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Behavioural response and winter survival of mated and unmated diapausing females of the *Tetranychus atlanticus–urticae* complex (Acari, Tetranychidae)

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ABSTRACT

Behavioural responses were studied in mated and unmated females of a Dutch strain of the spider mite *Tetranychus urticae* which were destined to enter diapause. Observations were confined to the period between acquirement of the winter coloration by the females (a few days after the last moult) and their entering of artificial hibernation sites offered to the mites on the host leaves. Unmated females were found to stay longer on the leaf surface than mated females; they entered the hibernation sites significantly later than mated females. The delay in the search for hibernation sites shown by unmated females may be seen as a behavioural adaptation to enhance the chance of being fertilized before hibernation. Winter survival of mated and unmated diapausing females of the same strain of mites was studied both in the laboratory at a constant temperature of 2 ± 1°C and outdoors under natural climatic conditions in Amsterdam during the winter of 1990–1991. Survival was high under both conditions for mated as well as unmated females; no significant differences in survival were found between both types of female. Observations on post-diapause females of *Tetranychus atlanticus* (a mite belonging to the *T. urticae* complex) sampled from strawberry fields near Moscow in spring, showed that at most 10% of the females of this natural spider mite population were unmated. Both mated and unmated females had survived winter temperatures of −28 to −30°C.

Key words: *Tetranychus urticae*, *Tetranychus atlanticus*, spider mites, diapause, behaviour, winter survival.

INTRODUCTION

Females of the *Tetranychus atlanticus–urticae* complex from the temperate zones exhibit a winter diapause which is mainly induced by short photoperiods (see Veerman (1985) for a review). Diapause is induced during the larval and nymphal stages; adult females destined to enter diapause stay on the host plant for only a few days before they start searching for overwintering sites. During this period they mate, feed a little and undergo a change of colour, from greenish to orange–

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red. In contrast to summer females (and non-diapausing strains of the same species) they do not lay eggs (Hanstein, 1901; Vasiljev, 1910; Linke, 1953; Nuber, 1961). Once the colour has changed and the hind-gut has been emptied the mites become positively geotactic (Foott, 1965) and negatively phototactic (Bondarenko, 1958; Hussey and Parr, 1963). They start to leave the plants and develop a tendency to hide in dark places. Only females may overwinter, as observed already by Banks in 1900 (cited in Vasiljev (1910)). Hanstein (1901) was the first to notice that in spring, fertilized females produced males and females, whereas apparently unfertilized females produced only males.

Cold hardiness has been relatively well studied in diapausing females of *Tetranychus urticae* Koch. In apple orchards in British Columbia, Morgan (1952) found that 37.2% of diapausing *T. urticae* females that wintered in colonies under the bark scales of scaffold limbs and the trunk survived a temperature of −30.5°C. Survival was somewhat higher (46.0%) for females hibernating below the snow line, hidden under fallen leaves on the ground around the tree base. In outdoor experiments Bondarenko (1958) showed that diapausing females of a strain from Leningrad could withstand minimum temperatures of −27°C; when exposed to −32°C, however, no mites survived. In Uzbekistan some mortality occurred in a population of the cotton spider mite (*T. urticae*) at −17°C, while complete mortality of the population was found at −29°C (experiments of M.S. Gershun, cited in Ivanov (1951)). Ivanov (1951) noticed that diapausing populations of *T. urticae* in Uzbekistan were not able to survive in places which were protected from precipitation. The importance of high humidity to survive winter diapause was demonstrated for *T. urticae* in laboratory experiments by Parr and Hussey (1966).

It is not known whether any differences exist in the diapause characteristics and cold hardiness between mated and unmated females of *T. urticae*. The question whether fertilization is necessary for the successful overwintering of female *T. urticae* was raised by Cone *et al.* (1986), but was not investigated by these authors. Cone *et al.* (1986) found that from a total of 64 overwintered females, collected from hop yards at Prosser, Washington, none produced an all-male progeny. Apparently, all were fertilized the preceding autumn. The authors suggested that if unfertilized females do not survive winter, we might have another potential means of evaluating physiological changes necessary for survival.

The aim of the present research was to investigate whether there are any differences in behaviour between mated and unmated diapause-destined females of the *T. atlanticus–urticae* complex and whether fertilization prior to entering diapause affects winter survival of these mites. The size of insect and mite populations entering the overwintering stages and the subsequent survival of these stages, play a major part in determining the population levels encountered in the following spring and summer (Leather *et al.*, 1993). Therefore, detailed knowledge of the overwintering habits of economically important mites and insects may be valuable in terms of control and prediction.

