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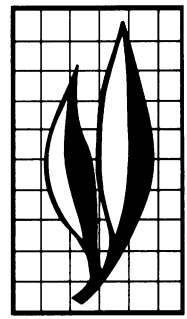
UNIVERSITY OF CALIFORNIA DIVISION OF AGRICULTURE AND NATURAL RESOURCES



ABSTRACT

Differences in premating behavior patterns and timing, both within and between populations, were observed among reciprocal crosses of five populations of the western predatory mite, *Metaseiulus occidentalis* (Nesbitt). One population that was subjected to three selections for enhanced premating isolation showed no selection response.

Postmating isolation in five of the eight pairs of reciprocal crosses of *M. occidentalis* colonies resulted in the deposition of shriveled eggs and reduced numbers of apparently normal eggs. Reciprocal crosses usually exhibited different degrees of incompatibility; no apparent pattern with regard to geographic origin of the colonies was found in the degree of postmating isolation.

The potential impact of postmating isolation on population dynamics was evaluated in reciprocal crosses of two populations using life table techniques. One colony was a strain that had been artificially selected in the laboratory for resistance to permethrin (Immature Selection-38), the other a population collected from a California pear orchard (McCall Pears). In the Immature Selection female (IS) X McCall Pear (MP) male cross, IS females produced fewer eggs than MP females in the reciprocal cross. Of the eggs deposited by the IS females mated to MP males, substantially more eggs shriveled than in the reciprocal cross. In addition, most of the surviving F_1 progeny in the IS female X MP male cross were males. The net reproductive rate (R_o) of the MP female X IS male cross was 10.58, but only 0.92 for the reciprocal cross. The intrinsic rate of increase (r_m) of the MP female X IS male cross was 0.213 and zero for the reciprocal cross.

The wide geographic distribution of *M. occidentalis* throughout western North America enhances the likelihood that genetically distinct populations have developed. The data pre-

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Marjorie A. Hoy and Frances E. Cave

Premating and Postmating Isolation among Populations of *Metaseiulus occidentalis* (Nesbitt) (Acarina: Phytoseiidae)[1]

INTRODUCTION

Metaseiulus (= *Typhlodromus* or *Galendromus*) *occidentalis* (Nesbitt) is an effective native biological control agent of spider mites in deciduous orchards and vineyards in western North America (Hoyt 1969; Flaherty and Huffaker 1970; Huffaker, van de Vrie, and McMurtry 1969; Hoy 1985a). It has a wide geographic distribution and exhibits considerable variability in its biological, morphological, and ecological attributes. It is morphologically very similar to *Typhlodromus longipilus* Nesbitt, and discrimination between the two species has been difficult until recently. However, Hoying and Croft (1977) evaluated populations of "*M. occidentalis*" from western North America and the Netherlands (where it has been introduced) and found that complete reproductive isolation existed between a *T. longipilus* population from New Jersey and each of two populations of *M. occidentalis* from central Washington state and the Netherlands. Their morphological and breeding data indicated that *M. occidentalis* is distributed from Colorado in the east to California, Oregon, Washington, and British Columbia in the west, while *T. longipilus* is restricted to the eastern United States (Hoying and Croft 1977).

Metaseiulus occidentalis populations vary in morphological structures (Davis 1970; Hoying and Croft 1977; Schicha 1978). Davis (1970) found that specimens of *M. occidentalis* from some orchards in Utah "have unusually long dorsal setae and thus resemble *T. longipilus* Nesbitt rather than *T. occidentalis*." Females in some Utah orchards had four pairs of ventrianal setae, while other populations had three. The prominence of the ventrianal pores also appeared to vary between populations. Hoying and Croft (1977) found a population of *M. occidentalis* from southern California to be notably smaller than the other populations measured. Schicha (1978) found no qualitative morphological differences in three populations of *M. occidentalis* collected from Australia (where it was introduced), but quantitative differences were found within strains.

Ecological and physiological attributes vary among populations of *M. occidentalis*. Diapause attributes are variable; critical photoperiod differed between two populations of *M. occidentalis* from California and Washington (Hoy and Flaherty 1970). Photoperiodic response curves of four populations of *M. occidentalis* from California, Utah, and Washington were also different (Croft 1971).

Populations of *M. occidentalis* vary in their responses to pesticides. Responses to organophosphates (Hoyt 1969; Croft and Jeppson 1970; Hoy and Knop 1979; Hoy 1985b) and sulfur (Hoy and Standow 1982) have been found to differ between populations within a relatively small geographic area, perhaps because dispersal is slow and rare. Studies of dispersal of a

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carbaryl-resistant strain of *M. occidentalis* out of California almond orchards suggest that this predator may disperse only about 800 m within three years of release; trapping of predators coming into the orchards indicated that dispersal may be rare (Hoy, Groot, and van de Baan 1985; Hoy 1982, 1985b). Populations within individual orchards or vineyards seem to respond to local pesticide selection pressures as the level of resistance observed appears to be related to the pesticide use history in the specific orchard or vineyard from which they were collected and may vary between colonies collected from adjacent sites (Hoy and Knop 1979; Hoy 1982; Hoy and Standow 1982; Hoy, Groot, and van de Baan 1985).

Whether these differences in morphological, behavioral, and toxicological attributes represent a normal range of variation within a widely distributed species or indicate that subspecies have developed remains to be determined. Geographic races, subspecies, and sibling species have been found in other phytoseiids. McMurtry, Mahr, and Johnson (1976) found that a population of *Amblyseius potentillae* (Garman) from apple orchards in the Netherlands was reproductively compatible with a colony collected from citrus in Italy. The two populations differed, however, in their responses to photoperiod and relative humidity. *Typhlodromus citri* Garman and McGregor and *T. arboreus* Chant were each shown to have a reproductively incompatible sibling species through crossbreeding studies by Mahr and McMurtry (1979). These authors found that normal eggs were produced in the control crosses, but shriveled eggs were produced in some crosses between different strains.

Congdon and McMurtry (1985) clarified, for the first time, that *Euseius hibisci* (Chant) is actually a complex of three species. Populations from citrus were primarily *E. tularensis* (Congdon and McMurtry), and *E. hibisci* was found primarily on avocado. A third species was not described. All three species were very similar morphologically, but reproductively isolated; this identification of distinct species explained a number of anomalies observed in biology and behavior.

Croft (1970) crossed four strains of *M. occidentalis* (from Washington, California, and Utah) and found partial reproductive isolation in certain crosses, manifested as reduced oviposition rates, increased production of shriveled eggs, increased mortality during development, and sex ratio changes.

Reproductive isolation subsequently has been found between other populations of *M. occidentalis*. Hoy and Knop (1981) found partial reproductive incompatibility in crosses of base colony (WA-0) males and laboratory-selected permethrin-resistant females (WA-18); the reciprocal crosses were apparently normal. The incompatibility made mode-of-inheritance tests difficult to conduct, because the females produced few eggs and some of the deposited eggs shriveled shortly after deposition. The reproductive incompatibility between the base colony (WA-0) and the permethrin-selected colony was first noted in preliminary crosses between the WA-8 and base colonies; the eight rounds of selection required approximately one year to accomplish. Crosses of the permethrin-selected colony with a permethrin-susceptible strain from a California almond orchard were also incompatible, as were crosses between females of the WA-0 colony and permethrin-susceptible males from a colony from British Columbia (BC) (Hoy and Knop 1981). A cross between BC males and females collected from a California almond orchard was also incompatible. In all the above examples, reciprocal crosses were compatible.

