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The western cherry fruit fly, Rhagoletis indifferens Curran, was studied to determine the suitability of the sterile insect technique for its control. To obtain insect material, field collection of maggots is preferred to sifting of soil or rearing on artificial diet.

The western cherry fruit fly is strictly univoltine; only 1.1 per cent adult emergence occurred without chilling under laboratory conditions at 26.7° C and photoperiod of 19L:5D. Per cent emergence increased with longer periods of chilling. Synchronization of emergence was maximized after about 200 days at 3° C. Time to emergence decreased with increasing days of chilling; after a minimum of 200 days of chilling at 3° C, flies emerged after an average of 26 days at 26.7° C.

Flies exhibited a pre-mating and pre-oviposition period in the laboratory, during which flies spent

little time on cherries. The presence of a male pheromone was demonstrated.

The number of eggs laid under laboratory conditions ranged from 0 to 325 and averaged 62 per female. A reduction in egg hatch of about 99 per cent occurred when females were mated to males that had been exposed to 8 krad of Co-60 gamma irradiation as 1-3 day-old adults. Longevity of male flies decreased significantly with increasing doses of irradiation. Females were more sensitive to irradiation than males: they were infecund after a dose of 5 krad or more. The longevity of females was only slightly reduced by irradiation as high as 16 krad. By screening, pupae can be separated into groups that are about 75 per cent male, and 90 per cent female; but females can be released with males if flies are irradiated as 1-3 day-old adults.

Sterile males were more competitive in ratios of 1:1 and 4:1 than 8:1 in laboratory cages: the total number of matings was about the same with 8:1 ratios as with 4:1. Females were less receptive to males after several matings, so that with a constant number of females, the number of matings by unirradiated males was reduced in the presence of sterile males. Irradiated males mated about 80 per cent as frequently as normal males. Males irradiated as pupae were less than half as competitive as males irradiated as adults. Sperm

from the last-mated male had precedence, but some mixing of the sperm occurred. Field cage studies showed about 94 per cent reduction in infestation with 20:1 sterile to normal male ratios.

The low economic threshold, the small dispersal capability, and favorable radiobiology of the flies make this insect an attractive candidate for the sterile insect technique. The technique may be used alone, or in an integrated control program in combination with chemicals. Post-harvest release of flies would efficiently prevent build-up of the population in the remnant of cherries left after mechanical harvesting.

Gamma Irradiation of the Western Cherry Fruit Fly for the Sterile Male Control Technique

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I. INTRODUCTION

A. The Insects

Tephritid fruit flies -- The cherry fruit flies are members of the family Tephritidae (formerly Trypetidae), and are in the tribe Trypetini and the subfamily Trypetinae (Bush 1966). The members of the Tephritidae are called peacock flies, or more commonly fruit flies. Tephritids can be recognized by the characteristic subcosta of the wing which is bent forward apically at a nearly right angle and then fades out before reaching the costa (Borror and DeLong 1964). Most tephritids have spotted or banded wings, and most species of Rhagoletis can be separated on the basis of wing banding as well as other characters (Foote and Blanc 1963, Bush 1966). For instance, R. indifferens Curran can be separated from R. cingulata Loew by the apical spot, which is free in the wing of cingulata, but is connected to the nearest band in indifferens (Blanc and Keifer 1955). Very rarely an indifferens with a free spot is encountered; however, this atypical wing is not identical to that of the eastern species. R. indifferens can also be separated from the other members of the cingulata species group by the presence of black shading on the

posterior surface of coxa I, and a black rather than yellow epandrium (Bush 1966).

