each of the 40 virgin females and males were transferred to a fresh bean leaf disc (20 mm diameter) in a rearing unit. The 40 couples were continuously observed under a stereomicroscope (Leica MZ8, magnification 25X) with cool light and the sequence of pre-mating behaviors of both sexes was recorded. After the beginning of copulation, i.e. when female and male reached the venter-to-venter position, they were observed every 5 min for a period of 1 min and the mating status – i.e. whether in copulation or not – was recorded. The duration of copulation was determined. After the couple's separation observations were continued for a

further period of 5–6 h to study whether the two individuals would mate again.

*Examination of spermathecae*

In phytoseiid species a certain period of time following insemination is needed before the wall-like structure surrounding the spermatophoral material of an endospermatophore is formed within a spermatheca (Schulten 1985). Preliminary experiments (Koveos, unpublished) have shown that after copulation endospermatophores of *K. aberrans* were clearly visible in the bodies of mounted females after approximately 5 min following insemination and they were still visible even after a period of 10 h. In the present study each experimental female was mounted in Hoyer's medium 5–6 h after mating, and subsequently observed under a microscope (Leica DMLS, magnification 400X). In addition, 10 virgin females developed from the egg through the adult individually and 10 females randomly collected from the stock colony were also mounted and examined. The number of inflated (expanded without spermatophores) and/or inseminated (expanded with spermatophores) spermathecae was recorded and ranked according to one of the following five categories proposed by Amano and Chant (1978a): a. both spermathecae inflated and inseminated (2-2 type), b. both spermathecae inflated and one inseminated (2-1 type), c. both spermathecae inflated and not inseminated (1-1 type), d. one of the spermathecae inflated and both not inseminated (1-0 type) and e. both spermathecae not inflated and not inseminated (0-0 type).

## Results

*Phases of mating behavior*

The phases of mating behavior of *K. aberrans* are schematically shown in Figure 1. Before the first contact, females were generally more quiet, whereas males were more active, moving rapidly over the leaf surface. In most of the pairs studied the time period from the transfer of the two individuals onto the leaf disc to their first contact ranged from 2 to 10 min.

*Phase 1*

The initial approach involved three ways (Figure 1, Phase 1-I (a, b, c)). Male and female met with their anterior parts (gnathosoma to gnathosoma) (a), laterally (male's gnathosoma to female's lateral part of idiosoma) (b) or posteriorally (male's gnathosoma to female's posterior part of idiosoma) (c). In most cases males encountered females that remained still or they met while both were in motion. Only once out of 40 cases a female approached a stationary male. Upon encountering a female (Phase 1-II (a, b, c)), the male

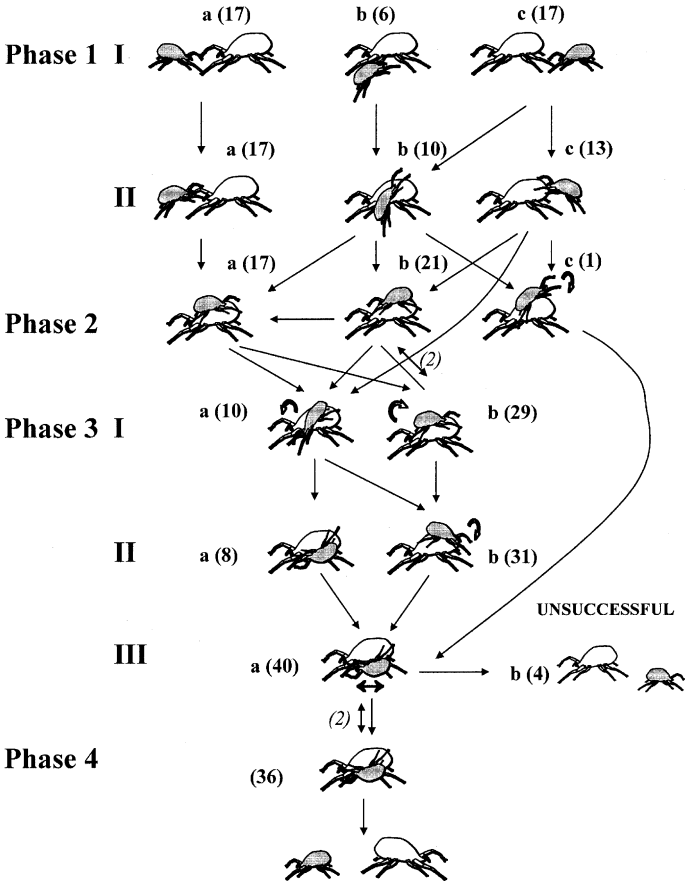


*Figure 1.* Diagrammatic representation of the mating behavior of the predatory mite *K. aberrans*. Phase 1: Initial meeting (approach); Phase 2: Climbing on the female's dorsum; Phase 3: Reaching the mating position (venter-to-venter); Phase 4: Mating position. Numbers in the parentheses indicate the number of pairs that followed each phase.

touched with his forelegs and pedipalps, either the female's gnathosoma (a), the lateral part (b), or the posterior part (c) of the idiosoma. Due to the small size of the individuals we could not determine the exact part of the female's body, which was touched repeatedly.