Hoy and Standow (1982) had difficulties conducting a mode-of-inheritance test of sulfur resistance using two colonies of *M. occidentalis* collected from California. They found that crosses between sulfur-resistant females (Raven colony, collected from a San Joaquin Valley vineyard) and sulfur-susceptible males (Berkeley blackberries) were partially reproductively

incompatible: only 16 of 36 crosses produced any F_1 larvae, and 10 of 36 crosses yielded at least one shriveled egg. In the 10 crosses that yielded at least one shriveled egg, three produced only one or two larvae.

Mueller-Beilschmidt and Hoy (1987) evaluated activity levels of a colony collected from California almonds (Wild strain collected near Modesto in April 1985) and a laboratory-selected permethrin-resistant strain (IS-38) of *M. occidentalis* originally collected from a Washington apple orchard. The initial cross between the two colonies was successful, but when the cross was repeated one month later, reproductive incompatibility prevented an analysis of the F_1 progeny. Why the incompatibility occurred in the second cross but not in the first is unknown.

Reproductive isolation is known to develop through either premating or postmating isolating mechanisms. We analyzed detailed observations of 15 pairs each of virgin males and females of four colonies of *M. occidentalis* to determine if intraspecific variability exists in premating behavior (Hoy and Cave 1985). Behavioral sequences were categorized using a scheme adapted from Amano and Chant (1978).

While mating behavior proceeds continuously and divisions in it are somewhat arbitrary, an outline is useful as a framework for comparison (fig. 1). During step I, the male encounters the female. There are three possible encounter routes: male and female meet head to head,

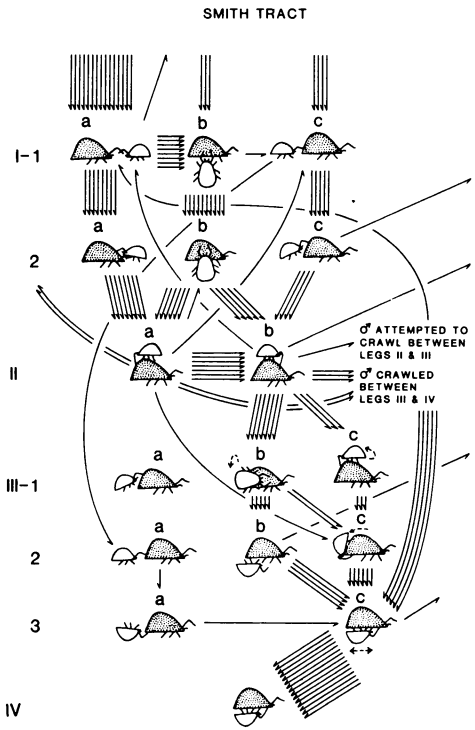

Fig. 1. Mating behavior sequence for 15 pairs of the Smith Tract colony of *M. occidentalis*.

male encounters side of female, or male encounters posterior of female. The male repeatedly touches the female with his forelegs and palps after encounter. This tapping may provide the male and female with tactile or chemosensory recognition cues. As the female may run away during the initial encounter, step I may be repeated. If the female does not run away, the male proceeds to mount the female's dorsum. Sometimes the male may leave even if the female does not run away.

During step II, the male mounts the female's dorsum, where he drums with his forelegs and palps. Again, it is likely that chemical or tactile cues are exchanged. The female typically remains quiet during this interval, but some females continue moving about the leaf and may become very active. These agitated females run quickly and may use their fourth pair of legs in an attempt to flick the male off. Step II thus appears to involve species-specific cues by both sexes, and acceptance by the female in the cases where she does not displace the male.

In step III, the male may move to the venter of the female, by one of three routes, and continue to use his palps and forelegs to tap or touch the female. In route a, the male touches the female from the rear, flips over, and attempts to reach the venter-to-venter position. In route b, the male crawls sideways under the female, and in route c the male turns, faces posteriorly, and crawls under the female. If the male remains with the female, he typically makes small back-and-forth movements under the female.

In step IV, the female typically becomes quiescent. During this interval, the male transfers sperm via his spermatodactyl from his genital opening to one or both of the female's sperm receptacles between coxae III and IV. The female typically accommodates the male in the venter-to-venter position by slightly raising her body off the substrate, particularly in the rear. About halfway through step IV, the male may change position slightly. This is probably associated with the movements necessary for the male to transfer a new spermatophore into the second spermatheca of the female on the opposite side. There is no apparent preference for the process to begin on one side or the other.

Behavioral sequences were found to vary significantly within and between four colonies of *M. occidentalis* (Hoy and Cave 1985). This variability generally contrasts with the highly repetitive patterns previously reported for phytoseiid mites (Lee and Davis 1968; Putman 1962; Amano and Chant 1978; Overmeer, Doodeman, and van Zon 1982), although Amano and Chant (1977) noted that more time was required for pairs to establish the venter-to-venter position when males were old, and the percentage of males that crawled under or climbed on females from the front also decreased as males aged.

The partial reproductive incompatibility observed in diverse crosses of *M. occidentalis*, as well as the variability in other traits that have been examined (diapause attributes, mating behavior, pesticide resistance, and anatomical characters), suggests that *M. occidentalis* exists as discrete populations. It is not known, however, if any populations are completely reproductively isolated. If so, there are several potential practical implications. Pesticide-resistant strains of *M. occidentalis* are being mass-reared and released into deciduous orchards and vineyards throughout western North America. The persistence of the pesticide-resistant strains will depend on the degree of reproductive isolation achieved between them and the native susceptible populations. Currently isolation is achieved by using pesticides selective for the released strains. Exploiting genetically determined reproductive isolating mechanisms could reduce the number of pesticide applications required for maintaining pure colonies.

In this paper we evaluate the degree of premating and postmating isolation between five populations of *M. occidentalis*, report the results of artificial selection for premating isolation in one colony, and evaluate, through life table statistics, the impact of postmating isolation between two colonies.

MATERIALS AND METHODS

Colony Sources and Culture Methods

Five colonies of *M. occidentalis* were evaluated: Livingston Almonds (LA), initiated from 469 individuals collected from eight almond orchards near Livingston, California, during July 1983; Almont Almonds (AA), initiated with 54 mated females collected from an almond orchard near Chico, California, in April 1984; McCall Pears (MP), initiated from 31 mated females collected from a pear orchard in El Dorado County, California, in October 1982; Smith Tract (ST), initiated from 180 diapausing mated females collected from an apple orchard 19 km north of Wenatchee, Washington, in October 1984; and Immature Selection-38 (IS), which originated from an apple orchard in Wenatchee, Washington, in November 1977 and had undergone 38 selections in the laboratory for permethrin resistance.