The family Tephritidae is divided into two major groups (Bateman 1972). The first group includes temperate-zone, generally univoltine and monophagous (or oligophagous) speices which diapause in the pupal stage. The second group is comprised of the non-diapausing, multivoltine, polyphagous species that are usually associated with warmer tropical and subtropical regions. The latter flies, primarily species of the genera Dacus, Ceratitis, and Anastrepha, have a food supply and acceptable climatic conditions available throughout the year. Temperate-zone flies, primarily Rhagoletis spp., live in areas where the climate is too cold or too dry for them to survive without diaapusing for part of the year (Bateman 1972, Smyth 1960). The temparate-zone flies have adapted to these climatic limitations, and, in so doing, have further restricted their activity to a univoltine exploitation of a particuliar host fruit, available in suitable condition for only a small part of the year. The univoltine life cycle of these frugivorous flies is thus adaptive to their monophagous (or oligophagous) habits. Christenson and Foote (1960) discuss biological races of fruit flies and whether several species should be considered monophagous or oligophagous.

Smyth (1960) lists eight families of plants in which North American species of Rhagoletis have been found to breed.

Cherry-infesting Tephritidae -- A number of species in the genus Rhagoletis are pests; Boller and Prokopy's (1976) review covers 11 economically important species. Four species of this genus commonly infest cherries: the European cherry fruit fly, R. cerasi L., (which is found in Europe only); the black cherry fruit fly, R. fausta (Osten Sacken); the (eastern) cherry fruit fly, R. cingulata; and the western cherry fruit fly, R. indifferens. The maggot found in cherries was often referred to in the early literature as R. pomonella (Walsh) (the apple maggot) (Cordley 1889, Davis 1889, Slingerland 1899). However, there is only one substantiated case of the apple maggot infesting cherries (Shervis et al. 1970).

The four species of cherry fruit flies listed above are often grouped together on the basis of their syntrophy. Bush (1966) emphasizes that this is an artificial grouping from an evolutionary viewpoint. On the basis of morphology he placed R. cingulata and R. indifferens in the cingulata species group. R. fausta and R. cerasi are not closely related to each other or to the above species.

In the western United States, R. indifferens was for many years referred to as R. cingulata (Eide 1947, Zwick et al. 1970), or as R. cingulata indifferens (Blanc and Keifer 1955, Harper 1966). Blanc and Keifer (1955) listed anatomical differences between the two forms. Bush (1966) listed further differences and suggested use of Rhagoletis indifferens, the name Curran (1932) had given to cherry fruit flies occurring on wild cherries in the West. The common name, western cherry fruit fly, was approved by the Entomological Society of America (Blickenstaff 1970).

Hosts of the North American cherry fruit flies -- The three species of North American cherry fruit flies (R. cingulata, R. indifferens, and R. fausta) are native insects that do not occur elsewhere in the world (Bush 1966). They lived exclusively on native hosts until the planting of Prunus avium (sweet cherry) and P. cerasus (sour cherry) in backyards and orchards. Wasbauer (1972) cataloged the hosts of the cherry and other fruit flies.

Prunus pennsylvanica (pin or fire cherry) is the main native host of R. fausta in the East (Severin 1918, Pettit 1931, Glasgow 1933); while P. emarginata (western pin, or bitter cherry) is the preferred host in the West (Frick et al. 1954, Bush 1966). It has also been reared from P. serotina (black cherry, Farleman 1932), and

P. virginiana (choke cherry, Pettit 1931) in the East.

R. cingulata prefers P. serotina (Glasgow 1933, Ladd 1933). Farleman (1933) listed P. pennsylvanica and P. virginiana as hosts in Michigan, but in New York Glasgow (1933) reported that he was unable to rear any adults from these two species even though he had witnessed oviposition into the fruits of the latter. Bird (1927) listed P. pennsylvanica as the host of R. cingulata in Manitoba, and Pettit (1931) reported rearing "a very few" cingulata from pin cherry. Bush (1966) stated that he had never found cingulata larvae in the fruits of P. virginiana even when this species was growing among heavily infested P. serotina. R. cingulata has certainly been swept from P. virginiana, but it is questionable whether it has ever been reared from the fruit of this tree.

