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DOES FEMALE MATING HISTORY AFFECT MATE CHOICE OF MALES IN THE TWO-SPOTTED SPIDER MITE *TETRANYCHUS URTICAE*?

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ABSTRACT — Males of the two-spotted spider mite *Tetranychus urticae* (Acari: Tetranychidae) attempt to copulate with mated females unreceptive to copulation. However, only the first copulation results in fertilization when the interval between the first and second copulation is longer than 24 h. Therefore, such male copulation behaviour does not directly contribute to male fitness. A previous study examined indirect effects on male fitness, but no effect was detected. A proximate explanation for males attempting to copulate with mated females may be the inability of males to discriminate between females that have recently copulated and those that had copulated earlier. Thus, here I tested male preference for females that had copulated 30 h ago and those that had copulated 6 h ago under dual choice conditions. Males chose equally both types of females, which supports the proximate explanation of male discrimination inability. In conclusion, this study suggests that males attempt to copulate with mated females because they are unable to perceive female mating history.

KEYWORDS — *Tetranychus urticae*; Tetranychidae; male; mated female; copulation; mating history

INTRODUCTION

Natural selection should favour individuals that have behavioural traits providing them with higher fitness than their conspecifics (Krebs and Davies, 1993). Therefore, whether given behavioural traits are adaptive or not should be discussed in terms of their costs and benefits. For example, sexual coercion, such as forced copulation, frequently occurs to compensate for male reproductive loss (Clutton-Brock and Parker, 1995). However, if male copulation attempts do not directly contribute to male fitness, the ultimate and proximate functions of such behaviour need to be thoroughly investigated.

Males of the two-spotted spider mite, *Tetranychus urticae* (Acari: Tetranychidae), often attempt to copulate with mated females unreceptive to copulation (Oku, 2010). In *T. urticae*, however, only the first mating results in fertilization when the intervals between the first and second copulation are longer than 24 h (Helle, 1967). Thus, this male copulation behaviour does not directly contribute to male fitness. Oku (2010) examined whether such male copulation behaviour indirectly enhances male fitness using the proportion of females among offspring as an index, but no effect was detected. Therefore, this male copulation behaviour is either non-adaptive or its adaptive benefits are cryptic and difficult to

detect. Although it is known that mated females incur fitness costs in the presence of males (Oku, 2010; Macke *et al.*, 2012), it still remains unclear why males attempt to copulate with mated females. A proximate explanation for such male copulation behaviour may be that males are unable to discriminate between females that had recently copulated and those that had copulated longer ago (Oku, 2010; Macke *et al.*, 2012). To test this explanation, I examined male ability to perceive female mating history.

MATERIALS AND METHODS

Mites

Tetranychus urticae (Acari: Tetranychidae) was reared on Lima bean plants (*Phaseolus lunatus* L. cv. Jackson Wonderbush) in a greenhouse (25 ± 5 °C, 50 – 70 % relative humidity, L 16 : D 8) at Wageningen University, The Netherlands.

The life cycle of *T. urticae* consists of egg, larva, quiescent larva, protonymph, quiescent protonymph, deutonymph, quiescent deutonymph and adult stages. Since *T. urticae* is arrhenotokous, virgin females can produce only sons, while mated females can produce both daughters and sons (Boudreaux, 1963). There are some behavioural differences between males arising from virgin females and males arising from mated females in *T. urticae* (Ohzora and Yano, 2008). Therefore, only males arising from virgin females were used in this study. To obtain adult *T. urticae* males arising from virgin females, quiescent deutonymph females were randomly selected from stock cultures. They were transferred onto leaf discs placed on water-saturated cotton wool, and after adult emergence, allowed to oviposit in a climate cabinet at 25 ± 5 °C and 50 – 70 % relative humidity, with a L 16 : D 8 photoperiod. When the mites had reached to the quiescent deutonymph stage, they were transferred onto new leaf discs and kept in the climate cabinet until being used for the experiment.

Perception of female mating history by males

To test whether males are able to discriminate between females that had recently copulated and

those that had copulated earlier, 86 virgin females that had emerged within one day were individually transferred onto bean leaf squares (8 × 8 mm). One unmated male (2 d old) per leaf square was introduced onto half of the leaf squares to allow copulation with the females. It was observed for 1.5 h whether copulation took place or not. When copulation occurred, the males were removed from the leaf square after the copulation was completed. Two pairs that did not copulate within the 1.5 h observation time were excluded from the experiment. After one day, new unmated males were introduced onto the second half of the leaf squares for copulation and observed for 1.5 h whether copulation took place or not. After 4 h, one female copulated 4 h ago and one female copulated 28 h ago were transferred in pairs onto bean leaf squares (10 × 10 mm) on water-saturated cotton wool (n = 41). One female of each pair was randomly marked with ink to be able to discriminate between females having different mating histories and allowed to acclimatize for 2 h in the climate cabinet. Then, one unmated male (1 d old) was introduced onto each leaf square. The male behaviour was observed for 30 min and it was recorded which female was first touched by the male (*i.e.* female copulated 6 h ago or female copulated 30 h ago) indicating male choice (Oku 2010). When males catch mated females, 75 % of them succeed in copulation (Oku, 2010). Four males did not touch a female within the observation time and were thus eliminated from the analysis. To determine whether the choice of the males differed significantly from a 1:1 ratio, the data were analyzed using a binomial test in the statistical package R version 2.10.0 (R Development Core Team, 2010).

RESULTS AND DISCUSSION

To examine perception of female mating history by males, a dual-choice experiment was performed using females that had copulated 6 h ago and females that had copulated 30 h ago. In *T. urticae*, when the first copulation was established less than 24 h ago, the second copulation is sometimes effective (15.4 % of 26 cases; Helle, 1967). Therefore, males are expected to prefer the former females over the latter females. However, in my experiment, males equally

chose both females (19 : 18; binomial test: $P = 1$), indicating that males of *T. urticae* are unable to discriminate between females that had copulated 6 h ago and those that had copulated 30 h ago. This discrimination inability is likely the proximate explanation why males of *T. urticae* attempt to copulate with mated females.

Since there is a limit to the number of mating times per day in *T. urticae* males (Krainacker and Carey, 1989), males should incur some costs for fertile copulation. If so, the results of my experiment then raise the question, why the males cannot discriminate between females that recently copulated and females that copulated longer ago. Males of *T. urticae* are attracted to sex pheromones of virgin females (Rasmy and Hussein, 1994). Although it has been shown that the attractiveness differs between virgin and mated females in *T. urticae* (Oku, 2010), mated females may be contaminated with the pheromones of virgin females. Moreover, possibly, the cost of copulation with mated females is small. Alternatively, natural selection on discrimination between females of different mating history may not be strong enough. Previous studies had observed male copulation behaviour under experimental conditions in the laboratory (Oku, 2010; Macke *et al.*, 2012). Under field conditions, however, mated females often disperse from the natal colony and found a new colony (Hussey and Parr, 1963), whereas males tend to stay in the natal colony (Enders, 1993). Therefore, although Puttaswamy and Channabasavanna (1979) reported that males of *T. ludeni* attempt to copulate with mated females under field conditions, *T. urticae* males may rarely encounter mated females in the field. In sub-social spider mites, such as species in the genus *Stigmaeopsis*, mated females often stay in the natal colony (Saito, 1986). Thus, it would be interesting to compare male copulation behavior between spider mites having different dispersal strategies, such as between *T. urticae* and *Stigmaeopsis* spp..

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