MATERIALS AND METHODS

Spider mites

All experiments conducted in Amsterdam, The Netherlands, were performed with a strain of the twospotted spider mite, *T. urticae* (the Dutch strain 'Sambucus'), kept in the laboratory from 1961 onwards.

The observations in Moscow, Russia, were made on natural populations of the Atlantic spider mite, *Tetranychus atlanticus* McGregor, a mite belonging to the *T. urticae* complex and a dominant species in many regions of Russia (Popov, 1985). Post-diapause females of *T. atlanticus* were collected from strawberry fields near Moscow and brought to the laboratory for experimentation.

Observations on behaviour

Behavioural responses of mated and unmated females of a Dutch strain of *T. urticae*, destined to enter diapause, were investigated during the first weeks of adult life. For the experiment (performed in November 1990) females of the 'Sambucus' strain of *T. urticae* were allowed to lay eggs for 24 h on detached leaf cultures of *Phaseolus vulgaris* L. The eggs were kept at 25°C under continuous light for 4 days, after which they were ready to hatch. During post-embryonic development the mites were exposed to a short-day regime (L : D 10 : 14) at 20 ± 0.5°C, which is known to induce diapause in practically 100% of fertilized females. The experiment was repeated in January 1991 at 19 ± 0.5°C.

For observations on behaviour, females in the last quiescent stage (teleiochrysalids) of exactly the same age (which could be checked by examining the condition of the cuticle just prior to ecdysis) were placed on fresh leaf cultures, either with or without males. The sex ratio (female : male) was 3 : 1 in the first experiment and 1 : 1 in the second. On each leaf a small piece of roof-shaped black paper was placed to serve as an artificial hibernation site. Pilot experiments have shown these black paper hoods to be well suited for this purpose. In the first experiment 15 leaves were used with 17–18 female teleiochrysalids on each leaf in both variants (with and without males); in the second experiment 12 leaves were used with 22 female teleiochrysalids per leaf on average.

Dispause incidence was determined on each leaf culture and behaviour and the position of individual mites on the leaf were observed daily under a stereomicroscope. Observations were made over a period of 5–6 days and began 6 days after ecdysis, when all females had acquired the orange–red winter coloration.

Observations on survival

Survival of both mated and unmated females was determined in a hibernation experiment under laboratory conditions as well as outdoors under natural winter conditions in Amsterdam, The Netherlands. Mated and unmated diapausing females of *T. urticae* obtained from the above experiments were kept in the cold for various periods of time. Equal numbers of mated and unmated females, contained in plastic boxes, were placed in a climatic room in constant darkness at $2 \pm 1°C$. Another group of mites, also consisting of equal numbers of mated and unmated females, was placed outdoors in a tent near the laboratory in Amsterdam. The periods of cold treatment and overwintering under outdoor conditions are given in Table 2. Air temperatures were registered by a thermograph. After cold treatment, survival of the mites was determined at room temperature under a stereomicroscope.

From post-diapause females of *T. atlanticus*, sampled in spring from strawberry fields near Moscow, Russia, the sex ratio of their offspring was determined to examine whether unmated females could overwinter in a continental area of Europe, where air temperatures during winter may drop to -30 or even $-35°C$. The mites were sampled in May 1994; the lowest temperatures measured in the Moscow area in the winter of 1993–1994 were between -28 and $-30°C$. Seventy-seven adult overwintered females were put individually on leaf discs (diameter 15–17 mm) of strawberry. Each leaf disc was confined to a glass vial and floated on water. Each female was allowed to lay 20–25 eggs. After 3 days the females were removed from the leaf discs; the eggs were reared at $24 \pm 0.5°C$ in a temperature- and light-controlled incubator. The sex ratio and egg mortality were determined in each replicate. If females produced only males and the egg mortality was low it was concluded that these females had been unmated.

RESULTS AND DISCUSSION

Behavioural responses of mated and unmated females of T. urticae *on entering diapause*

Newly emerged adult females of *T. urticae* which were induced to enter diapause did not differ in appearance from the 'summer' (egg-laying) form. The first 2–3 days after ecdysis they fed intensively. The orange–red 'winter' coloration appeared on the third to fourth day after ecdysis; the change in pigmentation was complete in all individuals on days 5–6. The diapause incidence in mated and unmated females of *T. urticae* reared under a diapause-inducing short-day regime is presented in Table 1.

