

# Oviposition by sterile codling moths, *Cydia pomonella* (Lepidoptera: Tortricidae) and control of wild populations with combined releases of sterile moths and egg parasitoids

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## ABSTRACT

This paper provides data on the number of nonviable *Cydia pomonella* (L.) eggs that are present in orchards receiving sterile moths and the potential for these eggs to support populations of the parasitoid *Trichogramma platneri* Nagarkatti. In the laboratory, non-irradiated female codling moths laid ca. 214 eggs in their lifetime while females irradiated with 330 Gy laid only 93 eggs. Persistence data collected in the field indicated that the majority of nonviable eggs were no longer suitable for parasitization after 1 week. With a release rate of 1,000 sterile females per hectare per week we estimated that 30,000-40,000 nonviable eggs per hectare would be present in orchards at any given time. When a combination of sterile moths and parasitoids were released into large field-cages fruit damage was less than seen when either tactic was used alone.

**Key words:** *Cydia pomonella*, sterile insect release, oviposition, biological control, parasitoid

## INTRODUCTION

The codling moth, *Cydia pomonella* (L.) (Lepidoptera: Tortricidae), is the key pest of apples and pears in the Pacific Northwest (Madsen and Procter 1982). Control programs for this pest have traditionally relied on organophosphate insecticides. However, resistance to these chemicals is increasing (Varela *et al.* 1993), as is pressure from environmental and worker safety groups to limit or eliminate the use of pesticides in fruit production (Calkins *et al.* 1998). In response to these pressures, apple pest management in the western USA has focused on the use of sex pheromones to disrupt codling moth mating (Knight 1995). In Washington State, an estimated 15,000-16,000 ha were treated in 1998, up from close to 11,000 ha in 1997. Total area treated with codling moth mating disruption in western North America was  $\approx$ 24,500 ha in 1998 (Anonymous 1998). In addition, the use of entomopathogens [e.g., bacteria (Knight 1997) and nematodes

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(Warner 1997; Lacey and Chauvin 1998)] and parasitoids is being evaluated for use in combination with mating disruption in areas where high codling moth populations are present, or as supplementary tactics to control secondary orchard pests such as leafrollers (Lepidoptera: Tortricidae) (Lawson *et al.* 1997).

An alternative to mating disruption is the sterile insect technique being implemented in southern British Columbia by the Okanagan-Kootenay Sterile Insect Release (SIR) Program to eradicate the codling moth (Dyck *et al.* 1993; Bloem and Bloem 1998). Insects are mass-reared and sterilized with gamma radiation in Osoyoos, BC, and then released twice per week into  $\approx 3,500$  ha of apples and pears in the south Okanagan, Similkameen and Creston Valleys. The SIR Program releases both sterile males and sterile females. In 1996, the release rate was  $\approx 1,000$  moths (sex ratio 1:1) per ha twice per week for about 20 weeks from early May to mid-September (Bloem *et al.* 1997). Unlike sterile release programs for fruitflies where released females can injure fruit during oviposition (Franz and Kerremans 1994), releases of sterile codling moth females have no impact on fruit quality and may help to control wild populations by attracting and engaging feral males (White *et al.* 1976).

Knipling (1992) suggested that the synergistic suppression of a pest population is possible when sterile insects and parasites are concurrently released. For control of codling moths, the combined release of sterile insects and *Trichogramma* (Hymenoptera: Trichogrammatidae) egg parasitoids was first suggested by Nagy (1973). Recently, releases of *Trichogramma platneri* Nagarkatti have been used to control lepidopteran pests in avocado (Oatman and Platner 1985) and codling moths in walnut orchards in California (N. Mills, U.C. Berkeley, personal communication). *T. platneri* has also been used to control oblique-banded leafrollers, *Choristoneura rosaceana* (Lepidoptera: Tortricidae) in apple orchards in New York (Lawson *et al.* 1997). In British Columbia, native *T. platneri* have been collected in apple orchards that are currently being treated with sterile codling moths (S. Bloem, unpublished results).