*Phase 2*

The male kept in touch with the female, climbed on her dorsum in one of the three ways shown in Figure 1 (Phase 2a, b, c), while the female remained quiet and moved in only a few cases. Nine pairs followed both ways (Phases 2a and 2b), that is after the male climbed on the female it first touched the posterior part of the female's body and then turned around so as to touch the anterior part. In all cases but one, the male climbed on the female's dorsum and

remained there for a few seconds. In one pair (Phase 2c) the male after encountering the female laterally climbed on top, got across the other side and then stopped at the mating position (Phase 3-IIIa), bypassing phases 3-I and 3-II. Only one male bypassed Phase 2 and followed directly the Phases 3-Ia, IIa, IIIa without climbing on the female's dorsum.

*Phase 3*

After reaching the top of the female, the male turned down either sideways (Phase 3-Ia, IIa) or posteriorally (Phase 3-Ib, IIb) to move into the mating position. As soon as the paired individuals took the venter-to-venter position (Phase 3-IIIa), the male displayed left-right movements for a while and in most cases the female walked rapidly on the leaf until both female and male remained quiet (Phase 4).

*Phase 4*

Female and male remained still for $230.5 \pm 13.4$ (mean $\pm$ SE) min (Table 1) and we assume that sperm transfer took place from the male's genital opening via the spermatodactyl to the female's spermathecae. During this phase, the male made some sudden movements every now and then. Towards the end of the stationary period the female began to run tremulously, while the male was quiet or moved its body left–right. Finally, the male moved away from the female and afterwards they did not meet again for the rest of the observation period (approximately 6 h).

Four of the 40 observed pairs did not complete Phase 3-III: the female rejected the male and the couple did not meet again (Phase 3-IIIb), despite repeated attempts (2–5 times) of three males to reach the mating position (Phase 4).

## *Duration of mating phases*

The time to first contact after transfer of the two mites onto the leaf surface was on average $8.2 \pm 1.5$ (SE) min (Table 1). The male remained for a few seconds on the female's dorsum and after approximately 1.7 min from the first contact, the pair reached the mating position. The paired mites moved on the leaf surface for approximately 7.5 min and then remained stationary in the mating position for almost 4 h (Table 1).

*Table 1.* Duration of different behavior phases during mating of newly emerged virgin females and unmated males of *K. aberrans*.

| Phase | Mites tested | Mean duration ($\pm$ SE)(min) |
|---|---|---|
| Time to 1st contact (Phase 1) | 40 | $8.2 \pm 1.51$ |
| Time from 1st contact to mating position (Phase 2) | 40 | $1.7 \pm 0.29$ |
| Time from mating position to stationary phase (Phase 3) | 36 | $7.5 \pm 1.83$ |
| Time from stationary phase to separation (Phase 4) | 36 | $230.5 \pm 13.36$ |

*Examination of spermathecae*

Three of the 36 females that completed mating were damaged during the microscopic slide preparation and therefore their spermathecae were not examined. Twenty of the remaining 33 females had one of their spermathecae inflated and inseminated (1-1 type) according to Amano and Chant (1978a), six had both spermathecae inflated and only one inseminated (2-1 type), six had both spermathecae inflated and inseminated (2-2 type) and only one female had one inflated spermatheca but not inseminated (1-0 type). None of the females had more than one spermatophore per spermatheca. All virgin females had no inflated or inseminated spermathecae (0-0 type). One out of ten individuals selected randomly from the stock colony had both spermathecae inflated and inseminated (2-2 type) (one of the spermathecae was inseminated with one spermatophore, the other with two spermatophores). In six of the stock colony females both spermathecae were inflated and only one was inseminated with a single spermatophore (2-1 type), in three females both spermathecae were inflated but not inseminated (2-0 type).