No significant difference was found in diapause incidence between mated and unmated females in either of the two tests ($p > 0.05$). The difference in diapause incidence between both tests may be due to the small difference in temperature; diapause induction was probably slightly suppressed by the higher temperature.- No effect of the status of the females (mated or unmated) was observed in either test. In earlier experiments, in 1984, diapause was induced in unmated females of *T. atlanticus* and *Tetranychus sawzdargi* Mitrofanov under short-day photoperiods (S.Ya. Popov, unpublished data).

TABLE 1

Diapause incidence in mated and unmated females of the Dutch strain 'Sambucus' of *T. urticae* reared at 19 and 20°C, L:D 10:14.

Test	Temperature (°C)	Replicates (number of leaves)	Number of females per leaf[a]		% Diapause[a]	
			Mated	Unmated	Mated	Unmated
1	20 ± 0.5	15	15.8 ± 2.1	17.7 ± 1.4	89.1 ± 8.6	89.6 ± 7.5
2	19 ± 0.5	12	21.6 ± 1.7	22.4 ± 1.4	100	100

[a](± SD).

Characteristic diapause-related behaviour was already shown by a number of females before the change of colour. On the second day after ecdysis some, still green-coloured, females began to aggregate on the leaves in groups of five to seven individuals. These aggregations were established earlier in the case of mated females than in the case of unmated females.

Migration into the artificial hibernation sites of both mated and unmated females is shown in Fig. 1. Migration started 1 day later in unmated females than in mated females. At 20°C (Fig. 1A) after 2 days, 65.1% of the mated females were hiding in the shelters, compared to only 4.6% of the unmated females. On days 3–5 some of the mated females returned to the leaf where they fed a little; nevertheless, the difference between mated and unmated females in the tendency to migrate to a sheltered place is noticeable. In the second experiment, performed at a slightly lower temperature (19°C, Fig. 1B), the percentage of mated females that had migrated to the shelters after 2 days was 74.5%, compared to 10.4% of the unmated females. After 3 days, migration to the shelters was almost complete in mated females; a slow but steady increase was observed in unmated females over the whole period of 6 days. The results indicate that the tendency to migrate to hibernation sites is stronger and develops earlier in mated than in unmated diapausing females of *T. urticae*. It is possible that mating stimulates migratory behaviour in diapausing females. The delay in migration to hibernation sites shown by unmated females may be seen as a behavioural adaptation to enhance the chance of being fertilized before hibernation. Apparently the increased chance of being fertilized by staying longer on the exposed leaf surface outweighs the greater risk of being discovered by a predator.

Winter survival of mated and unmated diapausing females of the T. atlanticus–urticae *complex*

To investigate whether mating influences winter survival, groups of mated and unmated diapausing females of the 'Sambucus' strain of *T. urticae* were kept for various periods of time in cold conditions. In the first variant they were kept in a climate room at a constant temperature of 2 ± 1°C, in the second variant they

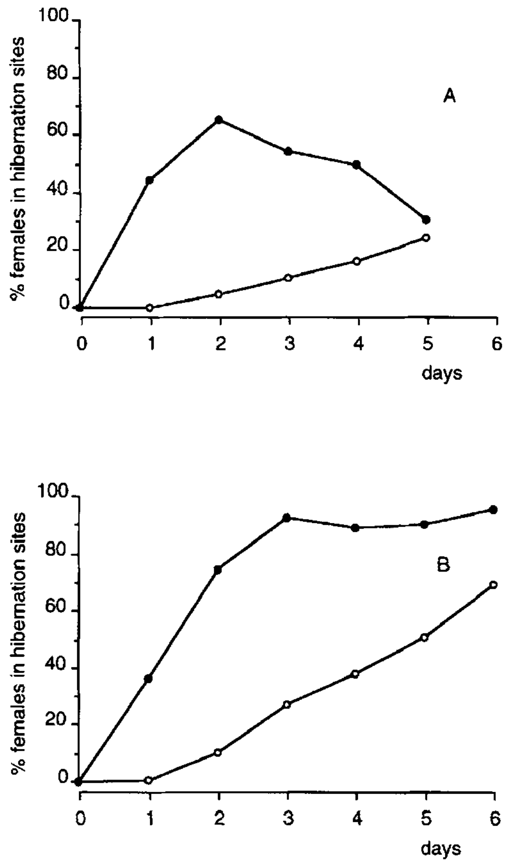

Fig. 1. Percentage of mated (filled circles) and unmated (open circles) diapausing females present in artificial hibernation sites at (A) 20°C and (B) 19°C. Observations started after completion of the colour change of the females on the sixth day after ecdysis. (See 'Materials and methods' for experimental details).

were exposed to natural winter temperatures in a tent near the laboratory in Amsterdam. The results of the experiment are shown in Table 2.