R. indifferens was originally described from P. emarginata (Curran 1932). This is the preferred host, although it also infests P. virginiana var. demissa (Frick et al. 1954, Banham 1971). All three species of cherry fruit fly have been found infesting both sweet and sour cherries and P. mahaleb (trees from the mahaleb rootstalk). There are also reports of R. indifferens infesting species of plums: Ellertson (1961) found an infestation in P. subcordata (pacific plum, at the

Dalles, Oregon), and in P. salicina (Japanese plum, at Hood River, Oregon). Don Berry (personal communication) said that western cherry fruit flies had infested commerical plums in 1957 in Medford, Oregon. Cordley (1889) also reported maggots in plums in Michigan.

Emergence of adult flies -- The cherry fruit fly adults emerge in the spring. Timing of emergence can be predicted by summation of thermal units received (Müller 1970, Jubb and Cox 1974, AliNiazee 1976). Frick et al. (1954) found that the first flies could emerge any time after May 15 and before June 1 in the Yakima Valley of Washington. Emergence of the last fly usually occurred by July 1, but cool temperatures in late May and early June caused the final emergence to occur in mid-July.

S. C. Jones[1] found similar emergence patterns in the Willamette Valley of Oregon: emergence of the first fly occurred from mid-May to mid-June, but in 8 out of 16 years it occurred during the first week of June in the central and southern parts of the Willamette Valley. Extreme dates recorded for emergence of the first fly were May 14 and June 21. Emergence of the last fly usually occurred in mid-July, rarely in August. In all cases emergence patterns resembled a bell-shaped curve, with a definite peak and low numbers at the beginning

[1]Annual report on cherry fruit fly for the Agricultural Experiment Station, Oregon State University, unpublished. 1940:12, 1945:11, 17.

and end.

The sex ratio of western cherry fruit flies approximates 50:50, but may vary from year to year. Frick et al. (1954) found ratios in field emergence cages to be 57:43 (males:females), 49:51 and 51:49 in three different years. The ratio for flies that emerged in their laboratory was 44:56. Jones[2] found that the sex ratios varied from 42:58 to 51:49 for seven years of field emergence in the Willamette Valley. The composite sex ratio of 13,635 flies was 48:52.

Boyce (1934) found that female walnut husk flies emerged earlier than males after cold (but not after mild) winters. Analysis of data obtained by S. C. Jones for the western cherry fruit fly (see Appendix A), indicates that males emerged first after colder winters and females emerged first after milder winters.

R. indifferens and other cherry fruit flies are obligatorily univoltine insects. Frick et al. (1954) recorded less than one per cent emergence (under field conditions) without chilling. This is in contrast to the apple maggot, R. pomonella, which can be reared continuously using 16 or more hours photoperiod (Prokopy 1968a), and a fraction of the population that pupates

[2]Annual report on cherry fruit fly for the Agricultural Experiment Station, Oregon State University, unpublished. 1938:22, 1939:3, 1940:23-25, 1941:13-16, 1942: 13-14, 1943:20-21, 1944:17-18.

early in the season may give rise to a partial second generation (Illingworth 1912a, Phipps and Dirks 1933, Dolphin et al. 1970). As discussed earlier, members of the genus Rhagoletis are highly adapted to their host fruits, and the strictly univoltine behavior of R. indifferens may be due to the shorter fruiting season of cherries compared to apples.