Colonies were maintained in the laboratory at 25° to 28°C under an 18-hour daylength on paraffin-coated paper disks placed on water-soaked cotton. Colonies were fed all stages of two-spotted and Pacific spider mites (*Tetranychus urticae* Koch and *T. pacificus* McGregor) brushed from pinto bean (*Phaseolus vulgaris* L.) foliage grown in a University of California greenhouse in Berkeley.

Screening for Premating Incompatibility

Intra- and inter-strain variability in premating behavior had been reported previously for four of the five colonies observed in the current evaluation (Hoy and Cave 1985); summaries of these same strain (homogametic) crosses are included elsewhere in this report (tables 1 and 2) to facilitate comparisons. In addition, baseline mating behavior data were obtained for a fifth colony (Smith Tract) before evaluating the reciprocal (heterogametic) crosses (fig. 1).

Virgins were obtained by rearing *M. occidentalis* larvae, one per disk, on bean leaf disks infested with the two-spotted spider mite, which served as prey. A single virgin female and male were placed on a clean bean leaf disk 1.27 cm in diameter (1.3 cm^2) for behavioral observations at 26° to 28°C and 40% to 60% ambient RH, under a stereoscopic dissecting microscope. Single pairs of 1- to 2-day-old virgin females and males were observed continuously on the bean leaf disks until mating occurred or 45 minutes had elapsed. A pair that terminated a premating sequence before attaining quiescence was monitored for the full 45 minutes; pairs thus could be observed for portions of more than one sequence.

A diagram of the variations of behavior patterns in the premating sequence developed in earlier tests (Hoy and Cave 1985) served as a score sheet (fig. 1). The specific sequence and time involved in each phase of the sequence was recorded for each pair during observations, beginning when the male was introduced. Acceptance of the male was defined as point at which the female showed no signs of agitation, characterized by running or kicking with the rear legs, and settled quietly into place (= quiescence). After quiescence, the pair was checked frequently to measure the duration of the apparent copulation. Fifteen pairs were observed for each of the homogametic (intracolony) crosses and ten pairs were observed for each of the reciprocal (heterogametic) crosses.

Times for the steps in the premating sequences for the five colonies were compared using analysis of variance (ANOVA), and means were separated by Duncan's multiple range test (LeClerg, Leonard, and Clark 1962). Pairs of reciprocal crosses were compared by group comparison t-test. Analyses included time from start of observation to first contact, start to contact in sequence leading to successful sperm transfer, contact to venter-to-venter position

(I-1 to III-3), and venter-to-venter to quiescence (III-3 to IV), and time spent in apparent copulation. To evaluate the rate of successful sperm transfer, each female was slide-mounted in Hoyer's mounting medium after the pair had separated. The number of sperm receptacles that were inflated and the number of spermatophores in each were recorded. The mating was termed "successful" if both receptacles had one (or more) apparently normal spermatophore.

Selection for Premating Isolation

Selection for enhanced premating isolation was conducted with colonies of *M. occidentalis* that had demonstrated low mating success in preliminary screenings. These colonies, McCall Pear (MP) and Smith Tract (ST), were collected from California and Washington, respectively, and to the best of our knowledge were both native populations unrelated to any release colony that may have come from our laboratory. Colonies were maintained as described above.

In observations of 10 pairs, 50% of the ST females rejected MP males the first time they gained a venter-to-venter position during the observation period (fig. 2b). "Rejection" was defined as the successful removal of the male from the venter of the female by the active, agitated movements of the female. Therefore, we decided to attempt to select for ST females that would reject males from the MP colony. Selection was conducted so that females that rejected MP males during a 45-minute test interval also had to accept ST males within a 3-hour interval. The selected colony was referred to as the Nonmating colony (NM).

To conduct a selection, we isolated virgin females of the ST colony with males of the MP colony for a period of 45 minutes. A single pair was isolated on a bean leaf disk (1.27 cm diameter or 1.3 cm^2). At the end of 45 minutes, each female that was not in a venter-to-venter position (suspected rejection of the MP strain) was transferred to another leaf disk. These suspected nonmating females were held and checked after 48 hours to be sure they were not gravid or had not deposited eggs. (Unmated *M. occidentalis* females do not deposit eggs [Hoy and Cave 1986].) Same-strain crosses of the three colonies (NM, ST, and MP) were evaluated simultaneously as controls. All selections were conducted at 26° to 27°C under continuous fluorescent light; 275 to 350 females were selected each time.

In the second part of the selection, nonmating females were isolated with males of their own strain, one pair per leaf disk, for a 3-hour period. Disks were checked every 20 to 30 minutes and mating status was recorded. Pairs *in copula* after 3 hours were allowed to finish mating. All females were again isolated, one per disk, to determine whether mating was successful, as demonstrated by deposition of at least one egg. Once eggs were deposited, these females were used to initiate the next generation of the NM colony. Selections were conducted every other generation for a total of three selections.

Survey for Postmating Incompatibility

Initial screenings of eight pairs of reciprocal crosses were performed to determine the extent and degree of postmating incompatibility between the five colonies. Fifty female deutonymphs were isolated, five per bean leaf disk (2.06 cm diameter), for each reciprocal cross. Disks were infested with *T. urticae* as prey. After 48 hours (when all females were adult), four males were added to each disk and left on the disks for the duration of the test. Counts were made of apparently normal eggs and shriveled eggs 48 and 96 hours after males were added. Calculations of eggs per female were adjusted for mortality and losses due to runoff by averaging the number of females at the start and end of each 48-hour scoring period.

For each pair of reciprocal crosses, the numbers of normal eggs per female deposited during the scoring interval were compared using a group comparison t-test.

A second set of each reciprocal cross was set up as described above, but 24 hours after males were added, we removed and slide-mounted the females in Hoyer's medium to count the number of spermatophores deposited in each female's sperm receptacle. Mating was termed successful if both sperm receptacles held a spermatophore.

Effects of Postmating Isolation on Life Table Attributes

Based on the survey just described, reciprocal crosses of the McCall Pear and Immature Selection-38 colonies were chosen for a detailed evaluation of the effects of postmating incompatibility. Female deutonymphs of each colony were isolated, one per disk, on 1.27-cm-diameter bean leaf disks for 48 hours until adults had emerged. Each adult female was then moved to a fresh disk, and a single young male was added. Leaf disks were prepared 1 to 2 days before the predator pairs were placed on them; disks were cut from uninfested bean leaves and two or three adult female *T. urticae* and *T. pacificus* were added to each disk to deposit eggs. When the predators were transferred to the leaf disks after 24 hours, the disks contained young spider mite eggs (and only two or three females) as prey; this facilitated inspection of the leaf disks for shriveled predator eggs. The predator pair was moved daily to new disks with a fresh supply of spider mite eggs (0 to 24 hours old) until the female died. Males were not replaced if they died or ran off the disk. The numbers of apparently normal and shriveled eggs deposited by each predator female on the disk from which the predator pair had just been moved were counted each day. Each disk was checked 6 days after egg deposition to determine the number of progeny that reached maturity, their sex, the number of eggs that failed to hatch, and the number of immatures that failed to develop. Twenty-four females were used for each of the reciprocal crosses and same-strain controls. Data were analyzed by ANOVA and means were separated by Duncan's multiple range test.

