REVIEW

Sexual selection and mating behavior in spider mites of the genus *Tetranychus* (Acari: Tetranychidae)

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Abstract As sexual selection is a coevolutionary process between males and females, various morphological and behavioral traits have evolved in each sex. In the tetranychid mites *Tetranychus urticae* Koch and *T. kanzawai* Kishida (Acari: Tetranychidae), males can mate repeatedly, whereas females normally accept only the first copulation for fertilization. Since early times, it had been reported that males engage in precopulatory mate guarding and combat against conspecifics for females to enhance their reproductive success. On the other hand, it was believed that females do not have opportunities to choose their mates. In the last 10 or so years, however, several new findings related to mating behavior were reported. Some of the findings reinforce our established knowledge, whereas some of them explode it. Here, I review the mating behavior of *T. urticae* and *T. kanzawai* by incorporating recent findings and then propose a new direction for future research.

Keywords Female mate choice · Male combat · Mate guarding · Sexual harassment · *Tetranychus* · Tetranychidae

Introduction

Sexual selection is a coevolutionary process between males and females. Normally, males produce enough sperm to inseminate multiple females, whereas females produce larger ova in smaller amounts than the sperm produced by males (Andersson 1994). Therefore, selection favors males that have traits allowing them to compete with conspecific males for fertilizations (Darwin 1871). For example, well-developed weapons and aggressive ability in males are outcomes of male-male competition (Andersson 1994; Thornhill and Alcock 1983). On the other hand, females choose their mates based on male target traits (Darwin 1871) and gain direct/indirect benefits by mating with attractive males (Andersson 1994). Female mate preferences act as a selective pressure on male target traits. Through such processes, various morphological and behavioral traits have evolved in each sex (Andersson 1994; Thornhill and Alcock 1983). In order to understand how sexual selection has led the evolution, it is essential to clarify mating behavior.

Several species of tetranychid mites (Acari: Tetranychidae), such as the *Tetranychus* genus, are serious agricultural pests worldwide because their host plant range is extremely broad (Bolland et al. 1998). Hence, their biological and ecological traits including mating behavior have been reported since early times (reviewed by Boudreaux 1963; Cone 1985; Ewing 1914; Huffaker et al. 1969; Osakabe 1967; Van de Vrie et al. 1972). The mating behavior, such as precopulatory mate guarding and male combat (see the details below), is conspicuous in the *Tetranychus* genus. The mites show sexual dimorphism (Fig. 1), which is evidence of sexual selection (Slatkin 1984). Unfortunately, however, only a few studies had investigated the behavior of *Tetranychus urticae* Koch in the twentieth century (see Enders 1993; Everson and Addicott 1982; Potter 1979). In the last 10 or so years, several new findings related to mating behavior have been reported in not only *T. urticae* but also *T. kanzawai* Kishida. Some of the findings reinforce our established knowledge, whereas some of them

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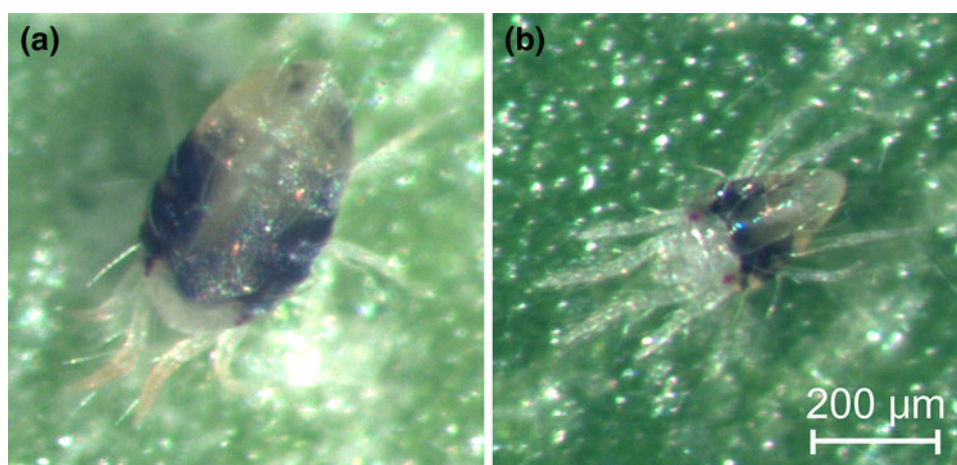
explode it. Here, I review the mating behavior of the two species by incorporating recent findings and propose a new direction for future research.