## Discussion

The first step of mating behavior in *K. aberrans* is the approach of a female by a male which occurs only a day after the female's emergence. Preliminary tests showed that newly emerged females of *K. aberrans* on the first day of their adulthood reject males, whereas both females and males spend much time feeding, possibly related to the need of food intake for sexual maturation (Pappas, Broufas and Koveos unpublished). Under field conditions males emerge before females and therefore may fulfill the need for food intake before mating. In other phytoseiid mites such as *G. occidentalis* (Laing 1969), *P. persimilis* and *A. andersoni* (Amano and Chant 1978a) and *Euseius mesembrinus* (Dean) (Abou-Setta and Childers 1987) mating occurs immediately after females' emergence and males display intense feeding activity before mating.

In our experimental units *K. aberrans* males approached females either from the front, from behind or from aside (Figure 1). Similar variability in initial approach of males to females has been reported in other phytoseiid species such as *P. persimilis* (Amano and Chant 1978a), *T. pyri* and *A. andersoni* (Overmeer et al. 1982), *G. occidentalis* (Hoy and Cave 1985) and *A. womersleyi* (Tsunoda 1994).

The mating phases of *K. aberrans* observed in 29 out of 40 pairs (i.e. following phase 3-lb) were similar to the '*Amblyseius–Typhlodromus*' type described by Amano and Chant (1978a), and also reported in the phytoseiid species *Euseius scutalis* (Athias–Henriot) (ElBadry and Elbenhawy 1968), *G. occidentalis* (Lee and Davis 1968), *Neoseiulus fallacis* (Garman) (Rock et al. 1976), *A. andersoni* (Overmeer et al. 1982) and *T. pyri* (Zaher and Shehata 1971). In 10 pairs the 'sideways' variation in the '*Amblyseius–Typhlodromus*'

type was observed, in which the male climbed on the female's dorsum and then crawled over her side to the ventral position, as described by Hoy and Cave (1985). In *A. womersleyi* most pairs followed the main '*Amblyseius–Typhlodromus*' type of mating whereas a few pairs followed the '*Phytoseiulus*' type in which the male moved directly under the female without climbing on her dorsum (Tsunoda 1994). In our study in one pair the male after encountering the female laterally climbed on one side of the female's idiosoma but not on her dorsum and subsequently moved to the venter-to-venter (mating) position. This behavioral sequence could be considered as a variation of the '*Phytoseiulus*' type, since after his first contact with the female, the male crawled underneath her without passing the 'face to face' position described by Amano and Chant (1978a). Thus, in *K. aberrans* as in other phytoseiid species considerable variation in mating behavior was observed. Intraspecific or even inter-population variation in mating behavior seems to be common in the Phytoseiidae (Hoy and Cave 1985).

In our study the time until first contact between the two sexes was 8.2 min, which is substantially shorter than the 15 min reported for *A. andersoni* and *T. pyri* (Overmeer et al. 1982). This interspecific variation could be related to innate species characteristics or to the fact that we observed mating behavior at a higher temperature (25 °C) than the temperature of 20–22 °C used in Overmeer et al. (1982). In *A. andersoni*, which follows the main type '*Amblyseius–Typhlodromus*' mating behavior, males climb on the females' dorsum and stay there for 2 min or less before moving to the 'venter-to-venter' (mating) position (Overmeer et al. 1982). In *K. aberrans* males spent approximately 30 s on the females' dorsum before moving to the 'venter-to-venter' position. Total time from first contact to the start of mating was 1.6 min, similar for *A. andersoni* and *P. persimilis* (Amano and Chant 1978a). The period from first contact to initiation of copulation seems a species–specific characteristic, rather than related to the behavioral sequences described in the '*Amblyseius–Typhlodromus*' and '*Phytoseiulus*' mating types. Moreover, in *P. persimilis* virgin females tend to accept more readily unrelated males than related ones (Enigl and Schausberger 2004), indicating that relatedness between the individuals could significantly affect the time from first contact to the start of copulation. In our study we tried to avoid inbreeding in the stock colony. However, we cannot exclude the possibility that some of the pairs tested may be closely related.

The mean duration of mating in *K. aberrans* was approximately 230.5 min, comparable to *Typhlodromus exhilaratus* Ragusa (243 min) (Castagnoli and Liguori 1991), but substantially longer than in *E. scutalis, A. womersleyi* and *A. andersoni* (30, 138 and 185 min, respectively) (ElBadry and Elbenhawy 1968; Amano and Chant 1978a; Tsunoda and Amano 2001). In *N. californicus*, *N. cucumeris*, *A. colimensis* and *T. pyri*, copulation lasted 351–500 min (Overmeer et al. 1982; Castagnoli and Liguori 1991; Orlando and McMurty 1992). Also in species showing the '*Phytoseiulus*' type of mating behavior, the duration of mating is variable: 90 min in *Phytoseiulus macropilis* Banks,

148 min in *P. persimilis* and 145 min in *Neoseiulus bibens* (Blommers) (Prasad 1967; Amano and Chant 1978a; Schulten et al. 1978; Enigl and Schausberger 2004). These literature data indicate that there is no consistent relationship between duration of copulation and type of mating behavior.

