

SEXUAL BEHAVIOR OF *Matsucoccus josephi*
(HOMOPTERA: MARGARODIDAE)
Asynchronous Adult Male Emergence
and Release of Female Sex Pheromone¹

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(Received October 10, 1989; accepted February 5, 1990)

Abstract—The daily emergence patterns of *Matsucoccus josephi* adults and third-instar male larvae raised on artificially infested saplings of *Pinus halepensis* were determined. A single peak of emergence was found for adult males between 0300 and 0500 hr. Adult females emerged throughout the day, with maximum emergence between 0500 and 0700 hr. Two daily emergence periods were observed in third-instar male larvae, one between 0300 and 0900 hr and the other between 1700 and 2100 hr. Airborne pheromone emitted by adult virgin females was collected using a flow system. No significant differences were recorded in the attraction of the male to crude pheromone collected at different times of day. A single female, virgin or half an hour after mating, was sufficient to attract the males in an olfactometer system. From minor differences in pheromone release throughout the day, and from the lesser degree of attraction by females half an hour after mating, it is assumed that there is no mechanism controlling the daily release of the female sex pheromone. Reduction of pheromone emission after mating is suggested.

Key Words—*Matsucoccus josephi*, Homoptera, Margarodidae, sexual behavior, pheromone release.

¹Contribution from the Agricultural Research Organization, The Volcani Center, Bet Dagan, Israel. No. 2743-E, 1989 series.

INTRODUCTION

The Israeli pine bast scale *Matsucoccus josephi* Bodenh. and Harpaz is the most noxious pest of *Pinus halepensis* Mill. and *P. brutia* ssp. *eldarica* (Medw.) Nahal in Israel (Mendel, 1987). The scale occurs on all aboveground parts of the tree. During feeding it secretes a poisonous saliva that disrupts the water transport in the tree and frequently causes its death (Mendel and Liphschitz, 1988). In its latent phase the scale population occurs mainly on the partly scaly bark section of the stem, whereas during the epidemic phase it infests most of the shoots (Golan et al., 1983).

The feeding stage of the male in the genus *Matsucoccus* is shorter than that of the female. At the end of the feeding period the male develops into a third-instar larva that leaves the feeding spot to look for a pupation site, the forest floor in the case of *M. josephi* (Bodenheimer and Neumark, 1955; Mendel et al., 1989). The emergence of the adult males is synchronous with that of the adult females and is usually related to the temperature and its effect on the pine host (Mendel et al., 1990; Riom and Fabre, 1977). Like several other species of *Matsucoccus*, the adult males emerge from the litter to fly or walk on the stem and crown in search of emerging females (e.g., Golan et al., 1983; McKenzie, 1942; Riom and Fabre, 1977; Unruh, 1985). Most known species are attracted to the female sex pheromone, a phenomenon first recorded by Doane (1966) in the males of the red pine scale, *M. resinosa* Bean and Godwin. Evidence of its presence has since been demonstrated in several *Matsucoccus* spp. (Sternlicht and Dunkelblum, unpublished; Young and Qi, 1983; Young et al., 1984; Park et al., 1986) and was identified for *M. resinosa*, *M. matasummuriae*, and *M. thumbergiana* (Lanier et al., 1989).

The biology and morphology of males and females of the more common *Matsucoccus* species (Beardsley, 1968; Bodenheimer and Neumark, 1955; Boratinski, 1952; Ray, 1982; Siewniak, 1976) and male morphology of several fossil species (Koteja, 1984) are known. The adult males live about half a day (Beardsley, 1968; Mendel et al., 1989; Siewniak, 1976; Riom and Fabre, 1977) and females for several days and even several weeks (e.g., Bodenheimer and Neumark, 1955; Riom and Fabre, 1977). Females may be inseminated during the first 10 days after emergence (Bodenheimer and Neumark, 1955). However, little is known about the daily emergence pattern of the adults and their sexual behavior.

The objectives of the present study were to elucidate several unfamiliar aspects of the reproductive biology of *Matsucoccus*: the release pattern of sex pheromone in *M. josephi*, and the emergence pattern of the adults. This provided also the opportunity to study the emergence pattern of third-instar male larvae.