RESULTS

Screening for Premating Incompatibility

When mating behavior sequences of single pairs were observed (fig. 2), differences were found in sequences I and III in both homogametic and heterogametic crosses (table 1). For example, in the cross between the Immature Selection-38 colony (IS) and the Livingston Almond (LA) colony, 40% of the pairs exhibited sequence c of step III, whereas 10% followed this sequence in the reciprocal cross. Likewise, 20% versus 60% did "other" in step III (table 1). As shown in figures 1 and 2, *M. occidentalis* does not appear to have a highly stereotyped mating behavior.

Mean durations of two mating behavior sequences were significantly different among the five colonies tested (table 2). Mean time to first contact ranged from 5.6 to 12.7 minutes, with the LA colony taking the least time for males to encounter females (table 2). Likewise, the LA colony took the least time (mean = 62.3 minutes) from quiescence to separation. All other mean times were not significantly different. The proportion of the 15 pairs that successfully mated (had at least one spermatophore in each receptacle) ranged from 73% to 93% (table 2). Two females (of 15) in the ST X ST cross had more than one spermatophore per receptacle.

Among the reciprocal crosses, a significant difference in time to contact in successful sequences was found in crosses of the LA and ST colonies (table 3); 10.4 minutes elapsed

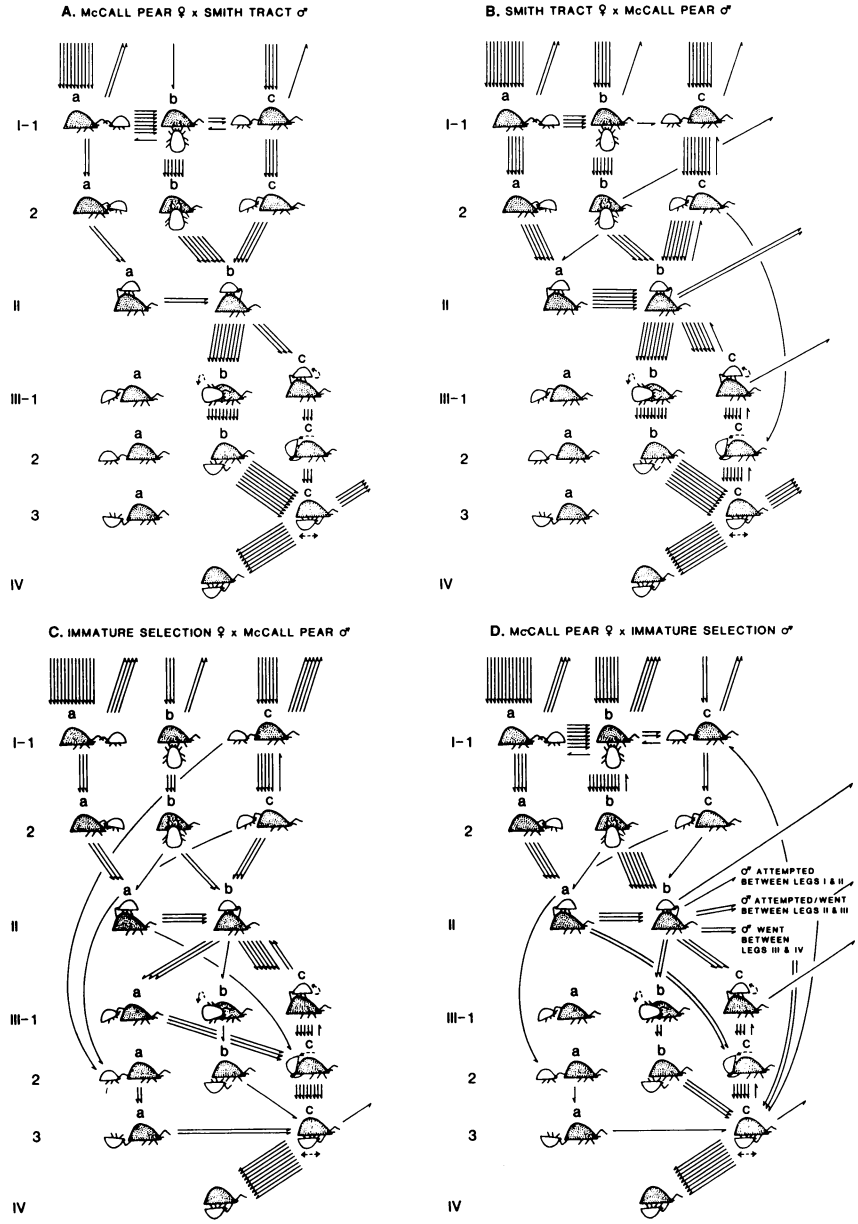

Figure 2. Mating behavior for 10 pairs each of A) McCall Pear female X Smith Tract male, B) Smith Tract female X McCall Pear male, C) Immature Selection female X McCall Pear male, D) McCall Pear female X Immature Selection male.

Table 1. PROPORTION OF MATING SEQUENCE TYPES IN CROSSES OF FIVE COLONIES OF *M. OCCIDENTALIS* USING YOUNG VIRGIN MALES AND FEMALES

Colony* ♀x♂	Pairs following sequence types in steps I and III (%)						
	Step I			Step III			
	a	b	c	a	b	c	Other
AA x IS	20	40	40	0	80	10	10
IS x AA	20	50	20	0	40	60	0
AA x LA	40	30	20	0	30	70	0
LA x AA	30	40	20	0	10	70	10
AA x MP	20	20	40	0	10	70	0
MP x AA	30	50	20	0	20	80	0
IS x LA	20	50	20	10	30	40	20
LA x IS	20	60	10	0	30	10	60
IS x MP	30	30	40	20	10	70	0
MP x IS	30	50	0	10	20	40	20
LA x MP	60	30	10	10	20	70	0
MP x LA	10	50	20	20	10	60	10
LA x ST	40	10	50	0	60	40	0
ST x LA	30	20	50	20	20	60	0
MP x ST	20	60	20	0	80	20	0
ST x MP	30	20	40	0	50	50	0
AA x AA†	27	53	20	0	40	60	0
IS x IS	40	40	13	0	27	53	20
LA x LA	40	40	20	7	33	60	0
MP x MP	40	40	13	0	27	67	0
ST x ST	33	47	13	7	20	40	33

* AA = Almont Almonds, IS = Immature Selection, LA = Livingston Almonds, MP = McCall Pears, ST = Smith Tract.
† Data for all homogametic crosses except ST X ST taken from Hoy and Cave (1985).

