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Possible ecological consequences of heterospecific mating behavior in two tetranychid mites

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ABSTRACT

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Interspecific mating between the two-spotted spider mite, *Tetranychus urticae* Koch, and the Banks grass mite, *Oligonychus pratensis* (Banks), was documented using laboratory populations. The incidence of mating between *T. urticae* males and *O. pratensis* females was 26.0%, while that for the reciprocal mating was 18.8%. The incidence of mating was affected by both male and female species. Such matings may have several important ecological consequences. Interspecific matings resulted in all-male progenies. Thus, progeny sex ratios may be distorted by misdirected mating behavior. In addition, heterospecific mating resulted in lower fecundity than conspecific matings in the two-spotted spider mite, although not in the Banks grass mite. Aerial dispersal behavior of the two-spotted spider mite was also affected. Under crowded conditions and deteriorating resource quality, female mites exhibit an aerial dispersal posture that helps them to become airborne, and allows them to disperse long distances. Forty-two percent of *T. urticae* females that mated with conspecific males exhibited this dispersal behavior, compared to only 3.6% for virgin females. The incidence of aerial dispersal behavior for females that mated with heterospecific males was intermediate (27.3%). The effects of these behavioral alterations on male and female fitness may depend on the population structure and resource distribution.

INTRODUCTION

Mixed populations of two species of tetranychid mites, the two-spotted spider mite (TSM), *Tetranychus urticae* Koch, and the Banks grass mite (BGM), *Oligonychus pratensis* (Banks), are often found on corn and sorghum plants in late summer in the Great Plains (Pickett and Gilstrap, 1985). The population dynamics and pest status of both species depend on successful dispersal and colonization of new habitats (e.g. Holtzer et al., 1984; Kennedy and Margolies, 1985). Their co-occurrence and similar life histories suggest the potential for interspecific interaction and competition between these mite species.

Life history characteristics of both mites are typical of colonizing species: high fecundity, rapid development and a female-biased sex ratio (Wrensch

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and Young, 1975). Spider mites are arrhenotokous; that is, virgin females produce only haploid male offspring, whereas mated females produce both haploid males and diploid females. Although progeny sex ratios of individual mated females vary considerably (Boudreaux, 1963; King, 1987; Wrensch, 1991), they generally produce two to three times as many daughters as sons (Laing, 1969; Overmeer, 1972). For haplodiploid species such as spider mites, the effective population number is maximized when the sex ratio is 2:1 females:males since, on average, two-thirds of the genes in the next generation come from females (see Hartl and Clark, 1990, pp. 86–87). Thus, female-biased sex ratios in spider mites tend to increase the effective population number, and to maintain genetic variability.

This system of sex allocation and the resulting female-biased sex ratio helps insure successful establishment of new colonies. A female-biased sex ratio increases the proportion of potential colonists because mated females serve as dispersers and founders of new populations (Mitchell, 1970). Despite the predominance of females in a population, mite mating behavior insures that most females will be inseminated. Adult males guard and defend quiescent female deutonymphs from other males, thereby gaining the opportunity to mate with adult females as soon as they emerge (Wrensch and Young, 1975; Potter et al., 1976). The incidence of guarding increases as the time of adult female emergence draws nearer (Cone et al., 1971; Potter et al., 1976).

Most guarded females are mated immediately after emerging, but females may remain receptive for at least 6 days after adult emergence (Potter and Wrensch, 1978). Although females may mate more than once, it is usually only the first insemination that is effective (Potter and Wrensch, 1978). Thus, mating generally precedes dispersal by adult females (Mitchell, 1970). This is critical to successful establishment of new populations, as the likelihood of encountering conspecific males with which to mate following aerial dispersal is slight. Unmated foundresses will produce male offspring with whom they may later mate, but fecundity and total production of female offspring is greatly diminished compared to that of mated females (Krainacker and Carey, 1990).

Although they are wingless, adult female mites of these two species are able to colonize distant habitats through behavior that enhances wind-borne aerial dispersal. When exposed to adverse environmental conditions and the proper ranges of light intensity and wind velocity, adult females assume a characteristic posture of raised forelegs and forebodies that facilitates their becoming airborne (Smitley and Kennedy, 1985; Margolies, 1987). Young adult females exhibit this behavior more often than older females, whereas males and immature mites rarely exhibit the behavior.