METHODS AND MATERIALS

Emergence Pattern. The emergence pattern of adult females and third-instar male larvae was determined by collections from 15 two-year-old saplings of *P. halepensis* growing in black polythene bags and infested with *M. josephi* ovisacs a month earlier. Each sapling was placed into a plastic tray (40 × 30 × 10 cm) lined with a sheet of paper. The emerging insects were removed from the plant or the tray with a fine brush and counted. The emergence pattern of the adult males was determined by counting the individuals emerging from masses of pupae collected from saplings and others kept in Petri dishes. The plants were maintained in a greenhouse under natural light with continuous temperature recording (Figure 1). Emerging scales were then collected at 2-hr intervals for three days, beginning at noon on June 29.

Airborne Pheromone Collection. Airborne pheromone emitted by adult virgin females of *M. josephi* was collected using a flow system. The scales were obtained from a mass rearing (Mendel et al., 1989). Two systems (A and B) were operated. In each system the females were maintained on Whatman No. 1 filter paper in three glass tubes closed at both ends with a copper wire screen. The tubes were placed in a glass cartridge. The cartridge was installed between a U-shaped tube containing active charcoal to purify the incoming air and a 50–80 mesh Porapak Q column (130 mm long × 10 mm diam. containing 1 g adsorbent) to trap the pheromone. The Porapak Q trap was connected to a small pump (Charles Austin Pumps, Weybridge, England) through a Dwyer flow meter equipped with a control valve. Air was drawn through the system at a rate of 1 liter/min. No significant breakthrough of pheromone was observed in this system. This was shown in an earlier experiment by adding a second Porapak Q column in line; bioassays proved that almost all active material was trapped in the first column (Z. Mendel and E. Dunkelblum unpublished). On July 29, system A was operated with 473 females, consisting of two groups: the first of 300 scales that had emerged after midnight and mainly during the early morning, collected around 0700 hr, and the second consisting of 173 females collected the previous morning (July 28). They were stored for 24 hr at 6°C. System B contained 321 tested females that had emerged in the early morning and were collected around 0700 hr. System A was operated for three days from 0330 hr on July 29 until 1230 hr on August 1. System B was operated for two days from 0830 hr on July 30 to 1230 hr on August 1. The Porapak column in each system was changed every 4 hr. Both systems were run at 26 ± 2°C under natural light. Lack of ovisacs indicated that the females were virgin. Every 4-hr collection was considered as a sample unit.

The adsorbed pheromone was eluted from the Porapak Q traps with 8 ml

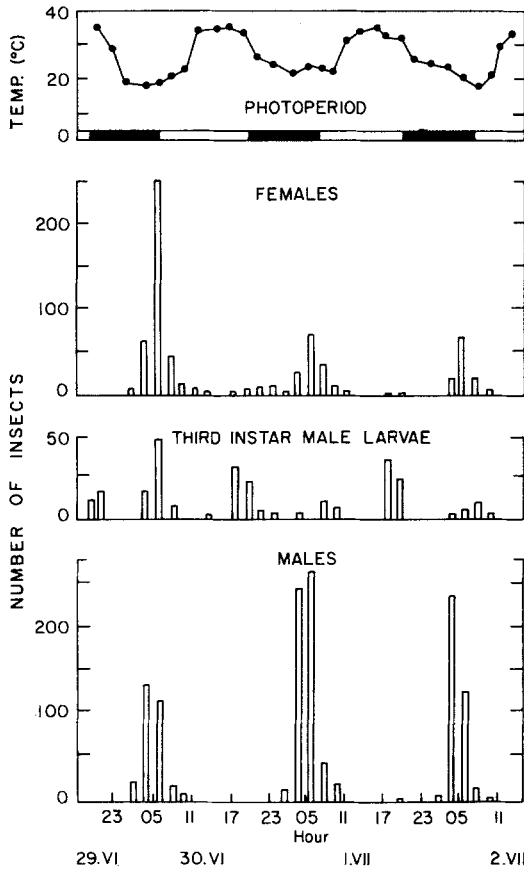


FIG. 1. Daily emergence pattern of adult females, adult males, and third-instar male larvae of *Matsucoccus josephi* in relation to the thermoperiod and the photoperiod (black: darkness).

distilled diethyl ether until 5 ml extract was collected. One milliliter of hexane was added to the ether extract, and the solution was concentrated to 1 ml at room temperature. For reuse, the Porapak Q columns were washed with 15 ml hexane and dried with a stream of nitrogen gas.