Table 2. DURATION OF MATING SEQUENCES IN FIVE COLONIES OF *M. OCCIDENTALIS* USING YOUNG VIRGIN MALES AND FEMALES

Behavior sequence and mean time (SD)	Colony* Almont Almonds	Immature Selection	Livingston Almonds	McCall Pears	Smith Tract	F value
Time to first contact (min)	11.0 a (4.9)	12.7 a (7.7)	5.6 b (4.9)	8.3 ab (4.8)	8.9 ab (5.2)	3.4†
Time to contact in successful mating sequence (min)	13.1 (6.1)	15.4 (8.1)	12.2 (8.0)	8.8 (3.8)	9.4 (5.1)	2.0
Time from contact to venter-to-venter (s)	35.8 (15.0)	47.9 (20.7)	43.1 (27.8)	40.6 (16.4)	48.1 (11.1)	1.1
Time from venter-to-venter to quiescence (min)	3.9 (5.0)	2.4 (4.4)	2.4 (3.7)	2.5 (3.1)	5.5 (5.7)	1.3
Time from quiescence to separation (min)	75.3 a (16.0)	76.7 a (10.8)	62.3 b (7.5)	75.2 a (8.1)	66.7 ab (19.5)	2.8†
Successful matings (%)‡	93	87	80	73	73	

* Fifteen pairs of each colony were observed. Data for Almont Almonds, Immature Selection, Livingston Almonds, and McCall Pears reported in Hoy and Cave (1985).
† Times significantly different ($P<0.05$; one-way analysis of variance). Means in a row followed by different letters are significantly different (Duncan's multiple range test; LeClerg, Leonard, and Clark 1962).
‡ Percentage of females with both spermathecae filled.

between start of the test and contact in successful matings of LA females with ST males, whereas 22.8 minutes elapsed for the reciprocal crosses. Significant differences in mean times from quiescence to separation were found for the IS X LA and IS X MP reciprocal crosses (table 3). IS females mated with LA males spent 83.6 (±8.1) minutes in the venter-to-venter position, whereas pairs in the reciprocal cross spent only 64.7 (±11.2) minutes. Likewise, in the MP female X IS male cross, the time spent in quiescence to separation was 87.8 (±4.6) minutes versus 74.0 (±9.6) minutes for the reciprocal cross. No other mean sequence durations were significantly different (table 3).

Mating success, defined as the transfer of at least one spermatophore to each of the two sperm receptacles, ranged from 30% to 90%. The lowest success rate was found in the LA female X IS male cross. Only 50% of the pairs were successful in each of the IS X MP reciprocal crosses. Of the ST X MP reciprocal crosses, 70% were successful; selection for nonmating was subsequently conducted with the ST female X MP male cross, because not only were few spermatophores transferred but 50% of the females rejected MP males after they had achieved the venter-to-venter position during the observation interval (fig. 2b, step III-3). In contrast, ST females rejected ST males only once (fig. 1, step III-3).

Selection for Nonmating Between Two Colonies

The percentage of ST females that failed to mate with males of the MP colony during the test interval did not increase in three selections (table 4). In fact, the percentage not mating declined from 32.9 to 26.5 to 22.0 during the three selections, whereas the percentage of ST control females mating with ST males was 30.0, 26.7, and 50.0, respectively, for the three selections.

Survey for Postmating Incompatibility in Eight Reciprocal Crosses

Postmating incompatibility, when present, was generally stronger in one reciprocal cross than the other (table 5). Five of the eight reciprocal crosses between different colonies of *M. occidentalis* yielded significantly different mean numbers of eggs per female (table 5). For example, AA females mated to LA males produced only 0.86 (S.D.= 0.22) egg per female compared to 4.63 (0.92) eggs per female in the reciprocal cross during the 48- to 96-hour interval after mating. In the AA female X LA male cross, 9 of 47 eggs (19%) deposited shriveled, whereas 2 of 203 eggs (<1%) shriveled in the reciprocal cross. Mating success (96% and 100%) was nearly the same, however, if the number of females with both spermathecae containing at least one spermatophore is used as an indicator of mating success. In all five crosses in which the reciprocal crosses yielded significantly different numbers of eggs per female, mating success was better than 92%. These data suggest that copulation and spermatophore transfer were successful but that reproductive incompatibility occurred at some subsequent stage.

The AA and LA colonies, both collected from California almond orchards, were reproductively incompatible in both directions, although to different degrees in the reciprocal crosses (table 5). The AA X MP reciprocal crosses were incompatible in one direction (table 5), and these colonies were also collected from California. The IS X LA and IS X MP reciprocal crosses were incompatible in both directions, although to differing degrees. The IS colony is a laboratory-selected colony originally collected from a Washington state apple orchard. Unpredictably, however, the ST X LA reciprocal crosses were compatible, even though the ST colony was from a Washington apple orchard and the LA colony was from a California

Table 3. DURATION OF MATING SEQUENCES IN EIGHT SETS OF RECIPROCAL CROSSES BETWEEN DIFFERENT COLONIES OF *M. OCCIDENTALIS* USING YOUNG VIRGIN MALES AND FEMALES

Colonies* ♀ x ♂	Time (S.D.) To first contact (min)	To contact in successful sequence (min)	Contact to venter-to-venter (s)	Venter-to-venter to quiescence (min)	Quiescence to separation (min)	Mating success• (%)
AA x IS	8.6 (7.5)	10.6 (7.2)	40.0 (11.4)	2.3 (2.3)	72.1 (6.6)	70
IS x AA	7.7 (4.0)	9.5 (3.8)	44.2 (25.2)	2.1 (1.6)	75.1 (6.2)	80
AA x LA	11.0 (7.3)	13.0 (7.6)	44.8 (16.6)	1.9 (1.7)	68.3 (4.8)	70
LA x AA	10.2 (8.4)	16.5 (9.2)	51.3 (39.5)	3.3 (3.8)	65.6 (14.4)	70
AA x MP	8.1 (6.6)	11.1 (6.1)	48.6 (40.4)	2.5 (3.4)	68.4 (19.0)	80
MP x AA	12.7 (12.8)	13.1 (14.6)	37.0 (14.5)	1.7 (2.6)	75.6 (16.7)	90
IS x LA	12.1 (4.6)	19.3 (11.7)	42.4 (14.9)	1.1 (0.9)	83.6 (8.1)§	80
LA x IS	11.5 (6.1)	12.4 (3.4)	45.2 (13.0)	3.3 (3.0)	64.7 (11.2)	30
IS x MP	9.5 (4.5)	12.4 (3.4)	38.3 (13.3)	2.5 (2.2)	74.0 (9.6)§	50
MP x IS	12.6 (8.5)	13.4 (9.8)	46.8 (14.7)	1.8 (2.1)	87.8 (4.6)	50
LA x MP	10.3 (7.3)	13.9 (8.3)	52.5 (42.2)	1.8 (2.1)	71.6 (16.9)	70
MP x LA	6.4 (4.4)	12.0 (9.9)	44.7 (18.5)	1.4 (0.8)	73.6 (13.3)	70
LA x ST	8.6 (6.6)	10.4 (6.3)§	48.4 (21.4)	3.6 (3.1)	69.7 (6.3)	90
ST x LA	4.1 (2.2)	22.8 (15.2)	44.4 (21.4)	4.6 (4.1)	68.0 (10.0)	60
MP x ST	7.8 (5.8)	14.0 (8.9)	43.0 (24.0)	4.9 (4.4)	70.0 (10.9)	70
ST x MP	4.8 (2.6)	15.1 (11.0)	39.8 (12.4)	4.9 (3.6)	55.0 (23.5)	70

* AA = Almont Almonds, IS = Immature Selection, LA = Livingston Almonds, MP= McCall Pears, ST = Smith Tract.
• Percent females with both spermathecae filled.
§ Means of the reciprocal crosses differ significantly at $P \leq 0.05$, group comparison t-test.