As part of a long-term study of interactions between *T. urticae* and *O. pratensis*, we examined the mating and dispersal behaviors when the species co-occur. These behaviors are critical for successful colonization. In this study we document some of the potential ecological consequences of such interspecific matings. Among the objectives of this study were to measure the propensities for interspecific mating, and to examine the consequences of such matings on the production of offspring. If heterospecific matings do not yield fecund female offspring, or if only sons are produced, the implications for individual fitness may be severe. Finally, we documented the influence of interspecific interactions on the incidence of aerial dispersal behavior by adult TSM females. Because of time and resource limitations, we did not examine the effect of these interactions on aerial dispersal behavior of BGM females.

MATERIALS AND METHODS

The TSM and BGM used in these studies were from laboratory cultures maintained on lima beans and corn, respectively. The TSM colony used to study the incidence of mating and aerial dispersal behavior was collected in Columbus, Ohio, approximately 2 months before these studies began. The BGM colony used in these experiments was started with mites collected in southwestern Kansas 3 months prior to the start of the experiments. These two colonies died out before the start of the study measuring offspring production. Therefore, the TSM colony used in this study was started from mites collected in North Carolina approximately 4 months earlier. The BGM used in the offspring production experiment were from a second BGM colony started from mites collected in southwestern Kansas 8 months before the start of the experiment. All rearing was done and behavioral observations made under room conditions of 25–50% RH and 28 °C.

Mating. Males which were observed guarding a quiescent deutonymph in the laboratory colony were transferred to individual 0.7-cm diameter corn or bean leaf disks. A 1-day-old virgin female was placed on each leaf disk occupied by a male; female TSM were placed on bean leaf disks, and female BGM on corn leaf disks. Each pair was observed continuously for 30 min, or until mating occurred, whichever came first. Females were scored as either mated or unmated. Although length of mating in TSM affects its efficacy (Overmeer, 1972), we were only concerned with the willingness to mate. Therefore, we considered mating to occur when the aedeagus was inserted for at least 5 s while the pair remained motionless.

A separate chi-square test was used for each of the reciprocal crosses to test the null hypothesis that mating does not occur between the two species. The significance of interactions among male species, female species and mating status (i.e., whether or not females mated) was assessed using a three-way analysis based on a log-linear model (Sokal and Rohlf, 1981, pp. 747–767). Chi-square tests were used to distinguish significant differences among mating incidence for specific mating types.

Offspring production. Groups of 10–25 female quiescent deutonymphs were collected and placed on 5×5-cm corn leaf sections (for BGM) or detached bean leaves (for TSM). Pairings were conducted on the following day, when all viable females had emerged as adults. Males were placed, one at a time, on a leaf or leaf section containing virgin females and observed for 15 min, or until mating (as previously defined) was observed. The males were then removed. Females that mated were removed immediately after disengagement and placed individually on a corn leaf section (for BGM) or a bean leaf (for TSM). Twenty-one mated females were collected for each possible cross. Mated females were allowed to oviposit for 7 days, and then removed. Subsequently, leaves or leaf sections were checked daily for 7–9 days until all offspring became adults, and their sex could be determined. The number and sex of adult F_1 offspring were recorded daily, after which the adults were removed.

Differences among crosses in the number of male offspring, female offspring, total offspring production and the sex ratio were assessed using factorial analyses of variance (ANOVA), with the species of the male and the species of the female considered as separate factors. Comparisons among means for specific treatments were made using the Student–Newman–Keuls' multiple range test (Steel and Torrie, 1960, pp. 110–111).

Aerial dispersal. The effect of mating on aerial dispersal behavior was examined for three groups of TSM females: (1) those previously exposed to TSM males; (2) those exposed to BGM males; and (3) females without exposure to males as adults (i.e., virgin females). The incidence of aerial dispersal behavior among conspecifically-mated BGM females was also measured. Groups of 10–25 TSM or BGM females were collected as quiescent deutonymphs between 08:00 and 15:00 h and placed on detached bean leaves (for TSM) or corn leaf sections (for BGM). TSM and BGM adult males that were observed guarding deutonymphs in their respective cultures were collected and placed on the leaves with the female quiescent deutonymphs (male:female ratio ca. 3:2). The males were introduced in sufficient numbers and given adequate time to insure that females exposed to males were mated before being tested. The incidence of aerial dispersal behavior among adult females was observed between 08:00 and 14:00 h on the following day in a 2.0-m/s wind (Smitley and Kennedy, 1985; Margolies and Kennedy, 1988). Females were monitored continuously for 2 h. Those that maintained the aerial dispersal posture for at least 10 s were scored as displaying the aerial dispersal behavior and immediately removed from the arena.