Because matings involving at least one sterile partner result in the production of nonviable eggs, a potentially large number of nonviable eggs could be present in orchards receiving sterile moths (Nagy 1973). Cossentine *et al.* (1996) report that nonviable codling moth eggs are suitable, although sub-optimal, hosts for *T. platneri* in the laboratory. Thus, it is possible that large numbers of nonviable eggs in orchards under sterile moth release might allow the establishment and maintenance of increased numbers of *T. platneri* (Cossentine *et al.* 1996).

In an effort to determine how many nonviable codling moth eggs are being actually laid in orchards under sterile insect release, provide an estimate of the population density of *T. platneri* that might be maintained on these eggs, and evaluate whether concurrent releases of *T. platneri* and sterile moths can improve control of wild codling moth populations over that of sterile moth releases alone, we:

- 1) collected data on daily and lifetime egg production by sterile females; 2) determined the persistence of nonviable eggs as suitable hosts for *T. platneri* under field conditions; 3) collected data on the number of nonviable eggs found in orchards under sterile moth release and compared these to predicted numbers; and 4) compared the amount of fruit damage that occurred when releases of *T. platneri* and sterile moths were made in large field-cages containing individual apple trees to control a known number of fertile codling moths.

## MATERIALS AND METHODS

**Test Insects.** Adult moths were provided by the codling moth mass-rearing facility in Osoyoos, BC. Shipments of *Trichogramma platneri* were purchased from Rincon-Vitova



Insectaries, Ventura, CA, as developing pupae inside eggs of the Angoumois grain moth, *Sitotroga cerealella* (Olivier) (Lepidoptera: Gelechiidae).

**Lifetime Egg Production by Colony Females.** Newly emerged (< 24 h) adult codling moths were sorted by sex and either left non-irradiated (N = normal) or irradiated (I) with 330 Gy (Cobalt<sup>60</sup>; Gammacell 220; Nordion Intl. Inc., Canada). Non-irradiated moths were packaged into Petri dishes and set-up as if they were to be irradiated to insure equal handling. Non-irradiated and irradiated moths were then paired into four treatments: N x N, I x I, N x I and I x N, female x male, respectively. Individual pairs were placed in clear 200 ml plastic cups with lids; a moist wick extending through the lid provided moisture and was re-wetted daily. The insects were allowed to mate and lay eggs at 25°C, 16L:8D and 55% RH until the females died. The total number of eggs laid per cup was counted and recorded. Ten pairs of codling moths per treatment per replicate were used and six replicates were completed, three replicates at each of two times. Egg count data were normalized using square root ( $\sqrt{n+0.5}$ ) transformation and subjected to a two-way (time x treatment) analysis of variance followed by a comparison of treatment means using Student-Newman Keuls' (SNK test) multiple range test (SAS 1985).

**Daily Egg Production by Colony Females.** Newly emerged adults were sorted by sex and either left non-irradiated (N) or irradiated (I) as above. Pairs of non-irradiated (N x N) or irradiated (I x I) females and males were placed in clear plastic cups (200 ml) and allowed to mate and lay eggs at 25°C, 16L:8D and 55% RH for 24 hours. The cups were briefly chilled (0-2°C) and the insects transferred to new cups daily for 7 days. The number of eggs laid per day by each female were counted and recorded. Twenty-five pairs of N x N and I x I were used per replicate and three replicates were completed. Egg counts were transformed as above and analyzed with a two-way (day x treatment) analysis of variance, followed by separation of treatment means using Student-Newman Keuls' (SNK) multiple range test.

**Persistence of Nonviable Moth Eggs in the Field.** Two apple orchards, one conventional and one organic in Summerland, BC, were used for this study. Five pairs of irradiated male and female codling moths were liberated into mesh sleeve cages with heavy wire frames (50 by 25 by 25 cm) that were placed over branches in the upper 1/3 of the canopy on five randomly selected trees in each orchard. The insects were allowed to mate and lay eggs in the cages for 72 h after which cages were removed and insects discarded.