A certain percentage of live pupae do not emerge the first spring, but remain in the soil and emerge one or more years later. Frick et al. (1954) found that 0.5 per cent or less did not emerge the first spring in the Yakima Valley. They stated that the percentage remaining dormant was proportional to the amount of low temperatures to which the pupae had been exposed, and noted that Yakima has four months with mean temperature of about 40° F (4.4° C), and one month with a mean temperature of about 45° F (7.2° C). The Willamette Valley of Oregon, on the other hand, has only one month (January) with a mean temperature below 4.4° C, and four more months with mean temperatures of below 7.5° C (Bates and Calhoun 1970). At Corvallis, Oregon, S. C. Jones[3] found as many as 138 flies emerging the second year from an emergence cage covering 4.1 m^2 of soil. He found second year emergence of 24, 27, 1, 7, and 43 per cent in five

[3]Annual report on cherry fruit fly for the Agricultural Experiment Station, Oregon State University, unpublished. 1936:10.

different years, and third year emergence of 0.3, 0.4, 0, 3.0, and 4.8 per cent (see Appendix B). The more southern Oregon population had a much greater percentage hold-over compared to the Yakima pupae. This is most likely due to the lower amount of chilling received by the Willamette Valley pupae, although there may be genetic differences too.

It has generally been suggested that cherry fruit flies have not infested commercial cherry growing areas of California (e.g. San Joaquin and Sonoma counties) because of their isolation (Mackie 1943). However, it may be that flies do not receive enough chilling in these areas and so are necessarily restricted to higher elevations in California.

Wild cherries frequently produce no fruits, at least in some parts of their range. In these areas selection for genes that control hold-over of pupae for the second year would be great. In commercial orchards, loss of the crop (due to frost or other insects) is infrequent. Selection for hold-over genes could still occur if few offspring survived to form pupae in a poor year (due to man-controlled or other factors), so that in the next year, a large percentage of the emerging flies were from hold-over pupae.

Behavior of adults -- Cherry fruit flies, apple maggots,

and other fruit flies are attracted to large sticky traps that are colored yellow (Prokopy 1972b, 1975b, Bateman 1976). For R. cerasi, a fluorescent yellow (Day-Glo Saturn Yellow) rectangular trap is 8 times as attractive as the standard McPhail traps with a 4 per cent solution of ammonium carbonate (Boller et al. 1971). Yellow reflects most light in the green area of the specturm, and is thus perceived by the fly as being similar to foliage. Saturn yellow has its peak in the region of 550 nm or yellow green (Prokopy 1972a). The attraction of tephritids to yellow is thus considered to be consistent with their attraction to large vertical areas of foliage (Moericke et al. 1975). Greany et al. (1977) found that Dacus oleae (Gmelin) was most responsive to rectangles painted with colors that have the greatest reflectance in the 580-590 nm region (orange), which is the color of some of the insect's host-fruit varieties. These studies have shown that the flies respond to the intensity of light of a certain hue.

Prokopy (1968b) found that the apple maggot was more attracted to large yellow objects and small red (or dark) objects; the flies respond to fruit visually, both to shape and color when they are ready to mate and oviposit. Adult R. pomonella are not attracted to fruit until mature (Prokopy et al. 1972). It appears that in

this fly, and in cherry fruit flies as well, the presence of the fruit on a tree may simply keep the fly in the area rather than the host tree being specifically attractive from a distance by odor or other trait.

Looking up into a cherry tree where R. indifferens is present, one typically sees females on leaves and males on cherries. Males wait on the cherries for females and may act aggressively toward other males (AliNiazee 1974b). In other species of Rhagoletis mating has been shown to occur at any time of the day when light intensity and temperature are adequate (Prokopy et al. 1972, Boller 1974). In many species of Rhagoletis, mating behavior occurs, or at least starts, on the fruit (Boyce 1934, Prokopy and Bush 1973, AliNiazee 1974b). However, Prokopy (1976) found that R. fausta mates on or near leaves.

Adult cherry fruit flies may feed on honeydew on leaves, on leaf nectaries, or on the fruit exudate after the female has bored into the fruit for oviposition (Frick et al. 1954, Prokopy 1976).