Note that Potter (1978) made an amendment to an earlier study (Potter et al. 1976a, b) by stating that the mites studied were not *T. urticae* but *T. cinnabarinus* (Boisduval). However, after Dupont (1979) indicated incomplete reproductive isolation between *T. urticae* (i.e., green form) and *T. cinnabarinus*, *T. cinnabarinus* was recognized as the red form of *T. urticae* (e.g., Everson and Addicott 1982). To avoid confusion, I regard *T. cinnabarinus* as a form of *T. urticae* in this article.

Biology

Tetranychus urticae and *T. kanzawai* are haplodiploid. Virgin females produce only sons, while mated females produce both daughters and sons. The sex ratio of offspring produced by mated females is female-biased, females:males ranging from 2:1 to 3:1 (Kondo and Takafuji 1982; Laing 1969; Overmeer 1972). Their life cycle consists of egg, larva, quiescent larva (protochrysalis), protonymph, quiescent protonymph (deutochrysalis), deutonymph, quiescent deutonymph (teleiochrysalis), and adult stages. The developmental period from egg to adult stages is around 10 days at 25 °C with a L16:D8 photoperiod (*T. kanzawai* on tea: Osakabe 1967; *T. urticae* on cotton: Kabiri et al. 2012). After a ca. 1 day pre-oviposition period, females lay 1–12 eggs per day for more than 20 days at 25 °C (on bean: Kondo and Takafuji 1985). Morphology differs between sexes. Although females are larger than males at the egg stage already (Macke et al. 2011), it is hard to detect the difference at a glance. Adult individuals clearly display sexual dimorphism (Fig. 1).

Tetranychus urticae and *T. kanzawai* are so small herbivores (body size of adult females is ca. 0.5 mm; Fig. 1)

and inhabit host plants. They lay silk threads while walking (Saito 1977, 1983), construct complicated webs over the leaf surfaces of the host plants, and live under the webs (Saito 1983). Individuals develop in their natal colony. After adult emergence, mating occurs there. Females normally accept only the first copulation for fertilization (Helle 1967; Oku 2008; Potter and Wrensch 1978; Satoh et al. 2001). Mated females disperse from the natal colony and establish new colonies (Hussey and Parr 1963). On the other hand, males can repeatedly mate (Krainacker and Carey 1989) and thus tend to stay at the natal colony (Enders 1993; Kondo and Takafuji 1982; Potter 1978). Consequently, although the operational sex ratio (OSR) is first female-biased, it becomes biased toward males as the colony matures (Potter 1978; Enders 1993). The details of mating behavior are given in the following paragraphs.

Although *T. urticae* and *T. kanzawai* have eyes, the visual capacity is limited. Their eyes can perceive wavelengths of light ranging from 350 to 600 nm (McEnroe and Dronka 1966, 1969; Naegele et al. 1966), but cannot resolve any images (McEnroe 1969). Setae on the whole body function as sense organs of touch and smell (Bostanian and Morrison 1973). These mites often use chemicals to perceive surrounding information (e.g., Grostal and Dicke 1999; Oku et al. 2003b, 2005; Pallini et al. 1999).

Precopulatory and copulatory behavior

Precopulatory mate guarding and copulation

Precopulatory mate guarding is one of male mating strategies to ensure their paternity, which has evolved in organisms in which female sexual receptivity is limited to a short time (Ridley 1983) or in organisms in which the first male's fertilization has an advantage in sperm competition (Yasui 1988). In *T. urticae* and *T. kanzawai*, males can

mate repeatedly (Krainacker and Carey 1989), while females accept copulation only once unless interrupted (Helle 1967; Oku 2008; Potter and Wrensch 1978; Satoh et al. 2001). Therefore, males guard quiescent deutonymph females, the stage immediately before adult emergence and sexual maturation (Oku et al. 2003a; Potter et al. 1976a; Satoh et al. 2001). The duration of the quiescent deutonymph stage is ca. 1 day at 25 °C with a L16:D8 photoperiod (*T. kanzawai* on tea: Osakabe 1967; *T. urticae* on cotton: Kabiri et al. 2012). Males search for females by using sex pheromones released by the females (Cone et al. 1971), the webs spun by deutonymph females (Penman and Cone 1972), and the body color of females (Royalty et al. 1993). Males continue to guard females until female adult emergence and then quickly copulate with them.