The leaves on each branch were examined for the presence of eggs. Leaves with eggs were marked by attaching small plastic tags with wires to the leaf petiole. No fewer than 10 ( $n = 10-22$ ) eggs per branch were tagged. Eggs were checked after 2, 5, 8, 11, and 14 days in both orchards. At each observation, egg status was coded as suitable for parasitization (= egg present and plump) or unsuitable for parasitization (= egg present and flat or egg absent). Field temperatures were monitored with electronic datapods (Kiwi Group, North Falmouth, MA). The experiment was repeated twice, once in early June and again in late July 1996. Persistence of nonviable eggs was compared between conventional and organic orchards and between seasons using analysis of variance.

**Density of Nonviable Eggs in Orchards Receiving Sterile Moths.** Apple leaves in five orchards in Summerland, BC, were examined weekly for 18 weeks (17 May - 20 Sept. 1996) for the presence of codling moth eggs. In mature, traditional plantings of Golden Delicious, Red Delicious, and McIntosh, 1,000 leaves were examined each week - 100 leaves per tree from the upper 1/3 of the tree canopy in 10 randomly selected trees per orchard. Ten apples from each of the 10 trees ( $n = 100$  fruit) were also examined each week for eggs. In high density plantings of Fuji and Royal Gala, 50 leaves and five apples per tree were examined at random from the entire tree canopy of 20 trees each week ( $n = 1,000$  leaves and 100 fruit).



When an egg was located, the leaf or fruit was collected and taken to the laboratory where it was held at 23°C, 16L:8D and 50% RH for 7 days to determine egg viability. The total number of leaves sampled per variety divided by the total number of eggs found was used to calculate the mean number of leaves required to be sampled in order to find one codling moth egg.

The mean number of leaves per tree (L/T) was estimated using the equation:  $L/T = (0.8)(td)^2$ , where 0.8 is a constant corresponding to heavy soil type; td is trunk diameter measured in mm (P. Parchomchuk, AAFC-PARC, Summerland BC, personal communication.). Trunk diameter was measured in five trees per variety at random. Spacing between trees was measured and used to determine the number of trees per ha. The expected number of codling moth eggs present was estimated by using the number of leaves per ha per variety, laboratory oviposition rates by irradiated females and field release rates for sterile codling moths (SIR Program, personal communication). We assumed that field oviposition was 50% of that obtained in the laboratory (Howell 1991 and refs. therein), and that 85% of the eggs laid on any given day were gone after 1 week and 100% were gone after 2 weeks (based on egg persistence data).

**Combination of Sterile Insect Release and Egg Parasitoids.** Large polypropylene mesh field-cages (3.65 by 3.65 by 3.65 m) (Chicopee, Gainesville, GA) were used to enclose single Spartan apple trees (mean height = 2.75 m) in an unsprayed orchard in Summerland, BC. All naturally occurring fruit was stripped from the trees. Several hundred thinning apples (3.5-5.0 cm diameter) were collected in mid-June from an unsprayed orchard in Oliver, BC. The fruit was washed, examined for insect damage, and a 30 cm length of cotton string attached to each fruit stem. The apples were then stored in paper bags at 0-2°C until needed. On the morning of the release, 50 apples were hung at random throughout the tree canopy inside each cage.

Shipments of *T. platneri* were stored in the dark at 15°C until prepared for release. On the day prior to release, ≈6,000 parasitized grain moth eggs were placed inside small (1 lb) paper bags; a dental wick soaked in a dilute honey solution (1 honey: 40 H<sub>2</sub>O) was added to each bag to provide moisture and carbohydrates to emerging parasitoids. Bags were stapled shut and stored in darkness at 25°C until the time of release. A sample of each shipment was kept in the laboratory to verify % adult emergence and sex ratio.