Eggs, Larvae, and Pupae -- The female flies lay eggs by inserting their ovipositor through the skin of the cherry and depositing a single egg just below the surface. The egg hatches in 5-7 days under field conditions (Johansen 1971), and 5-8 days under laboratory conditions (77 ± 2° F = 25° C, Frick et al. 1954). The young maggot makes its

way to the center of the cherry and feeds around the pit by rasping the tissues with its mouth hooks. There are three larval instars; the presence of the first two is not usually detected without dissection of the cherry, but the third instar makes one or more breathing holes in the cherry before leaving it. The larval stage lasts an average of 11 days at 77 ± 2° F (= 25° C, Frick et al. 1954). At the completion of larval development the maggots drop to the ground, where they burrow down 1-6 inches or more (AliNiazee 1974a). The skin of the third instar forms a puparium, and the insect overwinters as a pharate pupa.

Bateman (1976) has summarized the life table data developed for R. pomonella by Cameron and for R. cerasi by Boller (1966). In both cases the pupal mortality was very high due to predation and parasitism. The pupal stage lasts at least nine months so there is an extended time for disease, predators, or desiccation to destroy the pupae; and parasitism shows up as a mortality factor in this stage. The data indicate that except for the first and second instars, which are safely hidden near the pit of the cherry, there is moderate to heavy mortality in every life stage of the cherry fruit flies.

Early pest status and spread -- Cherry fruit flies are now the major insect pest of cherries in North America.

However, they were not a significant problem until about the turn of the century. Loew (1873) described Trypeta cingulata "from middle states". An earlier reference to Ortalis cerasi (Harris 1835) may be to R. cingulata. Slingerland (1902) cites correspondents from Massachusetts and New York who stated that they thought fruit fly maggots had worked cherries in their areas as early as 1865. However, the first infestation that can definitely attributed to a cherry fruit fly was reported by Hagen (1883) in Cambridge, Massachusetts. In 1889 cherries in northern Michigan were infested with maggots (Cordley 1889, Slingerland 1899).

In 1899 fruit fly infestations in cherry were widespread: in Geneva, New York (Lowe 1899), in Washington, D. C. (Chittenden 1904), and in Ithaca, New York, and in Belmont, Massachusetts (Slingeralnd 1899). Slingerland (1902) subsequently reported that infestations had occurred during the 3-5 years before 1899 in Massachusetts, New York, Pennsylvania, and Iowa. These infestations were all attributed to R. cingulata.

R. fausta was first collected from Mt. Washington, New Hampshire (Osten Sacken 1877). The first infestation of R. fausta occurred in 1904 in Victoria, B. C., and was mistakenly reported by Fletcher (1907) to be R. cingulata (Illingworth 1912b). Illingworth found that fausta was

as common as cingulata in New York in 1912. After further investigations he concluded that much of the damage attributed to cingulata was actually due to fausta. It did not occur on domestic cherry in Michigan as late as 1927 (Pettit 1927), but was first recorded in two counties in 1929 (Pettit and Tolles 1930). In Oregon fausta has never been reported from commercial cherries, though it is found on P. emarginata (Jones 1939, AliNiazee and Capizzi 1976). In Montana's Flathead Valley, fausta was the pest for many years (Strand 1934, Eichman 1936, Proverbs 1953). Frick and Simkover (1953a) reported that fausta was of very limited significance as a pest in Washington; it was a serious pest only at Cashmere. In British Columbia R. fausta has been a serious pest in the Kootenay district for many years (Ruhmann 1926, Twinn 1932). Andison (1952) recorded it in the Okanagon Valley, but it was absent from the rest of the lower mainland of British Columbia (Proverbs 1953); it was also absent from the Okanagan Valley 1952-64, but reappeared in 1965 (Banham 1972). Raine and Andison (1958) noted that R. fausta has been a persistent but minor pest on Vancouver Island, where its emergence is late, in sharp contrast to most other areas where fausta emerges before indifferens (Madsen 1970) or cingulata (Forsyth and Buriff 1969, Caesar and Spencer 1915).