When a male attempts to copulate with a female, the male slips under the female from behind and holds her legs with his front legs (Cone 1985). Then, the male opisthosoma is bent upward to bring the extruded aedeagus in contract with the female's genital opening. The copulation is so passive for guarded females that they do not refuse it. The copula duration is around 190 s (Oku 2008; Ozawa and Takafuji 1987).

When males engage in precopulatory mate guarding, they loose opportunities for other activities, such as searching for other females. Therefore, males employing precopulatory mate guarding should behave to maximize their reproductive success. Theoretical models predict that it is an optimum strategy for males to shorten guarding time until copulation for a given female (Grafen and Ridley 1983; Parker 1974). That is, males should choose females close to becoming receptive (Parker 1974). In *T. urticae*, Potter et al. (1976a) and Everson and Addicott (1982) showed that males prefer to guard older rather than younger quiescent deutonymph females. However, their findings do not always stand up. Saito (2010) observed that the experimental design of Potter et al. (1976a) was problematic. They prepared many differently aged quiescent deutonymph females and adult males in an experimental arena. This experimental setup allows older quiescent deutonymph females to be guarded frequently because they are exposed to males for a longer time than younger females (Saito 2010). The experimental design of Everson and Addicott (1982) also included uncertain factors in their experimental setup. Although they conducted dual choice experiments using a single male on leaf squares (i.e., experimental arena) with two differently aged quiescent deutonymph females, they reused the experimental arenas several times. Furthermore, they did not clarify the history of tested males and photoperiodic conditions for their experiments. It is possible that male experience alters subsequent guarding behavior (Oku 2009a). The mating behavior of *T. urticae* appears to have periodicity (Rasmy

and Hussein 1993). Recently, Oku and Saito (2013) reexamined whether *T. urticae* males discriminate between females closest to becoming receptive and younger females at 25 °C with an L16:D8 photoperiod. Although they conducted dual-choice experiments, as did Everson and Addicott (1982), only unmated males (2 days old after adult emergence) were used for the experiments. Moreover, age differences between two females were controlled by introducing them to the experimental arenas at different timings. The age differences were 3, 6, 12, and 23 h, and older females were always the same age. When the age differences were 3, 6, or 12 h, males showed no preferences for females, whereas males preferred older rather than younger quiescent deutonymph females only when the age difference was 23 h (Oku and Saito 2013). This result is not fully consistent with previous studies, by the same token, theoretical models. What the inconsistency in *T. urticae* means is still not known. At least, however, it is certain that *T. urticae* males prefer to guard quiescent deutonymph females close to adult emergence when older females are present with quite young quiescent deutonymph females.

Male combat

During the precopulatory period, non-guarding males have opportunities to take over quiescent deutonymph females. They often attempt to approach females already guarded by a conspecific male (Potter et al. 1976a). Guarding males usually do not tolerate the intruder males (Potter et al. 1976a, b), with male combat consequently occurring. In the aggressive interactions, males spread their first legs and extrude their stylet for attack (Potter et al. 1976a, b). These body parts are male weapons to combat with conspecifics. Although the male combat behavior has been officially reported only in *T. urtica,* males of *T. kanzawai* also combat in the same manner. Guarding males are more advantaged than intruder males (Potter et al. 1976a, b). However, intruder males are able to take over females when they beat guarding males. Male body size also influences the outcome of combat: larger males often defeat smaller individuals (Enders 1993; Potter et al. 1976a, b). When the OSR becomes male-biased, male combat occurs more frequently (Enders 1993).

Sometimes, guarding males tolerate intruder males, thus allowing more than one male to co-guard one female without male combat (Potter et al. 1976a, b). Sato et al. (2013) observed male precopulatory behavior of *T. urticae* using a video recording system and found that there were two types of guarding males. Many guarding males were disturbed by conspecific males and engaged in male combat, whereas some males were never disturbed by conspecifics and never responded to them. The latter males

may allow intruder males to become co-guarders, though there is no evidence that conspecific males are able to find females guarded by the latter type of males. The findings of Sato et al. (2013) are interesting from the viewpoint of male mating strategies. The factors that determine the male behavioral phenotypes remain unknown, but they will be reported soon in their subsequent work.