The influence of male exposure on the incidence of aerial dispersal behavior among TSM females was assessed using an R×C test of independence using the G-test (Sokal and Rohlf, 1981, pp. 744–747). The significance of differences among specific treatments was evaluated using chi-square tests.

The incidence of aerial dispersal behavior for conspecifically mated BGM and TSM females were compared using a chi-square test.

RESULTS

Mating. Significant numbers of interspecific matings occurred between TSM males and BGM females ($\chi^2=20.7$; d.f. = 1; $P<0.001$), and between BGM males and TSM females ($\chi^2=15.5$; d.f. = 1; $P<0.001$) (Table 1). The 3-way interaction between the male's species, the female's species, and the incidence of mating was also significant (adjusted $G=18.4$; d.f. = 1; $P<0.001$). The incidence of conspecific matings in both BGM and TSM were significantly higher and heterospecific matings lower than expected based on mating proclivities of males and females considered independently (Table 1). Deviations from these expectations measure the magnitude of the interaction between male and female main effects.

Offspring production. The minimum length of time for any mating was 10.8 s, sufficient for at least some sperm transfer to occur (Overmeer, 1972). Conspecific matings lasted 128 ± 11 (s.e.) and 118 ± 9 s for TSM and BGM, respectively, and heterospecific matings lasted 132 ± 17 and 80 ± 14 s for TSM females and BGM females, respectively. Heterospecific matings of BGM and TSM females produced only male offspring, while conspecific matings produced both male and female offspring. The mean sex ratios among F_1 progeny produced by TSM and BGM females mated with conspecific males were 75.2 ± 2.6 and 65.3 ± 5.5, respectively, and were not significantly different (ANOVA; $F=2.6$; d.f. = 1,40; $P>0.05$).

The number of male offspring was unaffected by the species of either the

TABLE 1

Percentage of mating between male and naive female BGM and TSM. Naive females had no previous exposure to males of either species. Expected percentages based on main effects only are indicated parenthetically (see text for explanation)

		Female	
		TSM	BGM
Male	TSM	62.0 a (50.5) $n=79$	26.0 b (37.4) $n=77$
	BGM	18.8 b (29.0) $n=85$	29.6 b (19.3) $n=81$

Percentages followed by the same letter not significantly different, chi-square tests for each mating combination, $P<0.01$.

TABLE 2

Mean (±s.e.) number of offspring produced by TSM and BGM females mated to hetero- and conspecific males. Sample size = 21 for each male–female species combination

	Male parent	Female parent	
		TSM	BGM
a. Male offspring			
	TSM	8.3±0.8 b	21.8±2.2 a
	BGM	24.4±2.6 a	5.6±1.2 b
b. Female offspring			
	TSM	27.1±2.6 a	0 c
	BGM	0 c	9.1±1.5 b
c. Total offspring			
	TSM	35.5±2.7 a	21.8±2.2 b
	BGM	24.4±2.6 b	14.7±1.9 c

Means within each offspring type (male, female and total) followed by same letter not significantly different; Student–Newman–Keuls' multiple range test; $P<0.05$.

male or the female parent ($F<1$ and $F=2.05$, respectively; d.f. = 1,80; $P>0.05$), but was influenced by the interaction between male and female species ($F=73.9$; d.f. = 1,80; $P<0.005$) (Table 2a). The number of female offspring was affected by the species of both male and female ($F=36.4$ and 36.4, respectively; d.f. = 1,80; $P<0.005$), as well as by the interaction between these factors ($F=146.8$; d.f. = 1,80; $P<0.005$) (Table 2b).

The species of the male and of the female significantly affected the number of total offspring produced ($F=14.4$ and 23.9, respectively; d.f. = 1,80; $P<0.005$) (Table 2c). There was no significant interaction between male and female species ($F<1$). TSM females mated with TSM males produced more total offspring than females with other mating histories (Table 2c). This was attributable to the greater number of females resulting from this mating compared to the number produced by BGM×BGM matings.