In several phytoseiid mites studied namely *P. persimilis*, *A. andersoni*, *N. bibens*, *A. womersleyi*, *T. exhilaratus*, *N. californicus*, *A. cucumeris* and *T. pyri* an inseminated spermatheca contains one spermatophore after 'successful' mating (Amano and Chant 1978a; Schulten et al. 1978; Overmeer et al. 1982; Hoy and Cave 1985; Castagnoli and Liguori 1991; Tsunoda and Amano 2001). Similarly in *K. aberrans* almost all inseminated spermathecae bore only one spermatophore. However, in one case a female randomly selected from the laboratory colony had two spermatophores within the same spermatheca. In *A. andersoni*, *P. persimilis* and *G. occidentalis*, even four spermatophores within a single spermatheca were reported as a result of multiple matings (Amano and Chant 1978b; Hoy and Smilanick 1979). In *T. pyri* and *A. cucumeris*, females of unknown reproductive history had up to two spermatophores within the same spermatheca (Overmeer et al. 1982; Castagnoli and Liguori 1991).

In all of the above-mentioned phytoseiid species, except in *G. occidentalis* (which was not studied), artificial interruption of copulation reduced the number and size of spermatophores in spermathecae, fecundity, oviposition period and the progeny sex ratio (ratio of daughters to sons) (Amano and Chant 1978b; Schulten et al. 1978; Overmeer et al. 1982; Castagnoli and Liguori 1991; Tsunoda and Amano 2001). In one pair of *K. aberrans* with an unusually short copulation (less than 20 min), only one of the spermathecae was inflated and no spermatophore was present in it.

In conclusion, in *K. aberrans* the three main types of the mating behavioral sequences known to occur in phytoseiids were observed, i.e. the main type and the 'sideways' variation of '*Amblyseius–Typhlodromus*' and '*Phytoseiulus*'. Whether this variability in mating behavior is an innate characteristic of *K. aberrans* with adaptive advantage remains to be determined. Furthermore, our results show that most females after one mating were inseminated with only one spermatophore, within a single spermatheca. Recent work showed that females of *K. aberrans* could mate 2–3 times in order to deposit their maximum number of eggs and in such cases more than one spermatophore may appear in one spermatheca (Koveos unpublished).

**Acknowledgements**

We thank three anonymous reviewers for their valuable comments on an earlier version of this paper. We also thank Dr George Papadoulis, Agricultural University of Athens, for verifying the identity of the species.

## References


Abou Setta M.M. and Childers C.C. 1987. Biology of *Euseius mesembrinus* (Acari: Phytoseiidae): life tables on ice plant pollen at different temperatures with notes on behavior and food range. Exp. Appl. Acarol. 3: 123–130.

Amano H. and Chant D.A. 1978a. Mating behaviour and reproductive mechanisms of two species of predacious mites, *Phytoseiulus persimilis* Athias–Henriot and *Amblyseius andersoni* (Chant) (Acarina: Phytoseiidae). Acarologia 20: 196–213.

Amano H. and Chant D.A. 1978b. Some factors affecting reproduction and sex ratios in two species of predacious mites, *Phytoseiulus persimilis* Athias Henriot and *Amblyseius andersoni* (Chant) (Acarina: Phytoseiidae). Can. J. Zool. 56: 1593–1607.

Castagnoli M. and Liguori M. 1991. Laboratory observations on duration of copulation and egg production of three phytoseiid species fed on pollen. In: Schuster R. and Murphy P.W. (eds), The Acari. Reproduction, Development and Life History Strategies. Chapman and Hall, London, pp. 231–239.

Duso C. and Vettorazzo E. 1999. Mite population dynamics on different grape varieties with or without phytoseiids released (Acari: Phytoseiidae). Exp. Appl. Acarol. 23: 741–763.

ElBadry E.A. and Elbenhawy E.M. 1968. Studies on the mating behaviour of the predaceous mite *Amblyseius gossipi* (Acarina, Phytoseiidae). Entomophaga 13: 159–162.

Enigl M. and Schausberger P. 2004. Mating choice in the predaceous mite *Phytoseiulus persimilis*: evidence of self-referent phenotype matching? Ent. Exp. Appl. 112: 21–28.