Female mate choice

Female mate choice is roughly divided into two types: direct and indirect mate choice (Willey and Poston 1996). In the former, females directly perceive male target traits and choose their mates. In the latter, females trigger male combat and then choose the winner as a mate. Indirect mate choice is likely to evolve when female behavior is restricted (Willey and Poston 1996), which is known to occur in other taxa of organisms (sea elephant: Cox and Le Boeuf 1977; fowl: Pizzari 2001; hermit crab: Okamura and Goshima 2010; Yamanoi et al. 2006; spider: Watson 1990). In these organisms, male aggressive ability ought to have been evolved not only by male-male competition but also by female mate preference.

In tetranychid mites, quiescent deutonymph females are immobile during the precopulatory period, and copulation occurs immediately after female adult emergence. Therefore, it was assumed that females have no opportunity to choose their mates during the precopulatory period (e.g., Enders 1993; Everson and Addicott 1982). However, a recent hypothesis proposed that T. kanzawai females indirectly choose their mate through male combat during precopulatory mate guarding (Oku 2009b). Potter et al. (1976a) stated that 'quiescent females already attended by a male mite commonly attract additional males' (page 709) in T. urticae, but no evidence exists to support this claim. Oku (2009b) experimentally confirmed that precopulatory mate guarding attracts conspecific males in T. kanzawai. Furthermore, to determine which males or females attract additional males, Oku (2009b) conducted dual-choice experiments for males in the following combinations: females with a male by the side vs. solitary females, females with an upside-down male on the back vs. solitary females, females with a glass bead on the back vs. solitary females, and females with a deutonymph individual on the back vs. solitary females. Males preferred to guard females with a deutonymph individual over solitary females, whereas they did not show any preference to other treated females. Therefore, she concluded that females guarded by a male attract conspecific males. As mentioned above, when more than one male attempts to guard a female, male combat often occurs. As a result, the strongest male wins the combat and guards the female, and after adult emergence, the female copulates with this male. In the context,

guarded females are assumed to release more chemical signals than solitary females to attract conspecific males (Oku 2009b). If this assumption is appropriate, guarded females should invest energy in attracting males at the expense of investment in other activities. Thus, Oku and Shimoda (2013) compared the oviposition rate immediately after adult emergence between guarded and solitary females in T. kanzawai. Because guarding males were removed from 'guarded females' before female adult emergence, the oviposition rate of virgin females was compared in their study. They detected a reduction of the oviposition rate in guarded females, indirectly supporting the assumption described above (Oku and Shimoda 2013). However, it remains unclear whether females obtain direct/indirect benefits by attracting additional males.

Although haplo-diploid organisms suffer less from inbreeding depression than diploid organisms, inbreeding depression does exist in haplo-diploid groups (Henter 2003). Actually, in T. urticae, inbreeding reduces female fecundity (Perrot-Minnot et al. 2004; Tien 2010) and egg hatchability (Helle 1965), and prolongs the developmental period for offspring (Tien 2010). Inbreeding can be avoided either by dispersal of one sex from its natal area or by kin recognition and avoidance of mating with relatives (Andersson 1994). The latter case can be seen from the viewpoint of mate choice. Tien et al. (2011) tested a hypothesis that sexual selection should favor T. urticae individuals that show a preference for copulation with unrelated mates using virgin adult females, their brothers, and unrelated males. Copulation with unrelated males was observed to occur more often than with related males, supporting their hypothesis (Tien et al. 2011). Although Tien et al. (2011) implied that virgin adult females chose their mate, they did not mention whether the females actually refused copulations with related males. Therefore, it remains unclear whether female mate choice resulted in the inbreeding avoidance. T. urticae females disperse from their natal colony after mating (Hussey and Parr 1963). When one mated female establishes a colony by herself, her offspring cannot avoid inbreeding. Perhaps, inbreeding depression might not work as a strong selective pressure in T. urticae.