Table 4. NO SELECTION RESPONSE FOR NONMATING (NM) BETWEEN SMITH TRACT (ST) AND McCALL PEAR (MP) STRAINS OF *M. OCCIDENTALIS* DURING THREE SELECTIONS

Date 1985	No. females tested	% non-mating	% mating with own strain•	Controls* % non-mating NM	ST	MP
6-8 May	325	32.9	58.9	—	30.0	26.0
27-28 May	275	26.5	75.3	33.3	26.7	30.0
18-20 June	350	22.0	66.2	20.0	50.0	33.0

* Pairs were observed for 45 minutes, and if the female was not *in copula*, she was held for 48 hours to confirm that she had not mated.
• Females that did not mate with males of the MP colony were then provided males from their own colony for 48 hours; mating was confirmed by the deposition of at least one egg.

almond orchard. The MP X ST cross was compatible in one direction and marginally incompatible in the other (table 5). No obvious pattern emerges with respect to geographic origin of the colonies that would allow one to predict which crosses will be compatible.

The MP and IS colonies were among the most incompatible, as indicated by the number of eggs produced combined with the number of eggs deposited that shriveled (table 5). The IS female X MP male cross yielded 46 shriveled eggs of a total of 99 eggs (47%) deposited and an average of 1.13 (±0.66) apparently normal eggs per female during the 48- to 96-hour postmating interval. The reciprocal cross also produced fewer apparently normal eggs (3.31 [±1.3] per female), as well as 10 shriveled eggs of a total of 171 (6%) deposited (table 5). However, mating success appeared normal, with 95.3% and 91.7% of females having both sperm receptacles containing spermatophores.

Table 5. SURVEY FOR POSTMATING INCOMPATIBILITY IN EIGHT RECIPROCAL CROSSES OF *M. OCCIDENTALIS* COLONIES

Colonies* ♀ x ♂	Total normal eggs	Total shriveled eggs	Mean normal eggs/♀ + (S.D.)	Mating success§	Compatible¶	Geographic origin and crop of female
AA x IS	112	3	3.02 (1.19)**	97.9	no	CA almonds
IS x AA	265	1	5.41 (0.63)	98.0	yes	WA apples
AA x LA	38	9	0.86 (0.22)**	95.9	no	CA almonds
LA x AA	201	2	4.63 (0.92)	100.0	?	CA almonds
AA x MP	55	19	1.30 (0.72)**	91.7	no	CA almonds
MP x AA	289	0	6.24 (0.82)	96.0	yes	CA pears
IS x LA	90	39	1.84 (0.57)**	100.0	no	WA apples
LA x IS	205	21	4.10 (1.14)	95.9	no	CA almonds
IS x MP	53	46	1.13 (0.66)**	95.3	no	WA apples
MP x IS	161	10	3.31 (1.30)	91.7	no	CA pears
LA x MP	292	0	6.78 (1.03)	100.0	yes	CA almonds
MP x LA	325	0	6.64 (0.22)	100.0	yes	CA pears
LA x ST	258	0	5.44 (0.41)	100.0	yes	WA apples
ST x LA	267	0	5.34 (0.37)	100.0	yes	CA almonds
MP x ST	272	5	5.55 (0.91)	93.3	?	CA pears
ST x MP	264	0	5.78 (0.60)	91.3	yes	WA apples

* AA = Almont Almonds, IS = Immature Selection, LA = Livingston Almonds, MP = McCall Pears, ST = Smith Tract; ten replicates of five females and four males were tested for each cross. Total eggs deposited was scored during a 48-hour interval beginning 48 hours after the experiment began.
+ Number of females adjusted for mortality by using midpoint of number alive at 48 and 96 hours.
§ Percentage females with both spermathecae filled
¶ Yes = more than 5 eggs per female *and* fewer than 3 shriveled eggs; ? = more than 3 shriveled eggs *or* fewer than 5 eggs per female; no = fewer than 5 eggs *and* more than 3 shriveled eggs per female.
**Means of the reciprocal crosses differ significantly at $P \leq 0.01$, group comparison t-test.

Effects of Postmating Isolation on Life Table Attributes

Comparisons of life table attributes of homogametic and reciprocal crosses of the MP and IS colonies of *M. occidentalis* are given in table 6. There were no statistically significant differences in the total number of eggs per female produced by these four crosses because variances were high, but there was a tendency for the IS female X MP male cross to deposit fewer eggs. The mean total number of eggs each female deposited over her lifetime ranged from 16.6 (IS female X MP male cross) to 23.7 (MP colony). However, the mean numbers of eggs per female per day alive were significantly different, with the IS female X MP male cross producing the fewest eggs. The mean number of live eggs deposited (eggs that hatched) per female also varied significantly, ranging from 10.8 (S.D. = 8.3) to 22.5 (15.0), with the fewest eggs produced by the IS female X MP male cross. The mean number of shriveled eggs deposited also varied significantly, ranging from 0.3 (1.0) per female for the MP colony to 5.3 (4.7) for the IS female X MP male cross. The mean numbers of apparently normal (unshriveled) eggs that failed to hatch were not significantly different among these crosses, ranging from 0.5 to 2.0 per female (table 6).

Once eggs hatched, significant differences in the mean number of immature deaths were found (table 6). The fewest immature deaths were found in the IS female X MP male cross (1.5/female). Mean total mortality of progeny (mortality of eggs and immatures) was not significantly different (table 6), but the mean numbers of adult progeny produced were significantly reduced for the IS female X MP male cross (8.6 progeny/female compared with 15.3

Table 6. POSTMATING INCOMPATIBILITY BETWEEN THE McCALL PEAR (MP) AND IMMATURE SELECTION (IS) STRAINS OF *M. OCCIDENTALIS*

♀ x ♂	Mean number/♀ (S.D.) MP x IS	IS x MP	MP x MP	IS x IS	F ratio
Total eggs	20.2 (14.5)	16.6 (12.8)	23.7 (15.2)	23.5 (17.7)	1.16
Eggs per day	1.9 a (0.7)	1.3 b (0.5)	2.5 a (0.5)	1.9 a (1.0)	11.72*
Live eggs	18.4 a (13.8)	10.8 b (8.3)	22.5 a (15.0)	20.8 a (15.3)	3.56*
Shriveled eggs	1.3 b (1.6)	5.3 a (4.7)	0.3 b (1.0)	0.7 b (1.5)	18.34*
Dead (unhatched) eggs	0.5 (0.8)	0.5 (1.1)	0.9 (2.1)	2.0 (4.7)	1.55
Immature deaths	1.8 bc (2.0)	1.5 c (2.1)	3.3 ab (3.6)	3.9 a (3.4)	3.92*
Total progeny mortality+	3.6 (2.9)	7.3 (6.9)	4.5 (4.6)	6.5 (6.8)	2.26
Total adult progeny	15.7 a (12.0)	8.6 b (6.4)	18.4 a (12.7)	15.3 a (11.3)	3.54*
♀ progeny	10.6 a (8.8)	0.9 b (1.9)	12.0 a (8.3)	8.0 a (6.6)	11.96*
♂ progeny	5.1 (3.6)	7.7 (5.7)	6.5 (4.7)	7.3 (5.4)	1.24
Sex ratio	2.1 a (1.0)	0.1 c (0.2)	2.1 a (1.3)	1.2 b (0.5)	24.40*
Last reproductive day	9.8 (5.6)	11.6 (7.3)	9.2 (5.8)	10.9 (6.9)	0.69

* Values significantly different ($P \leq 0.05$; one-way analysis of variance). Means in a row followed by different letters are significantly different (Duncan's multiple range test; LeClerg, Leonard, and Clark 1962).
+ Total progeny mortality = shriveled eggs + dead eggs + immature mortality.