Hoy M.A. 1979. Parahaploidy of the "arrhenotokous" predator, *Metaseiulus occidentalis* (Acarina: Phytoseiidae) demonstrated by X- irradiation of males. Ent. Exp. Appl. 26: 97–104.

Hoy M.A. and Cave F.E. 1985. Mating behavior in four strains of *Metaseiulus occidentalis* (Acari: Phytoseiidae). Ann. Entomol. Soc. Am. 78: 588–593.

Hoy M.A. and Smilanick J.M. 1979. A sex pheromone produced by immatures and adult females of the predatory mite *Metaseiulus occidentalis*, Acarina: Phytoseiidae. Ent. Exp. Appl. 26: 291–300.

Krantz G.W. 1973. Dissemination of *Kampimodromus aberrans* by the filbert aphid. J. Econ. Entomol. 66: 575–576.

Kreiter S., Tixier M.S., Croft B.A., Auger P. and Barret D. 2002. Plant and leaf characteristics influencing the predaceous mite *Kampimodromus aberrans* (Acari: Phytoseiidae) in habitats surrounding vineyards. Environ. Entomol. 31: 648–660.

Kumari M. and Sadana G.L. 1992. Mating behaviour of the predatory mite *Amblyseius alstoniae* Gupta (Acari: Phytoseiidae). J. Insect Sci. 5: 165–166.

Laing J.E. 1969. Life history and life table of *Metaseiulus occidentalis*. Ann. Entomol. Soc. Am. 62: 978–982.

Lee M.S. and Davis D.W. 1968. Life history and behaviour of the predatory mite *Typhlodromus occidentalis* Utah. Ann. Entomol. Soc. Am. 61: 251–255.

McMurtry J.A. and Croft B.A. 1997. Life-styles of phytoseiid mites and their roles in biological control. Ann. Rev. Entomol. 42: 291–321.

Moraes G.J. de, McMurtry J.A., Denmark H.A. and Campos C.B. 2004. A revised catalog of the mite family Phytoseiidae. Zootaxa 434. pp. 494.

Orlando A. and McMurty J. 1992. Mating behavior and reproductive mechanisms of *Amblyseius colimensis* Aponte and McMurtry (Acari: Phytoseiidae). Bol. Entomol. Venez. 7: 1–12.

Overmeer W.P.J. 1985. Alternative prey and other food resources. In: Helle W. and Sabelis M.W. (eds), World Crop Pests, Spider mites, Their biology, Natural Enemies and Control, Vol 1B. Elsevier, Amsterdam, pp. 131–139.

Overmeer W.P.J., Doodeman M. and Van Zon A.Q. 1982. Copulation and egg production in *Amblyseius potentillae* and *Typhlodromus pyri* (Acari, Phytoseiidae). Z. Angew. Entomol. 93: 1–11.

Prasad V. 1967. Biology of the predatory mite *Phytoseiulus macropilis* in Hawaii (Acarina: Phytoseiidae). Ann. Entomol. Soc. Am. 60: 905–908.

Rock G.C., Monroe R.J. and Yeargan D.R. 1976. Demonstration of a sex pheromone in the predacious mite *Neoseiulus fallacis*. Environ. Ent. 5: 264–266.

Sabelis M.W. 1985. Predator – Prey Interaction. Predation on Spider Mites. In: Helle W. and Sabelis M.W. (eds), World Crop Pests, Spider mites, Their biology, Natural Enemies and Control, Vol 1B. Elsevier, Amsterdam, pp. 103–129.

Schulten G.G.M. 1985. Mating. In: Helle W. and Sabelis M.W. (eds), World Crop Pests, Spider mites, Their biology, Natural Enemies and Control, Vol 1B. Elsevier, Amsterdam, pp. 55–65.

Schulten G.G.M., Vanarendonk R.C.M., Russell V.M. and Roorda F.A. 1978. Copulation, egg production and sex ratio in *Phytoseiulus persimilis* and *Amblyseius bibens* (Acari: Phytoseiidae). Ent. Exp. Appl. 24: 145–153.

Tsunoda T. 1994. Mating behavior of the predacious mite, *Amblyseius womersleyi* Schicha (Acari: Phytoseiidae). Appl. Entomol. Zool. 29: 141–147.

Tsunoda T. and Amano H. 2001. Female mate receptivity behavior in multiple matings of a predacious mite, *Amblyseius womersleyi* Schicha (Acari: Phytoseiidae). Appl. Entomol. Zool. 36: 393–397.

Zaher M.A. and Shehata K.K. 1971. Biological studies on the predatory mite *Typhlodromus pyri* Sch. (Acarina: Phytoseiidae) with the effect of prey and non prey substances. Z. Angew. Entomol. 67: 389–394.