On the morning of the release, non-irradiated (N) and irradiated (I) colony moths were counted, sexed, and placed in Petri dishes according to treatment requirements. Four treatments were randomly assigned to the field-cages: N = check = (five non-irradiated males and females); N + I = (N + 50 irradiated males and females); N + T = (N + one bag with ≈6,000 *T. platneri*); and N + I + T. Moths were transported to the field in a cooler and released into the cages in mid-afternoon (1530 hours [PST]). Moths were released into the cages by placing them into open (1 litre) paper cups hung horizontally at mid-canopy (separate cups were used for N and I moths), which provided a temporary shelter where the moths could warm-up and subsequently disperse. In cages receiving parasitoids, the paper bag was tied to an inner middle branch of the tree and 10-15 exit holes were opened in the bag with a dissecting probe.

Once per week, leaves were examined for developing or parasitized moth eggs, and thinning apples were examined for evidence of larval entries. After 4 weeks, all thinning apples were removed from the trees and held in the laboratory at 23°C, 16L:8D and 50% RH for 7 days. The number of damaged apples and larval entries per apple were recorded. The four treatments were repeated over four time periods with two-four replicates at each time, for a total of 10 replicates. To stabilize the variances, the number of damaged apples per treatment was transformed using arcsine ( $\sqrt{n/50}$ ) and the number of larval entries transformed using  $\log_{10} (n+1)$ . Data were analyzed by a two-way (treatment x time)

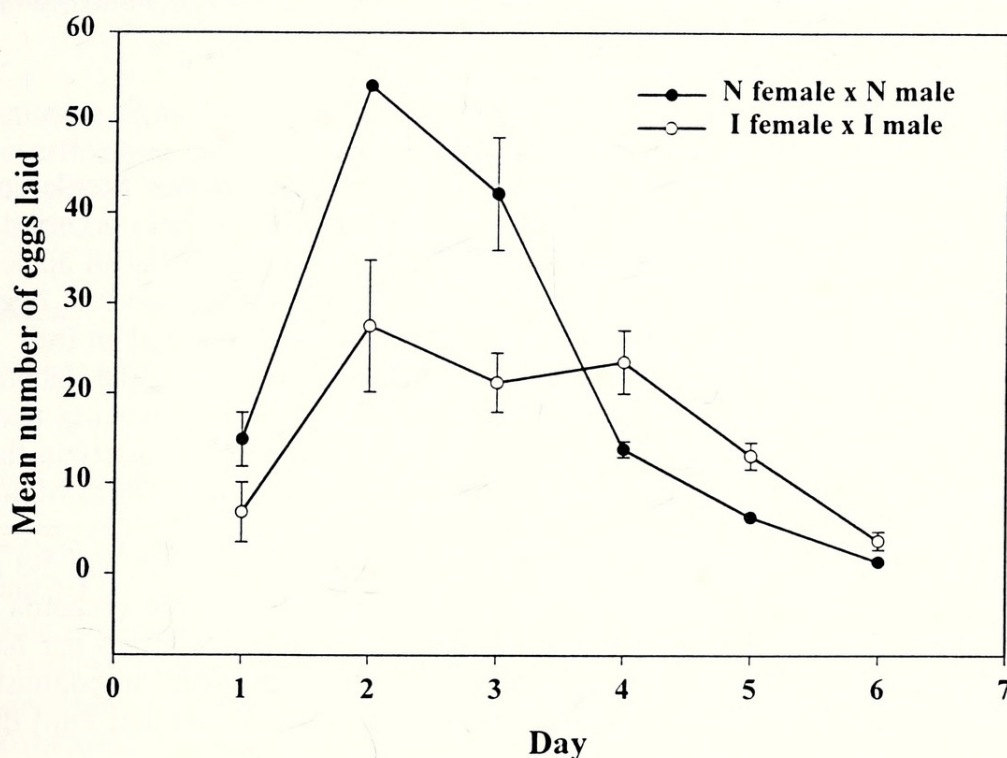


analysis of variance, followed by comparison of treatment means using Student-Newman Keuls' (SNK test) multiple range test.