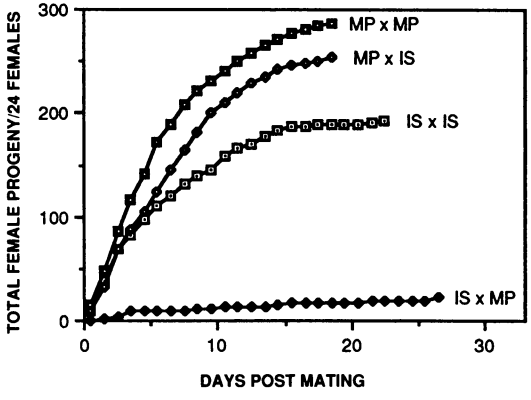

Fig. 3. Productivity of 24 *M. occidentalis* females from the Immature Selection (IS) and McCall Pear (MP) strains, and their reciprocal crosses, compared at 26° to 28° C under continuous light.

to 18.4 progeny/female in the other three crosses). These adult progeny had a highly skewed sex ratio: only 0.9 female was produced per female in the IS female X MP male cross compared with 8.0 to 12.0 females per female in the other three crosses (table 6). The mean numbers of male progeny produced were not different: 5.1 to 7.7 produced per cross. The sex ratios, as expected, were significantly different: 0.1 female:1.0 male was produced in the IS female X MP male cross. The IS colony produced 1.2 females:1.0 male, which is significantly different from the MP colony and the MP female X IS male cross. Both the MP colony and the MP female X IS male cross produced 2.1 females:1.0 male.

The 24 females in each of these four crosses were monitored daily until they died. Females deposited their last egg an average of 9.2 to 11.6 days after males were added; this was not significantly different among the crosses (table 6). Some females in each cross lived an unusually long time after they deposited their last egg. Thus, females died 0 to 63 days after depositing their last egg. In the IS X IS crosses, 12 of 24 females had more than four postreproductive days; 11 of 24 females in the IS female X MP male cross had a postreproductive interval longer than four days. Only five MP colony females had a postreproductive interval longer than four days, and seven MP females mated with IS males exceeded four postreproductive days.

Postreproductive intervals longer than approximately three days are unusual for *M. occidentalis*. It is unclear whether there is any significance to the fact that the IS females appear to have longer postreproductive intervals than MP females. Long postreproductive intervals may be due to the fact that females were supplied with only one male during this experiment; once that male died, he was not replaced. Since some *M. occidentalis* females need to mate more than once to deposit a full complement of eggs, some females may have terminated egg deposition prematurely (Hoy and Smilanick 1979; Hoy, unpublished). The postreproductive females that lived up to 63 days probably would have deposited a few more eggs and died within two to three days had a second male been added to the leaf disks shortly after they stopped depositing eggs. Longevities of 63 days are unusual, except for females that are in a photoperiodically induced reproductive diapause (Hoy and Flaherty 1970).

The cumulative number of female progeny per 24 females is shown in figure 3. The IS female X MP male crosses produced the fewest female progeny, while the MP colony produced the most. The MP female X IS male and the IS colony produced intermediate numbers of female progeny.

The differences in reproductive compatibility of these different crosses had a profound impact on life table statistics (table 7). The net reproductive rate (R_o) of the IS female X MP male cross was only 0.92, compared with 10.58 for the reciprocal cross and 11.96 and 8.04 for the MP and IS colonies, respectively. The mean generation time of the IS female X MP male cross was 16.9 days compared with 11.1 for the reciprocal cross and 10.4 and 10.6 for the MP and IS colonies, respectively. The intrinsic rate of natural increase (r_m) for the IS female X MP male cross was zero. For the MP female X IS male cross, it was 0.213, and for the MP and IS colonies, r_m was 0.238 and 0.196, respectively.

DISCUSSION

Premating behavior patterns are highly variable in the five colonies of *M. occidentalis* tested as well as among reciprocal crosses between these colonies (fig. 1, 2, table 1). The male may approach the female from the front, side, or rear, and males may move under the female by crawling down either the sides or posterior of the opisthosoma. There were no consistent

Table 7. SUMMARY OF LIFE TABLE STATISTICS FOR SAME STRAIN AND RECIPROCAL CROSSES OF THE McCALL PEAR (MP) AND IMMATURE SELECTION (IS) COLONIES OF *M. OCCIDENTALIS* AT 24° TO 26°C UNDER CONTINUOUS LIGHT

♀	MP	IS	MP	IS
x	x	x	x	x
♂	IS	MP	MP	IS
Net reproductive rate (R_o)	10.58	0.92	11.96	8.04
Mean generation time (T)	11.07	16.90	10.44	10.61
Intrinsic rate of natural increase (r_m)	0.213	0	0.238	0.196
Days for population to double(D_T)	3.25	—	2.92	3.53
Sex ratio (♀ : ♂)	2.07	0.12	1.85	1.10

differences in patterns among the different colonies, however, to suggest that significant premating isolation might be present (Hoy and Cave 1985; this paper). Premating behavior in *M. occidentalis* is thus much less stereotypical than the behavior patterns described for *Phytoseiulus persimilis* Athias-Henriot and *Amblyseius andersoni* (Chant) by Amano and Chant (1978).

Premating isolation could be due to preferences by males or females for individuals that are different in size, exhibit different activity patterns, or produce different chemical cues, or to combinations of these and other unknown characteristics. Adult virgin, mated, and deutonymphal females of *M. occidentalis* produce a contact sex pheromone (Hoy and Smilanick 1979). The chemical nature of the sex pheromone is currently unknown. It is also unknown whether variability in sex pheromone quantity or quality occurs among different populations and could thus influence mating success.

Selection to enhance premating isolation between ST females and MP males yielded no apparent selection response. The reasons are unknown but could be a lack of genetic variability for premating behavioral isolating mechanisms, insufficient numbers of selections on traits that are polygenically determined, selection of inappropriate colonies, or inappropriate selection criteria.