Tests of Attraction of Males to Airborne Pheromone Collections. Attraction of adult males to the crude pheromone extracts was tested in glass petri dishes (14 cm diam.). The Petri dishes were placed on white paper under diffuse overhead light at 19°–23°C. The samples of pheromone solution (10 μ l equivalent to five females) to be tested were applied to a double disk (7 mm diam.) of filter paper. After 5 min, the disk was placed in the Petri dish.

In experiment 1 we compared the attraction of the males, in a choice test, to six pheromone samples collected at different times (viz. 4-hr collections) during the first 24 hr of operation in system A. The six pheromone-treated disks were placed at even intervals around the wall of the Petri dish. Eight to 20 adult males, which had emerged in the early morning, were introduced into the dish using a fine brush. They were observed for 45 or 60 min. The number of males displaying courtship or mating behavior on any of the disks was recorded. This behavior was characterized by a typical dance on and around the disk and by attempts to inseminate the filter paper. The test was repeated 12 times.

In experiment 2 we used the same set-up as in experiment 1, but with only four disks per Petri dish: one impregnated with the tested extract and three control disks. The six 4-hr Poropack collections, each obtained from three or five columns (from different days and systems), were tested with five replications. The tests were conducted from 0630 to 1130 hr, using 10 adult males for each replicate. A total of 1000 males were used for the entire experiment. During that time the number of males displaying courtship or mating behavior on the disks was recorded every 30 min (a total of 10 observations).

Olfactometer Bioassays. Pheromone bioassays were conducted, using a modified version of an olfactometer used by Schlyter and Lofquist (1985), to compare the attraction of adult males to virgin and mated females. The system consisted of an entry chamber, where the males were released, followed by a Y tube with either the airborne pheromone or clean air (control). Pheromone effluvia and air were drawn by a vacuum pump from the two chambers, one of them containing females. The males were allowed to advance to the point of division and to select the branch leading to the pheromone or control chamber. Females were verified as mated or virgin by the presence or absence, respectively, of ovisacs. The mated females had been fertilized 30 min prior to the experiment.

RESULTS

Emergence Patterns. The adult males started to emerge at 0200 hr, with a single peak of emergence recorded between 0300 and 0500 hr and the last individuals emerging around 1000 hr. On a single occasion, two males (0.14% of the total) emerged between 1900 and 2100 hr (Figure 1). Emergence of females was observed in various numbers at most hours of the day, with a maximum emergence occurring between 0500 and 0700 hr. The females usually did not emerge in the afternoon, and only small numbers were collected during the first half of the night (Figure 1); approximately 3% of all the females emerged between 1230 and 0300 hr.

The daily emergence periods were observed for the third-instar male lar-

vae, one in the early morning between 0300 and 0900 hr and the other in the evening between 1700 and 2100 hr (Figure 1).

Attraction to Airborne Pheromone Collections. As shown in Tables 1 and 2, no marked differences were recorded in the attraction of males to airborne pheromone extracts collected at different times. In experiment 1 (Table 1) the sample collected between 0430 and 0830 hr was the most attractive (16.7% of the males); about half the males did not respond to any of the collections (Table 1). In experiment 2 (Table 2), males were almost equally attracted by all extracts, there being no marked differences between number of counts per treatment (number of times males displayed courtship or mating behavior with disks containing the sex pheromone from six collection periods). Only a small, but significant ($P < 0.05$) difference was found between the highest and lowest values, samples collected during 0030–0430 hr (22.8 counts), and 2030–0030 hr (15.7 counts), respectively.

Olfactometer Bioassay of Virgin vs. Mated Females. One single female, virgin or half an hour after mating, was sufficient to attract the male in the olfactometer system, whereas the control failed to attract any males (Table 3). In general, the attraction of males to virgin females was significantly ($P < 0.05$) greater than that of the mated females, but differences between the two groups were small. The relatively weak response in the tests of five virgin females and 15 mated females, 21% and 19%, respectively, was most probably due to the advanced age of the males in these tests (Table 3).