## RESULTS

**Lifetime Egg Production by Colony Females.** Irradiated female codling moths (I) laid 57% fewer eggs than did non-irradiated (N) females ( $F = 73.89$ ,  $df = 3, 39$ ,  $P = 0.0001$ ). However, the number of eggs laid by N and I females was independent of whether the male mating partner was irradiated or not. Non-irradiated females laid an average of  $216.3 \pm 8.8$  (SE) and  $212.2 \pm 11.6$  when paired with N and I males, respectively. Irradiated females laid an average of  $92.5 \pm 6.1$  and  $93.3 \pm 8.0$  eggs when paired with N and I males, respectively.

**Daily Egg Production by Colony Females.** The daily egg laying schedule was significantly different for I and N females ( $F = 36.84$ ,  $df = 5, 24$ ,  $P = 0.0001$  for day;  $F = 9.71$ ,  $df = 1, 24$ ,  $P = 0.0047$  for treatment) (Fig. 1). A more gradual increase in egg deposition was observed in I females, who by day 3 had laid only 58% of their total eggs, as compared to 84% for N females. By day 4, I and N females had laid 82.4% and 94.3% of total eggs, respectively. However, the greatest number of eggs was laid on day 2 after mating by both I and N females. The total number of eggs laid by I females in this experiment was similar to that recorded in the previous experiment, even though females were subjected to more handling (i.e., chilled and transferred to new oviposition cups every 24 h). This was not true for N females, which showed a 39% decrease in oviposition when handled daily.



**Figure 1.** Mean number of eggs ( $\pm$ SE) deposited per day by *Cydia pomonella* females ( $n = 75$ ) in the laboratory. Females and males were either non-irradiated (N x N) or treated with 330 Gy of gamma radiation (I x I). Points with missing SE bars have SE's smaller than the point.

**Persistence of Nonviable Moth Eggs in the Field.** No significant difference was found in the persistence of codling moths eggs laid by irradiated females in organic



versus conventional apple orchards ( $F = 3.13$ ,  $df = 1, 16$ ,  $P = 0.3715$ ); however, egg persistence was significantly shorter in both orchards in July than it was in June ( $F = 42.5$ ,  $df = 3, 16$ ,  $P = 0.0001$ ) (Table 1). In June, 20-25% of the eggs laid appeared fresh and suitable for parasitization by *T. platneri* after 1 week and 7-10% appeared fresh after 2 weeks. In July, when daily temperatures were warmer, only 5-6% of the eggs still appeared to be suitable for parasitism after 1 week and < 5% were suitable after 2 weeks (mean daily maximum temperatures were 26.3°C and 32.0°C in June and July, respectively).

**Table 1**

Persistence of nonviable *Cydia pomonella* eggs laid by sterile females on the foliage of apple trees in orchards in Summerland, BC, during June and July, 1996.

Days After Oviposition	% of Eggs Suitable for Parasitism <sup>a</sup>			
	June		July	
	Organic Orchard ( <i>n</i> =100)	Conventional Orchard ( <i>n</i> =75)	Organic Orchard ( <i>n</i> =102)	Conventional Orchard ( <i>n</i> =98)
2	81.0 a	98.7 a	71.6 a	83.7 a
5	34.0 b	53.3 b	15.7 b	28.6 b
8	20.0 b	22.7 c	5.9 c	5.1 c
11	-- <sup>b</sup>	12.0 d	5.9 c	-- <sup>c</sup>
14	10.0 c	6.7 e	3.9 c	3.1 c

<sup>a</sup> Mean percentages within a column followed by the same letters are not significantly different ( $P > 0.05$ ).

<sup>b</sup> Bees swarming in the orchard prevented data collection.

<sup>c</sup> An application of endosulfan prevented entry into the orchard.

