SEASONAL CHANGES IN RESIGHTINGS OF MARKED, WILD RHAGOLETIS POMONELLA (DIPTERA: TEPHRITIDAE) FLIES IN NATURE

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ABSTRACT

We observed individually marked, wild male and female apple maggot flies (AMF) on a host apple tree for 24 days. Although we resighted a fairly high proportion (30.6%) of 599 marked flies, we observed most flies (74.9%) only during the first week after marking and release. Following the onset of reproductive maturity, as evidenced by mating and oviposition, we saw males over more consecutive days than females. This presumably occurred due to male arrestment following contact with female marking pheromone deposited on fruit. Peak die time of mating by unmarked flies corresponded more closely with peak time of observation of marked males rather than marked females. We estimate some adult AMF may live up to 4 weeks in nature.

RESUMEN

Nosotros observamos por 24 días a machos y hembras salvajes de la manzana (AMF) marcadas individualmente en un árbol hospedero de manzanas. Aunque vimos de nuevo una proporción bastante alta (30.6%) de 599 moscas marcadas, observamos la mayoría de las moscas (74.9%) solamente durante la primera semana después de marcadas y sueltas. Seguido a comienzo de madurez reproductiva, demostrado por el apareamiento y la puesta de huevos, nosotros vimos los machos más días consecutivos que las hembras. Esto corrió presumiblemente debido a la cohibición de los machos después del contacto con feromonas depositadas por hembras en la fruta. El auge del tiempo de apareamiento de las moscas no marcadas correspondió más al auge del tiempo de observación de machos marcados que a hembras marcadas. Nosotros estimamos que algunos adultos de la mosca de la manzana pudieran vivir hasta 4 semanas en la naturaleza.

The apple maggot fly (AMF), Rhagoletis pomonella (Walsh), is a well-known pest of apples in northeastern North America and, in recent years, has been detected in many western regions, including California (Joos et al. 1984). This fruit-parasitic tephritid fly has attained its pest status primarily due to expansion of its host range from...
the native host, hawthorn (*Crataegus* spp.), to fruits more desirable for human consumption, such as apple, pear, and sour cherry (Boller & Prokopy 1976).

Scientific interest in this fly extends beyond the realm of immediate pest control to include empirical studies of physiology, behavior, and ecology (Dean & Chapman 1973, Doller & Prokopy 1976, Prokopy & Roitberg 1984). The AMF has proven to be an excellent subject for studies of foraging behavior (Prokopy & Roitberg 1987), visual ecology (Owens & Prokopy 1986), resource utilization (Reissig 1979, Averill & Prokopy 1987), and sexual selection (eg. Prokopy & Bush 1973, Opp & Prokopy 1986). Nevertheless, large gaps in our knowledge of the behavior and ecology of this fly in its natural environment still exist. For instance, we have yet to determine details of dispersal in relation to food, oviposition site, and mate foraging behaviors. In addition, we know little about individual variation in fly behavior over the host fruiting season in nature.

We undertook this study of marking and releasing wild AMF in nature to attempt to answer such basic questions as: How long will an individual fly remain on the same host tree? Does this residence duration differ between the sexes and change over the fruiting season of the host? Does the onset of reproductive maturity following eclosion affect residence duration?

**METHODS**

Site.—In early June, 1984, we chose a small, Early MacIntosh variety apple tree in an unsprayed apple orchard naturally infested with AMF on the campus of the University of Massachusetts, Amherst (Fig. 1). We pruned the tree, thinning the leaves so that all branches were clearly visible to an observer standing either on the ground or on a 2.5m ladder. By mid-July, 1500 apples were ripening on this tree, whose canopy was ca 5m tall X 5m diam. The two Early MacIntosh variety apple trees in closest proximity to the pruned tree (canopies within 2m) bore few or no fruit that season. In

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Fig. 1. Arrow denotes location of observation tree (O) in relation to other Early MacIntosh (E), MacIntosh (M), and Cortland (C) variety apple trees at Orchard Hill, University of Massachusetts, Amherst.
addition, trees of a later fruiting variety (MacIntosh) in the adjacent row (canopies ca 5m away) bore few or no fruit that season. The closest fruiting trees (Cortland) that season were located two rows away (ca 12m).