DISCUSSION

The emergence patterns of adult males and females of *M. josephi* are more or less synchronus. Although peak emergence of the males occurs 2 hr earlier than that of the females, the male may need this time to complete the emergence process and to locate host trees and females. This time gap may allow males to fly over long distances through the forest and reach other infested foci. Most females (97%) emerge during the time of the males' flight period. Thus, copulation is achieved on the emergence day, or at the latest, the next morning. Females of *M. feytaudi* display a similar emergence pattern, whereas male eclosion occurs between 1000 and 1600 hr (Riom and Fabre, 1977).

In the warm season, encounters between sexes occur during the early morning, when low temperature and high humidity enable the adult males of *M. josephi* to survive for many hours. From preliminary observations it seems that *M. josephi* males emerge and couple at temperatures above 9°C (Z. Mendel, unpublished). The low-temperature thresholds for flight of the male of the California red scale *Aonidiella aurantii* (Maskell) and the San Jose scale *Quadraspidiotus perniciosus* (Comstock) (Homoptera: Diaspididae) are 15–18°C (Rice and Moreno, 1970) and 16°C (Rice and Hoyt, 1980), respectively. In these

TABLE 1. NUMBER OF MALES (% OF TOTAL IN PARENTHESIS) ATTRACTED TO FEMALE SEX PHEROMONE COLLECTED AT DIFFERENT HOURS OF THE DAY^a

Time of the test (hr)	Number of tests	Total number of males	Time of pheromone collection (hours)								Males not responding to pheromone
			0030-0430	0430-0830	0830-1230	1230-1630	1630-2030	2030-0030			
0815-0900	6	64	4 (6.2)	1 (1.6)	1 (1.6)	7 (10.9)	8 (12.5)	12 (18.7)	31 (48.4)		
0930-1030	3	57	2 (3.5)	19 (33.3)	2 (3.5)	5 (8.8)	5 (8.8)	2 (3.5)	22 (38.6)		
1200-1245	3	32	0 (0)	5 (15.6)	0 (0)	1 (3.1)	0 (0)	7 (21.9)	19 (59.4)		
Overall total ^b	12	153	6 (3.9)b	25 (16.7)a	3 (2.0)b	13 (8.5)ab	13 (8.5)ab	21 (13.7)a	72 (47.1)		

^aThe experiment was conducted as a six-choice test in Petri dishes (for more details see text).

^bWithin the line means followed by the same letter are not significantly different (chi square test of *k* independent samples, Siegel, 1959).

TABLE 2. MEAN NUMBER OF MALES (COUNTS) ATTRACTED TO FEMALE SEX PHEROMONE COLLECTED IN DIFFERENT HOURS OF THE DAY^a

Collection interval (hr)	Male attraction	
	Number of tests ^b	Mean number of male counts
0030-0430	15	22.8 a ^c
0430-0830	15	19.7 ab
0830-1230	25	20.3 ab
1230-1630	15	20.6 ab
1630-2030	15	16.9 ab
2030-0030	15	15.7 b

^aEach test involved 10 males in a Petri dish with four disks: one impregnated with the test pheromone extract and three controls. The males did not respond to the control disks.

^bThe tests were conducted between 0630 and 1130 hr.

^cWithin column, means followed by the same letter are not significantly different ($P < 0.05$), Duncan's (1955) multiple range test.

TABLE 3. OLFACTOMETER ATTRACTION OF MALES TO VIRGIN AND MATED FEMALES OF *Matsucoccus josephi* VS. BLANK CONTROLS

Test object (no. of females)	Date	Hour	Number of males	Number (%) of males		
				Selecting female	Selecting the blank control	Failed to reach the dividing point (no response)
Virgin						
35	July 22	0945-1100	31	21 (68)	0	10 (32)
15	July 28	0915-1045	36	32 (89)	0	4 (11)
5	July 29	1345-1530	39	8 (21)	0	31 (79)
1	July 29	0700-0900	31	31 (100)	0	0
Combined (overall mean)				(67) ^a		
Mated						
15	July 28	1100-1200	42	8 (19)	0	34 (81)
5	July 29	0915-1115	22	16 (74)	1 (4)	5 (23)
1	July 30	0845-1015	33	17 (52)	0	16 (48)
Combined (overall mean)				(42) ^a		

^aThe overall treatment means (virgin vs. mated) were significantly different ($P < 0.05$) (determined by ANOVA; SAS Institute, 1982).