Aerial dispersal. Mating history significantly influenced the incidence of aerial dispersal behavior in TSM females (adjusted $G=191.5$; d.f. = 2; $P<0.001$). Virgin TSM females (i.e., those without adult exposure to either TSM or BGM males) displayed little inclination to disperse aerially; only 3.6% ($n=331$) assumed the aerial dispersal posture. The incidence of aerial dispersal behavior among TSM females that were exposed only to BGM males was 27.3% ($n=289$). These females were significantly more likely to exhibit aerial dispersal behavior than were TSM females with no male exposure ($\chi^2=67.4$; d.f. = 1; $P<0.001$). However, exposure to BGM males did not elevate the incidence of aerial dispersal behavior among TSM females as much as exposure to conspecific males ($\chi^2 = 17.1$; d.f. = 1; $P < 0.001$); 41.8% of TSM females exposed to TSM males exhibited aerial dispersal behavior ($n = 629$).

The difference between the incidence of aerial dispersal behavior among TSM females exposed to TSM or BGM males may be due to a lower incidence of interspecific mating compared to intraspecific mating, or to quantitative or qualitative differences in mating-related stimuli that promote aerial dispersal behavior. Additional experiments are required to distinguish between these alternatives.

Only 7.5% of BGM females mated with BGM males exhibited the aerial dispersal posture. This is significantly lower than the incidence of this behavior among TSM females mated to TSM males or to BGM males ($\chi^2 = 128.0$ and 44.5, respectively; d.f. = 1, $P < 0.001$), but higher than the incidence among virgin TSM females ($\chi^2 = 4.2$; d.f. = 1; $P < 0.05$). These levels of response are comparable to those reported by Margolies (1987).

DISCUSSION

Interspecific mating between TSM and BGM mites from our laboratory populations were common. Such matings have several potentially significant consequences for mite populations because they alter offspring sex ratios and dispersal propensities. Hybrid matings between TSM and a sibling species, *T. cinnabarinus*, result in diminished viability among F_2 eggs (Murtaugh and Wrensch, 1978). However, matings between TSM and BGM yielded no female offspring at all. In mixed populations where reproductively active males of one species appreciably outnumber those of the other, interspecific mating could yield a competitive advantage to the more abundant species by suppressing the sex ratio in the minority species, thereby decreasing its growth rate. This would also reduce the effective population size in the minority species by reducing the sex ratio below 2:1. Thus, the initial relative densities of the two species could play a major role in determining competitive balances between the species.

Heterospecific mating may diminish the individual fitness of males to the extent that the male's time and other resources are depleted. However, Krainacker and Carey (1989) observed that TSM males exposed to virgin TSM females ad libitum inseminated an average of 15.5 females during the first day as adults, and a total of 68.9 females after 8 days. Thus, the costs to males of heterospecific matings may be slight. The net effect of interspecific mating on male fitness will depend on to what degree and at what cost interspecific mating is avoidable, and the relative frequencies of sexually receptive females of both species. The opportunity costs associated with other misdirected reproductive behaviors, especially prolonged guarding of heterospecific females, could be more severe.

Aerial dispersal appears to be an adaptive response to habitat deterioration, and, hence, a potentially important life history trait. Modification of aerial dispersal behavior in TSM females through interaction with BGM males may directly influence the dynamics of mixed populations of the two species. Interspecific mating may induce aerial dispersal by TSM females, and thereby reduce mite density on the original plant. This appears to represent a form of direct competition mediated by interspecific mating behavior. McLain and Shure (1987) refer to this phenomenon as "pseudo competition", whereby misdirected mating results in the abandonment of a resource by one species.

The impact of modified dispersal propensities on the fitness of an individual female will depend on the distribution and abundance of suitable host plants, predator abundances, and on her reproductive potential. If a female is in a patch that is densely populated with another species, she may increase her fitness by dispersing if there is a sufficient likelihood of reaching a new patch with more abundant food resources or conspecific mates. If this probability is high, then heterospecific mating may provide useful information. However, if this probability is slight, then interspecific mating could represent misinformation that elicits an inappropriate dispersal response.

The relationship between interspecific mating and dispersal may reflect a recent species association for which time, selection intensity, or available genetic variability have not been sufficient to modify or eliminate. Pre-mating reproductive barriers were demonstrated for both BGM and TSM. Observed frequencies of conspecific mating were substantially greater than expected based on mating propensity of males and females considered independently, and heterospecific matings occurred less frequently than expected. Although these barriers may contribute to reproductive isolation of the species, they are far from complete. However, post-mating reproductive barriers were complete: no female offspring were produced by cross-mated females of either species. The eventual evolution of pre-mating reproductive barriers might be expected, especially in areas where mixed populations are common.

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