The first report of a western cherry fruit fly infestation was in 1908 at Stayton, Oregon; which was followed by one at Salem in 1909 (AliNiazee 1973). The first published report was by Wilson and Lovett (1913). The species became a serious pest in Oregon "around 1916" (Ellsworth 1943). It was first discovered at Hood River in 1929 (Marble 1939). S. C. Jones[4] found the western cherry fruit fly on P. emarginata in southern Oregon near Roseburg and Ashland. Commercial orchards were within three miles of infested wild cherry near Ashland, but at lower elevations. Commercial orchards in the Rogue River Valley were not infested until 1950 (Berry 1951, Messenger 1950).

The western cherry fruit fly did not reach the Puget Sound region of Washington until 1918 (Frank 1918). It had spread to the Palouse region of eastern Washington by 1924 (Melander 1924), and was found in five Washington counties by 1928 (Fleury 1928). It was not found on cultivated cherries in the Yakima Valley of Washington until 1942 (Eide 1945, Shipman 1951), nor in the Wenatchee area until 1950 (Frick et al. 1954). In British Columbia the western cherry fruit fly was first reported in the mid 1930's on Vancouver Island where it

[4]Investigations to determine the identity of fruit flies infesting cherries in the west. Supplement to the annual report on cherry fruit fly for the Agricultural Experiment Station, Oregon State University, unpublished. 1944:10-13.

caused serious damage in 1938 and 1939 (Downes 1952); it has remained a pest of varying severity (Twinn 1943, Andison 1952). The pest did not reach the Fraser Valley until 1947 when it was found at Sumas (Andison 1948). R. indifferens first appeared in the Kootenay district in 1962 (Arrand and Peters 1968) and in the Okanagan Valley in 1968 (Madsen 1970). The insect had been of only minor and sporatic significance in Montana (Cooley 1922, 1925) where R. fausta had been the major pest. More recently, however, indifferens has surpassed fausta as the primary insect pest of cherries in Montana (USDA 1964, 1968). Manis (1956) reported that both species were present in northern Idaho, while indifferens first appeared in southern Idaho cherry growing areas in 1956.

Difficulties in changing hosts -- The irregularity of cherry fruit fly infestations before 1899 in the East may be due in part to a lack of record keeping. Chittenden (1904) supposed that previous to 1899 fruit fly damage was commonly attributed to the plum cucurlio. However, such a scarcity of recorded infestations is an indication of a lower level of pestiferousness than is currently true for cherry fruit flies.

Shortly after the turn of the century, there were no good control techniques available, except for clean picking--the removal of all fruit from the tree--which

was not widely practiced. At the present time, in uncontrolled situations, infestation levels commonly reach 50 to 100 per cent (Frick and Simkover 1953a, Newcomer 1966, personal observation); sometimes the infestation may go from 2 to 3 per cent to 40 to 50 per cent in one generation (Parrott 1933). Furthermore, good control was difficult to achieve with lead arsenate the first year after an infestation had been allowed to develop (Hufford 1939). It seems extremely doubtful that the cherry fruit fly could have been an unnoticed pest for very long.

Slingerland (1902) noted that while considerable damage was done by the cherry fruit fly in 1900, it gave little trouble in 1901. This decline and the apparently sporadic nature of early outbreaks are at variance with present-day uncontrolled populations. The sporadic nature of early infestations must in part have been due to the difficulty the insect experienced in changing from wild to domestic hosts.

Similarly (as was outlined above) the appearance of R. fausta and R. indifferens was very much delayed in some cherry growing areas of western North America. It is not known whether new infestations have spread from the original ones at Stayton and Salem, Oregon, or whether the cherry fruit flies have moved from their

native hosts to domestic varieties independently in other parts of the West.