**Density of Nonviable Eggs in Orchards Receiving Sterile Moths.** Sterile codling moths were first released on 24 April 1996, and weekly sampling for eggs occurred from 17 May-20 Sept. 1996. The first egg was found on 21 June, on a McIntosh apple leaf. After this date, eggs were consistently found each week, with the number of eggs per apple variety ranging from 1-10 in 1,000 leaves. No eggs were ever found on fruit. Also, no embryonic development was ever observed after incubation in the laboratory, suggesting that all eggs found were laid by sterile females or by wild females that had mated with sterile males. The total number of eggs collected per apple variety in the 18-week sampling period was 19 in Red Delicious, 9 in Golden Delicious, 26 in McIntosh, 11 in Royal Gala, and 25 in Fuji.

As shown in Table 2, the number of codling moth eggs found per week was 2-3 times greater than the number we expected to find in the traditional apple orchards (Red Delicious, Golden Delicious, and McIntosh) based on the number of leaves per ha, the number of released sterile moths, and oviposition and persistence data. In contrast, the actual number of eggs found in the high density orchards (Royal Gala and Fuji) during our leaf sampling was about 40% less than expected.

**Combination of Sterile Insect Release and Egg Parasitoids.** There was a significant reduction in the proportion of damaged apples and the number of larval entries per treatment when irradiated codling moths (I), parasitoids (T), or both were added to the field-cages containing fertile codling moths ( $F = 12.4$ ,  $df = 3, 24$ ,  $P = 0.0001$  for apples;  $F = 15.0$ ,  $df = 3, 24$ ,  $P = 0.0001$  for larval entries) (Table 3). Both treatments reduced the number of damaged fruit by  $\approx 50\%$  and the total number of stings by  $\approx 60\%$ . The effect of simultaneous release of irradiated moths and *T. platneri* parasitoids appears to be additive.



When both treatments were used together the mean number of apples damaged was reduced by almost 84% and the average number of larval entries by  $\approx 90\%$  (Table 3).

Table 2

A comparison of expected versus actual number of *Cydia pomonella* eggs found in weekly samples of leaves taken during 17 May - 20 Sept. 1996 from apple orchards in Summerland, BC, under sterile insect release (1,000 leaves per orchard).

Orchard	Tree spacing (m)	Approx. trees/ha	Estimated leaves/tree <sup>a</sup>	Estimated leaves/ha	Expected eggs/leaf/week <sup>b</sup>	# eggs found/leaf/week
Red D.	5.3x3.8	490	226,600	111,034,000	1/2,095	1/947
Golden D.	3.7x3.7	730	310,250	226,482,500	1/4,273	1/2,000
McIntosh	7.2x3.6	390	338,000	131,820,000	1/2,487	1/692
Roy. Gala	2.9x0.5	6,800	7,400	50,320,000	1/949	1/1,636
Fuji	3.0x1.3	2,500	9,400	23,500,000	1/443	1/720

<sup>a</sup> Using estimated number of leaves per tree =  $0.8 [\text{trunk diameter (mm)}]^2$  provided by P. Parchomchuk, AAFC-PARC, Summerland, BC.

<sup>b</sup> Based on the following assumptions: i) 1,000 females per ha are present each week in orchards receiving sterile moths; ii) all eggs found during sampling were laid by irradiated females; iii) released females lay all of their eggs and then die after 1 week (based on data presented here and in Bloem *et al.* 1998); iv) the number of eggs laid by irradiated females in the field is 50% that recorded in the laboratory; v) 85% of the eggs laid by a given female are gone after 1 week and 100% are gone after 2 weeks.

Table 3

Reduction in *Cydia pomonella* damage due to the release of sterile codling moths at a 10:1 overflooding ratio, a single release of *Trichogramma platneri*, or a combination of both tactics in large field-cages containing individual apple trees, Summerland, BC, 1994-1995.