Postmating isolation among different colonies of *M. occidentalis* was found in five of eight pairs of reciprocal crosses, and these incompatibilities were generally more extensive in one of the reciprocal crosses than the other (tables 5, 6, and 7). The incompatibilities resulted in reduced numbers of eggs deposited, deposition of shriveled eggs that failed to hatch, reduced numbers of female progeny, and a highly skewed sex ratio in favor of males (tables 6 and 7). In the IS female X MP male cross, the net reproductive rate was dramatically reduced (to 0.92) with an intrinsic rate of natural increase of zero (table 7). If the IS colony, which is permethrin resistant, were released into a pear orchard where native permethrin-susceptible *M. occidentalis* behaved like the MP colony, loss of permethrin resistance would be unlikely, whether or not permethrin was applied. Unfortunately, it is difficult to predict which crosses will be partially reproductively incompatible (table 5), because geographic proximity alone does not provide a useful clue. However, it is clear that partial postmating isolation is widespread, although the degree exhibited among different reciprocal crosses is variable (tables 5, 6, and 7).

The causes of the postmating isolation are unknown. Females appear to have normal spermatophores deposited within their sperm receptacles. Likewise, there is no obvious deformity of the sperm receptacles in the females. The fact that homogametic crosses generally produce normal numbers of progeny suggests that males deposit normal quantities and nor-

mal quality of sperm. Reproductive incompatibility could be due to lack of penetration of eggs by sperm, lack of syngamy, incompatible sperm and egg cytoplasm, or incompatible genomes. *Metaseiulus occidentalis* is parahaploid, and all eggs must be fertilized if development is to occur (Hoy 1979; Nelson-Rees, Hoy, and Roush 1980; Hoy and Cave 1986). Early in embryogenesis of male progeny, half the chromosomes are heterochromatinized and extruded from the nucleus (Hoy 1979; Nelson-Rees, Hoy, and Roush 1980). Based on pesticide resistances as markers, it appears that the extruded chromosomes are paternal in origin (Hoy 1985b; Hoy and Standow 1982). The fact that normal numbers of males are produced in the IS female X MP male cross (table 6) suggests that sperm from the MP male is effective in initiating development of the eggs that eventually become males after the paternal genome has been eliminated.

The fact that few females develop successfully in these incompatible crosses could be due to either chromosomal or cytoplasmic factors. Normal development of females requires the functioning of both chromosome sets; in these incompatible crosses, the maternally and paternally derived chromosomes may be unable to function together to produce normal adult females. Because normal numbers of males are produced but very few females, the dead and shriveled eggs are probably nearly all females. The deposition of shriveled eggs suggests that female development may proceed for awhile before the female embryo dies, yielding shriveled eggs (table 6). However, reproductive incompatibility has often been found to be due to cytoplasmic factors, and this could be true in *M. occidentalis*. Our data do not allow us to discriminate among these hypotheses.

Reproductive incompatibility has been found in other species of mites. Incompatibility between local populations of the spider mite, *Tetranychus urticae* Koch, is common; sometimes populations from adjacent glasshouses are incompatible. Typically, a proportion of the F_1 females fails to deposit eggs or produces only a few eggs, and some of the eggs produced are inviable. As a rule, this incompatibility is not complete, varying from slight to almost complete, and if hybrids are propagated through inbreeding, the fertility usually improves in later generations for unknown reasons (deBoer 1982). DeBoer (1982) speculated that both chromosomal and extrachromosomal factors are involved in these incompatibilities. He suggested that, because many spider mite populations are founded by a single inseminated female and remain isolated for many generations, the likelihood that the semi-incompatible populations are maintained is enhanced.

Incompatibility between a number of arthropod species involves bacterial or viral symbiotes. For example, Yen and Barr (1973) found that cytoplasmic incompatibility in the mosquito *Culex pipiens* L. was due to the rickettsia-like symbiote *Wolbachia pipientis*. Likewise, Kellen, Hoffmann, and Kwock (1981) found that a species of *Wolbachia* was the causal agent of cytoplasmic incompatibility between strains of the almond moth *Ephestia cautella* (Walker). Hess and Hoy (1982) found two morphologically distinct forms of rickettsia-like organisms in the tissues of *M. occidentalis*; one, type A, was found in all the mites examined and did not appear to be associated with a pathogenesis. The second, type B, was found in approximately two-thirds of the mites examined, was both intracellular and extracellular, and was found in all ovaries and eggs of infected individuals, suggesting that transovarial transmission might occur. Mites considered diseased had a rectal plug, deposited few eggs, and were unable to walk normally; type B organisms were found throughout the body cavity and tissues. Sutakova and Ruttgen (1978) also described a polymorphous rickettsia, *Rickettsiella phytoseiuli*, in another phytoseiid mite *Phytoseiulus persimilis*. The relationship between these microorganisms and reproductive incompatibilities in phytoseiid populations is cur-

rently unknown; no experiments have been conducted with antibiotics or heat (which may eliminate the microorganisms) to determine whether the "diseases" or reproductive incompatibilities can be cured.

Single inseminated females of *M. occidentalis*, like *T. urticae*, can found new isolated populations that could remain isolated for many generations. Furthermore, *M. occidentalis* can tolerate the subsequent inbreeding with little apparent negative effect (Hoy 1977). Results from surveys of organophosphate and sulfur resistances in *M. occidentalis* from pear and almond orchards and vineyards in California, and the relatively slow dispersal of the carbaryl-resistant strain from release sites in almond orchards to adjacent orchards, support the hypothesis that *M. occidentalis* populations in California are genetically diverse and not panmictic (Hoy and Knop 1979; Hoy 1982, 1985; Hoy and Standow 1982; Hoy, Groot, and van de Baan 1985). Whether these different populations also differ in their ability to control spider mites is unknown; the efficiency of different predator colonies has not been compared.

Future efforts to enhance reproductive isolation between different populations of *M. occidentalis* as a component of a genetic improvement project should probably focus on postmating rather than premating isolating mechanisms. While mating behavior is variable within and between colonies of *M. occidentalis*, there did not appear to be qualitative differences among the colonies; the failure to obtain a selection response for premating isolation indicates that exploiting premating isolating mechanisms would be more difficult. In contrast, the degree of postmating reproductive isolation, in some crosses, resulted in dramatically reduced numbers of progeny. The manipulation of postmating isolating mechanisms could possibly have practical implications if we could identify the mechanisms.

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sented here and other data previously obtained on dispersal rates, discreteness of pesticide-resistant populations, and differences in diapause attributes of geographic strains indicate that *M. occidentalis* is subdivided into distinct populations, some of which are partially reproductively isolated from others through postmating isolating mechanisms. No clear pattern has emerged, however, that would allow us to predict which populations are completely compatible. Populations that are geographically distant may show little reproductive isolation, while others that are adjacent may be partially reproductively isolated, and differences may occur between reciprocal crosses. In the case of the permethrin-resistant strain (IS), the degree of reproductive isolation after release into orchards or vineyards that contain native *M. occidentalis* cannot be predicted. It would be desirable to have such reproductive isolation, because permethrin resistance is polygenically determined in this colony and outcrossing can result in loss of resistance. Thus, IS (permethrin-resistant) populations released into North American orchards or vineyards will have to be maintained as pure populations through selection with permethrin rather than through reproductive incompatibility because of our inability to predict whether postmating isolation will occur.

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