Marking Individuals.—The observation tree was checked daily until the first newly emerged adult AMF was sighted on June 24. Then, using mouth aspirators, we collected flies daily from the tree for 12 days (until July 5). These flies were brought to the laboratory for sex determination, measurement, and marking. Size was determined by measuring the length of the dorsal mesothorax using an eyepiece micrometer on a dissecting microscope. Each fly was immobilized briefly on ice and was marked individually with dots of one or two colors of Liquid Paper™ on the dorsum of the thorax. A symbol was then written on the Liquid Paper with a waterproof black felt pen (see Walker & Wineriter 1981). Preliminary laboratory studies had indicated that marks applied in this manner were non-toxic to the flies, yet were waterproof and durable. By using four colors singly and in two color combinations along with 49 different symbols, we were able to develop over 300 unique marks. Although we marked and released 327 female and 272 male AMF, not all flies seen on the observation tree over the course of the experiment were marked, either because they eluded capture or because they emerged or flew to the observation tree following the 12-day period of collection and marking. We released all marked flies on leaves of the observation tree at dusk on the day of collection.

Observations.—For 24 days after the first day on which flies were captured and released (i.e. until July 18), we censused the tree for marked flies. Censuses were conducted at one hour intervals between 0900 and 1700 hours when ambient temperature was above 21°C and below 33°C (the approximate activity thresholds of the flies) (Prokopy et al. 1972, Johnson 1988), except during periods of heavy rain. During the census periods, we also recorded the numbers of pairs of unmarked AMF in copula on the observation tree. We accumulated 148 census-hours over the 24-day period for an average of 6.2 census-hours per day.

To ensure that all portions of the observation tree were evenly censused for flies, we divided the tree into 8 approximately equal-area sections based on the natural limb structure of the tree. Leaves, fruit, and branches were examined for 5 min per section. With this method, we were confident that all areas of the tree were inspected each hour except the top sides of leaves located in the top 10% of the canopy.

Statistics.—To test for differences in resighting frequencies between the sexes and over the season, we used G-tests with Yates's correction for continuity on frequencies (see Sokal & Rohlf 1981). We used t-tests for unequal variances to assess both the differences in total numbers of days in which flies of each sex were sighted and the influence of fly size on mating and resighting.

RESULTS

Of the 599 marked AMF which were released, we saw 183 (30.6%) at least once during the 24 days of censure. The great majority of these flies (137 of 183; 74.9%) were seen only during the first week of observation. The remainder (46 of 183; 25.1%) were seen during the first week but then were absent for an intervening period of 1-2 weeks before resighting. We did not see equal proportions of marked male and female flies; significantly more marked males were seen (100 of 272; 36.6%) than marked females (83 of 327; 25.4%) (G = 8.52 with Yates's correction; p<0.001). Multiple sightings of males over time were also more common than of females; whereas only 4% of females were seen on more than two consecutive days, 24% of males were seen on more than two consecutive days. Thus, on average, individual males were seen over more days
(mean = 2.18 days; S.E. = 0.27) than females (mean = 1.37 days; S.E. = 0.09) (t = 2.85; p < 0.05; df = 181.0). The maximum number of consecutive days over which we saw an individual male or female was 14 and 7, respectively.

The oviposition and mating behaviors of male and female flies changed over the season. Early in the census season, before July 7, we did not observe either marked or unmarked females ovipositing into apples in the orchard. The apples were sufficiently ripe to allow oviposition because when apples from our observation tree were brought into the laboratory, our wild, laboratory-maintained AMF readily attempted oviposition (D. R. Papaj, Dept. Entomology, University of Massachusetts, Amherst, personal communication). Thus, we hypothesize that the flies observed in the field prior to July 7 were not ovipositing because they were not reproductively mature. This contention is supported by the fact that no flies were observed mating prior to July 7.

Prior to July 7, we detected no significant difference between the number of male or female flies observed on only one day versus the number of flies observed on more than one day (G = 1.13; p > 0.05). After July 7, the pattern of sightings of males and females differed (Fig. 2), though not significantly (G = 1.00; p > 0.05), probably due to low sample sizes (n = 17 females; n = 33 males). The primary difference in sighting frequency between males and females resulted not from a change in the frequency of seeing females (both before and after July 7, most marked females were seen on only one day; G = 0.95; p > 0.05), but was due to a change in the pattern of male sightings. Following the onset of oviposition, males were more likely to be seen for many days (G = 5.80; p < 0.05). The maximum time span over which a male was periodically re-sighted was 22 days, and the maximum time span for a female was 24 days.