Postcopulatory behavior

Postcopulatory mate guarding

In species in which females mate with more than one male, males engage in postcopulatory mate guarding to prevent rival males from mating with their mates (e.g., Dodson and Beck 1993; Singer 1987). In T. urticae, the second copulation becomes effective when the first copulation is

interrupted (Potter and Wrensch 1978; Satoh et al. 2001). Thus, Satoh et al. (2001) determined the minimum copula duration required to fertilize a female for the first copulation by artificially manipulating the copula duration (30–200 s). They found that *T. urticae* females produce female offspring when they copulate for more than 40 s and that the copula duration is not correlated with the number of female offspring, indicating that 40 s is enough time for fertilization. However, the natural copulation lasts around 190 s in *T. urticae* (Ozawa and Takafuji 1987). To clarify why the copula duration is so long, they also investigated the effect of an interval (40–1,320 s) between female copulations with two males on the paternity of the first male. In the experiment, the first copulation was interrupted at 60 s, whereas the second copulation was not interrupted. The paternity of the first males increased with an increase in the interval between the copulations. When the intervals were shorter than 150 s, 60 % of the first males fathered less than half of offspring ($n = 5$), whereas 26.6 % of them fathered less than half of offspring when the intervals were longer than 150 s ($n = 19$). From these results, Satoh et al. (2001) concluded that *T. urticae* males also engage in postcopulatory mate guarding to ensure their paternity.

In *T. urticae*, after copulation has begun, conspecific males often attempt to pull a copulating male apart from the female (Tien et al. 2011). This interrupting behavior supports the conclusion of Satoh et al. (2001). When the attempt is successful, a second male begins to copulate with the female. Probably, he will gain some paternity. Potter and Wrensch (1978) estimated that 14.3 % of females will receive two effective inseminations in a crowded population of *T. urticae*. While postcopulatory mate guarding is a tactic for copulating males to ensure their mating success, the interrupting behavior would be a tactic for other males to enhance their reproductive success. Until now, however, no one has examined which kinds of males employ the interrupting behavior and how males perceive that copulation has occurred around them.

Male sexual harassment

In many organisms, males coerce females to mate with them. The sexual coercion compensates for being inferior in male competition and/or female mate choice, whereas it imposes fitness costs on females (Clutton-Brock and Parker 1995). As an example of male sexual harassment, males make repeated attempts to copulate until females accept it, which reduces female feeding time and thereby results in low reproductive success of females (e.g., Liana 2005; Magurran and Seghers 1994; Sakurai and Kasuya 2008). In *T. urticae*, as described previously, only the first copulation results in fertilization when the copulation is not

interrupted. Because males can recognize the mating status of females (Oku 2010), males likely do not copulate with mated females. But in reality, many males attempt to copulate with mated females when virgin females are absent (Oku 2010). Thus, Oku (2010) examined the effects of male copulation with mated females on the fitness of both sexes in *T. urticae*. Since only daughters have genes derived from their father, the proportion of females among the offspring was used as an index of male fitness. It is common to use the oviposition rate within a certain period as an index of female fitness (e.g., Oku et al. 2002). No effects on male fitness were detected, whereas the oviposition rate of mated females was lower in the presence of a male than in the absence of a male. The result suggested that mated females were disturbed by males and subsequently spent less time feeding and/or ovipositing, although male behavior was not observed during the experiment. The reduction of oviposition rate in the presence of males was also reported by Macke et al. (2012). Although it still remains unclear why males attempt to copulate with mated females (Oku 2013), the male behavior toward mated females can be seen as sexual harassment (Macke et al. 2012; Oku 2010). In *T. urticae*, mated females disperse from the natal colony and establish a new colony (Hussey and Parr 1963). Although this dispersal was believed to be attributable to the avoidance of food deterioration (Kondo and Takafuji 1985; Oku et al. 2002), Oku (2010) hypothesized that mated females disperse from their natal colonies to avoid male sexual harassment.

Conclusion

The mating behavior of *T. urticae* and *T. kanzawai* obviously indicates how sexual selection contributed to the evolution. During the precopulatory period, adult males guard quiescent deutonymph females until female adult emergence. Precopulatory mate guarding also occurs in other taxa, such as crustaceans (Jormalainen 1998), which is for ensuring paternity. Male mites are able to distinguish at least females close to the adult emergence and quite young females. On the other hand, non-guarding males attempt to approach females already guarded by a male to take over the females. Then, males often fight using weapons (first legs and stylet), and males that win the combat guard the females. Although it will occasionally happen that non-guarding males spontaneously intrude, females incite male combat by attracting additional males during precopulatory mate guarding. Females indirectly choose their mates through male combat. A similar female mate choice during precopulatory mate guarding has been reported in a spider (Watson 1990) and a hermit crab

(Okamura and Goshima 2010; Yamanoi et al. 2006). Among these organisms, it is common that females are restricted to directly choose their mate. Male weapons and aggressive ability will result from male combat, but they will be target traits for female mate choice, too. Further studies are still needed to clarify whether females obtain benefits by attracting additional males. Moreover, the behavioral types of male mate guarding reported by Sato et al. (2013) include profound meanings of male mating strategies. There must be more we do not know yet.