No significant difference was observed in the survival of mated and unmated females after a stay of 136 days in the cool room ($p > 0.05$). The mortality was somewhat higher in the group of mated females due to desiccation; almost complete survival was found in a group of mated females after a shorter period of cold of 46 days (Table 2).

Mites stored under natural conditions showed almost 100% survival in both groups, even over a period of 101 days, from mid-November until the end of February (Table 2). It is noticeable that both mated and unmated diapausing females of the 'Sambucus' strain, that has been kept in the laboratory for 30 years, survived 6 successive days in February with minimum temperatures of −12, −13, −12, −14, −14 and −10.5°C.

TABLE 2

Survival of mated and unmated diapausing females of the Dutch strain 'Sambucus' of *T. urticae* at low temperatures

Variant	Conditions	Status of females	Period of cold treatment (days)	Females after treatment		Survival (%)
				Alive	Dead	
1	Cool room (1–2°C)	Mated	16.XI–1.IV (136)	44	13	77.2
		Unmated	16.XI–1.IV (136)	91	5	94.8
		Mated	14.II–1.IV(46)	74	2	97.4
2	Natural conditions, Amsterdam	Mated	16.XI–25.II(101)	117	0	100
		Unmated	16.XI–25.II(101)	110	0	100
		Mated	21.XI–25.II(96)	391	0	100
		Mated	31.I–25.II(25)	182	1	99.5
		Unmated	31.I–25.II(25)	269	0	100

To examine whether unmated females of the *T. atlanticus–urticae* complex are able to overwinter in the continental frost zone, some life history parameters were determined for overwintered females of *T. atlanticus*, sampled in May 1994 from strawberry fields near Moscow. Females that had just started feeding on the plants and that had not yet lost their red colour completely were individually put on leaf discs of strawberry. The eggs laid were reared to adulthood after which the sex ratio in the progeny of each female was determined (Table 3). The proportion of unmated females in the overwintered population appeared to be 10.4% (eight females out of 77). Five of the unmated females produced eggs without any egg mortality, while the egg mortality in the batches of the other three females varied between 17.6 and 58.8%. The mean egg mortality in eggs of mated overwintered females was lower than that of unmated females, but in three females it attained values between 52.4 and 88.9%. The sex ratio in the progeny of these three

TABLE 3

Life history parameters of overwintered females of *T. atlanticus*, sampled from strawberry fields in the Moscow region, Russia

Females tested		Unmated females %	Mated females			Unmated females	
Mated	Unmated		Eggs tested	Egg mortality (%)[a]	Proportion of females in progeny[a]	Eggs tested	Egg mortality (%)[a]
69	8	10.4	1472	5.7 ± 15.2	0.752 ± 0.132	153	14.9 ± 22.2

[a](± SD).

females varied from 0.43 to 0.70, while in all cohorts of mites the sex ratio varied from 0.35 to 1.0. The correlation coefficient between the egg mortality and sex ratio in the progeny was rather low ($r = 0.501$). In addition, on earlier occasions a small proportion of *T. atlanticus* females were always found to produce males only (S.Ya. Popov, unpublished data).

The present study shows that there are no clear differences in survival between mated and unmated diapausing females of the *T. atlanticus–urticae* complex and that unmated females as well as mated females of *T. atlanticus* can survive air temperatures as low as −28 to −30°C. In addition, in the case of phytoseiid mites it has been recorded that certain species in Canada and the USA may survive winter temperatures from −16 to even −43°C, depending on the species (see Veerman (1992) for a review).

Conclusion

Mated as well as unmated females of *T. atlanticus* enter diapause in response to short-day photoperiods. The migration of unmated diapausing females of *T. urticae* to hibernation sites is delayed in comparison with mated diapausing females. This may be understood as a behavioural adaptation which enhances the chance of being fertilized before hibernation.

The survival of mated and unmated diapausing females of *T. urticae* at temperatures below and above zero does not differ significantly; unmated females of *T. urticae* from the Dutch laboratory strain 'Sambucus' survived temperatures of −14°C, whereas unmated females of *T. atlanticus* from a natural population in Moscow could survive air temperature minima of −28 to −30°C.

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