cases the onset of flight at a relatively high temperature may explain why most of the flight of males occurs during the afternoon (San Jose scale) or evening (California red scale) (Rice and Hoyt, 1980; Rice and Moreno, 1970). In another group of scale insects, the mealybugs (Homoptera: Pseudococcidae), in California and in Israel most males of *Planococcus citri* (Risso) were caught in pheromone traps between 0500 and 0800 hr, mainly during the first 2 hr after sunrise (Moreno et al., 1984; Tauber 1987). In Sardinia, two flight periods for males of *P. citri* were recorded: the main one in the early morning and the other one in the evening (Ortu and Delrio, 1982). The flight of the males of *Pseudococcus calceolariae* (Maskell) in Italy continues throughout the daylight hours with two clear peaks, the main one being around sunset (Rotundo and Tremblay, 1976). The males of *P. citri* fly at temperatures above 16°C, a threshold coinciding with that of the above diaspidids. McLaughlin and Ashley (1977) suggested that the emergence rhythm of the males of the white peach scale *Pseudaulacaspis pentagona* (Targioni-Tozzetti) is modified daily by the prevailing temperature cycle, apparently to ensure maximum survival and mating by the short-lived males.

Another factor that may affect the diurnal course of flight of the males is wind velocity. There are usually no strong air currents in the early morning that might confuse the flight of the males of *M. josephi* towards the pheromone sources. For example, males of the California red scale are unable to fly upwind to a pheromone source when air velocity exceeds 1 mph (Rice and Moreno, 1970); males of the San Jose scale achieve active flight at wind velocities of less than 4 mph (Rice and Hoyt, 1980). Males of *M. pini* (Green) usually couple on the lee side of the stem (Siewniak, 1976). Although the dimensions of the males of *Matsucoccus* are larger than those of diaspidids or pseudococcids, the former need to move relatively long distances to locate the females, whereas the latter two groups may find the first female at a distance of a few millimeters.

The third-instar male larvae of *M. josephi* migrate from the canopy and the stem during the same hours as the adults, and also in the late evening. Thus, there are two daily emergence periods, both under optimal temperature and humidity conditions.

Most insect species characteristically mate during a specific period of the day (Shorey, 1974). Among Lepidoptera, many species release their sex pheromone or respond to the attractant at a particular time of day and display a typical mating rhythm with seasonal shifts due to changes in temperature and photoperiod (Roelofs and Cardé, 1974; Shorey, 1974). However, some species such as the silkworm, *Bombyx mori* (L.), release the sex pheromone shortly after emergence until copulation or deposition of unfertilized eggs (Steinbrecht, 1964). Continuous release of sex pheromone is prevalent in scale insects. Rotundo and Tremblay (1980) investigated the sex behavior of *P. citri* and *P.*

calceolariae and found that pheromone release is uninterrupted until copulation takes place. In the present study, the behavior in *M. josephi* was similar. Release of sex pheromone throughout the day suggests that the females are ready to mate at all hours. They attract the males and are ready for insemination even before completing their emergence from the exuviae of the second-instar larvae (Z. Mendel, unpublished). Minor differences in pheromone release throughout the day may explain the minor preference of some pheromone collections when all samples were examined in the six-choice test (Table 1). In *M. josephi*, *P. citri*, and *P. calceolariae*, sex pheromone release does not coincide solely with flight of the males. Hence, we assume that the absence of a mechanism controlling the daily rate of pheromone release during the preinsemination period of females from two different families, Pseudococcidae and Margarodidae, may be an indication of a general phenomenon among members of the Coccoidea superfamily.

Reduction of sex pheromone release after mating, which is a general phenomenon in the Insecta, was noted by Tashiro and Moffitt (1968) in the California red scale. The female of this scale ceases to be attractive within 24 hr after mating, while virgin females remain attractive for 84 days. In *M. josephi* the female may attract males during 10 days after emergence (Bodenheimer and Neumark, 1955). We found that half an hour after mating, the female still attracts males, but to a lesser degree than virgins, suggesting reduced pheromone release.

Acknowledgments—The authors express their thanks to Mrs. Fabienne Assael (Department of Entomology, ARO) for her help. The study was partly supported by the Jewish National Fund as project No. 131-0509.

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