The peak time of day in which marked flies were seen also differed between males and females. During the 1500 h census, we saw slightly more marked females than at any other time (mean = 1.08 females/census hour), whereas the greatest mean number of males were seen during the 1600 h census period (mean = 2.89 males/census hour).

Fig. 2. Proportion of marked female and male AMF seen once or more than once in relation to the onset of reproductive maturity on July 7. (Numbers of individuals.)
(Fig. 3). In addition, the latter census period, during which we saw the greatest numbers of males, was one of the periods in which the fewest females were seen. For each census period, a greater mean number of males than females were seen. The pattern of sightings of unmarked mating pairs corresponded more closely with the pattern of sightings of marked males than of marked females; most were seen at 1600 h, with a considerable decrease during the 1700 h census period (Fig. 3).

We observed very few marked flies in copula. Only 12 marked males (12% of all sighted marked males) and only 6 marked females (7.2% of all sighted marked females) were observed copulating, in every case with an unmarked partner. Only 1 marked female was seen to mate more than once (2 matings); 4 marked males (33% of all marked males observed mating) mated multiply during census periods. One marked male mated 6 times and the other 3 marked males mated twice.

Sighted, marked females did not differ in size from females which were not seen (t = -0.44, p > 0.05, df = 175.1). Marked males which were sighted were significantly larger than marked males which were not sighted (t = -2.00, p < 0.05, df = 224.9). Marked males and females which we observed mating did not differ in size from flies which were not observed to mate (males: t = -0.98, p > 0.05, df = 19.4; females: t = -0.84, p > 0.05, df = 6.6).

DISCUSSION

Dispersal prior to reproduction is fairly common in adult insects and is sometimes accompanied by the loss of flight ability once reproduction begins (Harrison 1980). In

![Graph](https://via.placeholder.com/150)

Fig. 3. Relationship between hour of day and average numbers of marked individual male and female and unmarked mating pairs of AMF seen on the observation tree over the 24 day observation period.
AMF, many pre-reproductive adults dispersed away from the site of emergence. Approximately 75% of the newly emerged AMF we marked left the host tree after being seen within the first week and were not seen again. The remaining 25% apparently left the host tree shortly after emergence but returned when reproductively mature, 1-2 weeks later. Using radiolabelled AMF, Neilson (1971) also found that many flies which dispersed outside of a naturally infested orchard early in the season later returned.

Similar dispersal behaviors of the immature adults of a close relative of the AMF, Dacus tryoni (Froggatt), the Queensland fruit fly, have been reported (Fletcher 1973, 1974). Using mark recapture methods in a naturally infested orchard, Fletcher (1973, 1974) found that 75% of D. tryoni left the orchard in their first week and did not return. In later weeks, as flies became mature, many re-entered the orchard. Although D. tryoni are larger and capable of longer dispersal flights than AMF (Neilson 1971, Fletcher 1974), the same general pattern of dispersal away from hosts prior to reproduction followed by return when reproductively mature occurs as we observed in the AMF. This pattern likely corresponds to the change from primarily food foraging behavior when reproductively immature to mate and host foraging behaviors when mature (Harrison 1980).

We detected distinct differences between wild male and female AMF in the tendency to remain on a host tree, with those differences magnified following the onset of fly reproductive maturity. In general, we resighted many more males than females, but the most striking differences between the sexes occurred after oviposition began. Following oviposition, female AMF deposit a marking pheromone on the surface of fruit that deters further egglaying (Prokopy 1972). Previous studies using field-caged flies showed this marking pheromone elicits female emigration from host trees (Roitberg et al. 1982, 1984). Just the opposite behavior, arrestment of activity, occurs in male AMF when they contact marking pheromone on fruit (Prokopy & Bush 1972).

Both before and after the onset of oviposition and deposition of marking pheromone, we found that female AMF were not likely to remain on a single host apple tree for more than one day. Although this effect may have been heightened by our thinning of tree leaves, we could not detect any increase in female emigration from the host tree which might have been due to contact with marking pheromone. The lack of fruit on immediately adjacent host trees may have caused females to remain on our observation tree longer than if suitable host fruit were available nearby, or may have resulted in longer dispersal flights by females to find new oviposition sites (see also Neilson 1971). Fletcher (1973) found that the length of time D. tryoni remained in an orchard was in great part determined by the quantity of fruit available for oviposition. Hendriks & Reyes (1987), however, felt that the length of time D. longistylus (Wied.) females spent on a host was influenced by encounters with patrolling males which were continually attempting forced copulations.