Treatment <sup>a</sup>	No. Apples Sampled <sup>b</sup> (n)	% Damaged Fruit <sup>c</sup> (mean $\pm$ SE)	% Reduction due to Treatment	No. Entries in 50 Apples <sup>c</sup> (mean $\pm$ SE)
N	500	32.4 $\pm$ 5.4 a	-	27.7 $\pm$ 6.8 a
N+I	500	13.4 $\pm$ 3.8 b	58.6	8.9 $\pm$ 3.2 b
N+T	500	18.2 $\pm$ 5.8 b	43.8	13.0 $\pm$ 4.8 b
N+I+T	500	5.2 $\pm$ 1.9 c	83.9	2.6 $\pm$ 1.0 c

<sup>a</sup> N = non-irradiated (fertile) codling moths (5 males and 5 females per cage); I = irradiated (330 Gy) moths (50 males and 50 females per cage); T = commercially available *T. platneri* ( $\approx 6,000$  per cage).

<sup>b</sup> Ten replicates with 50 apples per replicate.

<sup>c</sup> Means within a column followed by the same letters are not significantly different ( $P > 0.05$  SNK).

DISCUSSION

This paper documents the negative impact of gamma radiation on oviposition by codling moth females and provides a measure of the number of nonviable codling moth eggs that are present in orchards receiving sterile moths. It also examines the effect of combining a release of sterile codling moths with a single release of *T. platneri* in large field-cages. Our results showed that the combination of both tactics after 4 weeks



significantly reduced fruit damage caused by fertile codling moths (introduced into the cages) over that obtained when either tactic was used separately.

Data on other codling moth colonies indicates that fecundity per female generally varies between 132-162 eggs (Howell 1991 and refs. therein). However, non-irradiated females from the mass-rearing facility in Osoyoos, BC, were much more fecund than those reported in Howell (1991), producing an average of 214 eggs under laboratory conditions. This higher fecundity may be due to strain differences, better larval nutrition during mass-rearing, better handling of the adults, or a combination of these. Regardless, high fecundity in colony females is beneficial for mass-rearing and suggests that the SIR colony is healthy and vigorous. On average, females treated with 330 Gy laid only 93 eggs. These results support the findings of Proverbs and Newton (1962) and confirm that gamma radiation has a detrimental effect on oviposition. However, unlike results reported by Robinson (1974), the number of eggs laid by females was not affected by whether they mated with irradiated or non-irradiated males. This discrepancy might be explained by again suggesting that the current codling moth colony is more vigorous than the one used by Robinson in 1974, and as such, the negative effect of radiation on the ability of males to transfer sperm to females has been reduced.

It is interesting to note that irradiated females were less affected by handling than were fertile females. The fecundity of irradiated females was similar in both lifetime and daily oviposition experiments, even though in the second test females were moved to a new cup every 24 h. In contrast, non-irradiated females laid approximately 39% fewer eggs when they were transferred daily. The reason why irradiated females failed to show a decrease in oviposition with increased handling is not known, although it has been shown that irradiated moths are longer lived than non-irradiated moths (Proverbs and Newton 1962). It has also been suggested that irradiated insects are generally less active (Proverbs and Newton 1962). This may partially explain why irradiated moths have a lower recapture rate and are less competitive at mating than are non-treated moths (Bloem *et al.* 1998). However, less active insects may also be less affected by handling and thus longer lived in laboratory bioassays. The fact that we observed more gradual egg laying in irradiated females (Fig. 1) may be related to the detrimental effect of radiation on oocyte maturation or on their reduced activity level, or both (Proverbs and Newton 1962).