During the copulatory and/or postcopulatory period, copulating males engage in postcopulatory mate guarding to further ensure paternity, whereas non-copulating males attempt to interrupt the copulation to obtain paternity. This is because there are still possibilities for the latter males to fertilize at that moment. It is not rare that males employ both pre- and post-copulatory mate guarding. Males of a field cricket normally guard females after copulation to prevent their mates from remating with other males, but males occasionally guard females before copulation (Parker and Vahed 2010). Although the field cricket males transfer a spermatophore to females during copulation, they require time to replenish another spermatophore after copulation. When males find a female but do not yet have a spermatophore to transfer, they engage in precopulatory mate guarding until the replenishment is completed (Parker and Vahed 2010). Thus, selection is able to act on both pre- and post-copulatory behavior of males. Sexual coercion occurs to compensate for being inferior in male competition and/or female mate choice (Clutton-Brock and Parker 1995). However, male mites attempt to copulate with unreceptive mated females. Why this occurs still needs to be clarified. Dispersal of mated females from their natal colony would be partly because of the male sexual harassment.

Research on sexual selection and mating behavior has become more active in *T. urticae* and *T. kanzawai*. This is because general theories of sexual selection have developed rapidly in the last couple of decades (Andersson and Simmons 2006; Kuijper et al. 2012). Hopefully, the enthusiasm for studies on sexual selection in the spider mite *Tetranychus* genus will continue. Although *Tetranychus* mites are more often recognized as agricultural pests, they are suitable experimental materials. Their generation time is quite short, and they can be easily reared under laboratory conditions. These characteristics allow artificial selection for a specific trait in the laboratory (e.g., Yano and Takafuji 2002). In *T. urticae*, gene analysis is practicable because the genome has been completely sequenced (Grbić et al. 2011). Moreover, since their normal movement is walking, it is easy to analyze the behavior under the microscope. Thus, these mites are equivalent to *Drosophila* flies in their usefulness as a model organism (Belliure et al.

2010; Grbic et al. 2007). I hope that basic research will become increasingly common in *Tetranychus* and other genus spider mites.

Perspectives

Since behavioral and morphological traits are plastic, the phenotypes are altered by environmental factors and prior experiences. For example, predation risk reduces male-male competition (Kelly and Godin 2001) and female preference (Godin and Briggs 1996) in guppies. Among many taxa, it is known that fighting experiences modulate male aggressive behavior (Hsu et al. 2006). In the spider mite *Tetranychus* genus, there are a few studies examining the effects of predation risk and density experience on precopulatory mate guarding behavior (in *T. kanzawai*: Oku 2009a; Oku and Yano 2008). However, mating behavior reported until now is mostly fundamental. Naïve individuals were used for experiments under a simple environment. Therefore, the next step will be to investigate how environmental factors and/or prior experiences affect their mating behavior.

Furthermore, mating signals play important roles in sexual selection (Johansson and Jones 2007). As noted above, recent studies have suggested that chemical signals have a role during precopulatory mate guarding (Oku 2009b; Oku and Shimoda 2013). Moreover, chemical signals seem to be used in other situations, such as kin recognition and copulation interruption by males. However, we do not adequately understand their chemical communication, including having poor understanding of sex pheromones. In *T. urticae*, Regev and Cone (1975, 1976, 1980) identified farnesol, nerolidol, geraniol, and citronellol as components of the sex pheromone of quiescent deutonymph females. However, they squashed whole bodies of the females to extract chemical compounds; therefore, the extract may have included compounds unrelated to sex pheromones. Actually, Royalty et al. (1992) experimentally confirmed that farnesol, nerolidol, geraniol, and citronellol are not attractive to *T. urticae* males. These compounds probably do not function as actual sex pheromones (Royalty et al. 1992). Because spider mites are so small, it is technically difficult to detect chemical compounds from each individual. However, the investigation of chemical signals must be done to improve our understanding of the sexual selection and mating behavior of spider mites of the *Tetranychus* genus.

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