Male AMF tended to remain on the tree longer and were seen for more consecutive days in the latter than in the earlier part of the season. We hypothesized that once females had commenced oviposition, males frequently were contacting female marking pheromone on fruit. Contact with marking pheromone would arrest male activity on fruit (Prokopy & Bush 1972). Similarly, Johnson (1988) found that male AMF responded more strongly to the mating-oviposition stimulus of a red sphere trap than to the feeding stimulus of a yellow panel trap. By remaining on fruit, males increase the probability of encountering females arriving on the fruit to oviposit, and thus increase their opportunities to mate, since over 90% of matings occur on fruit (Prokopy et al. 1987) and most occur when females are in some phase of oviposition behavior (Prokopy & Bush 1973, Smith & Prokopy 1980). This observation is consistent with the hypothesis of Thornhill & Alcock (1983) that when females of a species multiply mate, males would be expected to search for mates near sites of female oviposition. Although we were not
able to document multiple female mating in this study, we expect multiple mating to occur in nature because laboratory studies have shown that female AMF benefit from multiple copulations in terms of increased fecundity and fertility (Opp & Prokopy 1986).

The peak time of mating by unmarked AMF corresponded more closely with time of observation of peak male presence than peak female presence (see also Prokopy et al. 1972). Since most matings on fruit are male rather than female initiated (Smith & Prokopy 1980), peak time of male abundance on fruit might be one of the primary factors governing diel mating patterns.

Using the maximum time span over which marked male and female AMF were sighted (24 days for females and 22 days for males), we conservatively estimate that, as adults, some flies may live up to 4 weeks in nature. Neilson & Wood (1966) estimated from field and laboratory cage studies that AMF adults may live up to 1 month when supplied with aphid honeydew. Although female size appeared to have no influence on longevity in our study, body size may have affected longevity of males because more large males were sighted over time than small males. We detected no interaction between body size and mating success for either sex, although body size is known to influence mating success in other dipteran species (Borgia 1981, Burk & Wobb 1983, Sivinski 1984).

This study provides information on individual fly activities in nature but raises many questions concerning AMF behavior. For example, although we know that AMF are not likely to remain on the host tree early in the season for more than one day, we do not know where these pre-reproductive individuals go. Furthermore, we do not have comprehensive information concerning the natural food of these flies and their food foraging behavior, although we know that protein is necessary to attain reproductive maturity (Webster et al. 1979). Finally, many questions remain concerning male-female interactions, especially the average numbers of times individuals mate on host plants. We know that most matings occur on fruit and are male initiated but we have no estimate of variance in individual mating success. We plan to address these and many more questions in future studies.

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PREDATION ON WATERHYACINTH WEEVILS AND OTHER AQUATIC INSECTS BY THREE WETLAND BIRDS IN FLORIDA

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Abstract

Common moorhens (Gallinula chloropus), boat-tailed grackles (Quiscalus major) and red-winged blackbirds (Agelaius phoeniceus) were collected monthly from September 1984 to August 1985 at a waterhyacinth (Eichhornia crassipes) infested lake in northcentral Florida. Contents of esophagi and gizzards were examined to assess predation on waterhyacinth weevils, Neochetina eichhorniae and N. bruchi, and other aquatic insects. Waterhyacinth weevils were rarely found in stomach contents of common moorhens, whose herbivorous diet consisted largely of coontail, hydrilla and duckweed. Although diets of the other two bird species varied seasonally, both consumed significant proportions of aquatic insects. Adults of Donacia leaf beetles were found to be very abundant in stomach contents of grackles and blackbirds (aggregate percent: \( \bar{x} = 17.2 \), \( \bar{x} = 26.9 \), respectively). Neochetina weevils were frequently found in gizzards of boat-tailed grackles and red-winged blackbirds (percent occurrence: \( \bar{x} = 52.5 \), \( \bar{x} = 41.5 \), respectively), but accounted for a relatively small proportion of the total diet (aggregate percent: \( \bar{x} = 1.0 \), \( \bar{x} = 6.3 \), respectively). Implications for biological control of waterhyacinth are discussed.