The SIR Program releases sterile moths for 20 weeks each year at the rate of  $\approx 2,000$  moths per ha per week. Both males and females are liberated and the sex ratio is consistently 1:1. As such, we can assume that  $\approx 1,000$  females per ha per week are present in orchards throughout the season. It is reasonable to expect a decrease in oviposition when sterile females are released into the field. Many biotic and abiotic factors will adversely affect egg production. When preparing Table 2, we assumed that released females survived 1 week, most field matings occurred between sterile moths (I  $\times$  I), oviposition in the field was 50% of laboratory totals, and that all eggs laid remained in the orchard for 1 week and 15% of them persisted for 2 weeks. As such, we might expect  $\approx 53,000$  eggs per ha at any given time during the release season (i.e., 50% of 93 eggs per I female in the laboratory = 46.5 eggs  $\times$  1,000 females = 46,500 eggs laid in any given week + 15% from previous week =  $\approx 53,000$  eggs/ha/wk). Jackson (1979) found that the upper leaf surface is always preferred for oviposition by wild females followed by lower leaf surface, fruit and stem. Unpublished data (S. Bloem) suggests that irradiated female preferences are no different than those reported by Jackson (1979).

The fact that we found 2-3 times as many codling moth eggs as we expected in the larger trees (Red Delicious, Golden Delicious, and McIntosh) can be explained, in part, by pointing out that our estimates were based on the assumption that eggs are laid randomly throughout the trees (total number of leaves per ha divided by the expected number of eggs laid per ha). In reality, codling moth females have an ovipositional



preference for the upper portions of apple trees. Richardson and Du Chanois (1950) and Wood (1965) report that 65-85% of codling moth eggs are laid in the upper half of the tree canopy depending on tree height. In our experiments, leaf samples were taken from the upper third of the canopy. As such, the number of eggs found per leaf in these varieties really only applies to the portion of the tree sampled and not to the entire tree. The actual number of eggs per leaf is probably lower and closer to the expected number, as found in the samples taken from Royal Gala and Fuji. Thirty thousand to 40,000 nonviable codling moth eggs per ha per week in orchards under sterile release is probably a more accurate estimate than the 53,000 as originally predicted.

Even though the simultaneous release of sterile moths (at a 10:1 overflooding ratio) and *T. platneri* still allowed some fruit damage to occur, the control provided by both tactics was significantly improved over the protection offered by a single tactic. These results suggest that releasing a generalist egg parasitoid might be a reasonable approach to use in combination with sterile moth release under certain conditions or at certain times of the year, particularly if the parasitoids are able to maintain good field populations by utilizing the nonviable eggs being laid by sterile females as replacement host material. However, our experiments were conducted inside large field-cages. As such, the effect of some biotic (e.g., predators) and abiotic (e.g., wind and rain) factors may have been modified. In addition, the cages confined the sterile moths to the vicinity of one tree and artificially concentrated oviposition (at the end of 4 weeks, a sample of 1,200 leaves found 1,163 non-viable eggs or 0.97 eggs per leaf). A concentrated distribution of nonviable eggs might have influenced host finding by the released *T. platneri* females and as a consequence the level of control provided may be different if evaluated under true field conditions.

The commercially recommended release rate for *T. platneri* is 200,000-250,000 per ha per week. This is significantly higher than the population that could be maintained on the 30,000-40,000 nonviable eggs being laid by sterile codling moths. However, the consistent availability of these eggs should support higher than normal parasitoid populations and prevent extinctions which typically occur throughout the growing season when natural host egg densities are low. Because *T. platneri* is a generalist parasitoid the "artificially" maintained populations could be expected to provide some measure of control against other lepidopteran orchard pests. Only a limited number of parasitoid releases may be necessary to establish resident populations, but they should be delayed until mid-June when egg laying by sterile moths occurs.

Although our data suggests that the level of control provided by the combination of tactics was additive it only represents a single generation effect (i.e., 4 weeks). Hence, our results do not rule out a possible synergistic effect which would manifest itself over time (Knipling 1992; Carpenter 1998). With increasing pressure from the urban public to reduce pesticide use and insure the safety of our food supply (e.g., the U. S. Food Quality Protection Act of 1996), growers and scientists are actively searching for tactics or combinations of tactics that satisfy environmental concerns yet remain cost effective (Carpenter 1998). It remains possible that a combination of *T. platneri* with sterile moth releases can improve the efficiency and cost effectiveness over either tactic used alone for codling moth control. Further investigation under actual field conditions would be necessary to determine if and when this occurs.

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