Eide (1947) observed a population of R. indifferens on wild cherries near Wenatchee which had not moved to a nearby commercial orchard over a period of 12 years. Frick (1957b) noted that the first appearance of R. indifferens in the lower Yakima Valley was at Toppenish, 20 miles from the nearest native hosts. He suggested that the fly was imported to that part of Washington rather than moving from local pin cherries. In California, Mackie (1940) reported that cultivated cherries within a few hundred yards of infested wild cherries in northern California had never been infested.

The distance between wild cherry and planted domestic trees is the most obvious factor which has hindered the movement of flies to new hosts. In California, wild natural hosts are limited to higher elevations (Mackie 1942, 1943), where there are back-yard trees but no commercial orchards. The distance to a potential host does not need to be great to make the probability of a fly reaching it small. Members of the genus Rhagoletis have not been shown to travel great distances: a kilometer or less is probably the maximum flying distance (Jones and Wallace 1955, Barnes 1959, Leski 1969, Boller et al. 1971). Dispersal will be

greatest in those years in which there is little or no fruit to detain the flies at the trees where they emerge (Boller and Prokopy 1976). In some areas where domestic trees are irrigated, native cherries growing at the same elevation have had complete premature fruit drop in some years (Banham 1971). Such areas can not be expected to support a high population of flies.

It may be that infested native hosts were close enough to commercial and backyard trees only in one or a few areas and spread from there only by chance movement (such as movement of infested fruits by man). The slow spread in the discontinuous western cherry growing areas can be explained by either (1) movement from one or a few original infestations, or (2) independent movements from native to domestic cherries in many areas. Either event is one of low probability and could explain the late appearance on domestic trees of cherry fruit flies in the Pacific Northwest and British Columbia.

Geography does not provide as acceptable an explanation in the East. Here the topography forms much less formidible barriers. Also, the evidence indicates that populations subsided in some areas (Slingerland 1902, Chittenden 1904), which would not be expected given the lack of control measures. Problems involving synchrony of fruiting and fly emergence, and physiological

compatibility of flies to domestic cherries must have hindered the movement to the new hosts. Genetic changes in the fly population must have been necessary before it could thrive on the new host. These genetic changes and their associated host specificity have been studied in the cherry fruit flies and other members of the genus Rhagoletis as possible examples of early stages of sympatric speciation (Bush 1966, 1969).

When a fly reached the area of a potential host variety, it may not have found it as suitable as its usual host. The fruit may not have been suitable for completion of development, so that no adults emerged the next year.

The maggots that first infested a new host would have carried genes for earlier-than-average emergence, but only a small number may have been physiologically capable of completing development through adulthood on the new host. The evidence to support this theory seems limited to cingulata. Simkover (1953) found that indifferens from either a wild or a domestic cherry population preferred domestic cherries to wild: more larvae developed in the domestic cherries.

A most serious obstacle to host changing was the time factor: domestic cherries fruit much earlier than native varieties. Particularly if the domestic plantings

are picked clean, there is little likelihood that flies will be present early enough to move to the earlier-fruiting domestic varieties. Perhaps it was necessary for a combination of unusual conditions to occur: (1) weather patterns that resulted in early fly emergence relative to domestic tree fruiting, (2) cherry trees not being picked clean due to market or other factors, and (3) low production of cherries on the native hosts causing an increase in dispersal. Frick and Simkover (1953a) noted that in 1950, when domestic cherries were first infested in the Wenatchee area, the harvest was extremely late; in fact, domestic fruit matured at about the same time as wild fruit in that year.

One can imagine a population of flies with a genetic component such that at least some flies have a great potential for dispersal. One can imagine that many flies could develop equally well on either wild or domestic fruits. But as far as the timing of emergence is concerned, it is clear that there are selective pressures that would force a population to adapt to either the early fruiting of domestic varieties or the late fruiting of wild trees, unless a bimodal or very extended emergence pattern occurred.

The history of infestations of the cherry fruit flies suggests that the move from wild to domestic

cherries was not an easy one. The founders of the new domestic races of cherry fruit flies may have been genetically much different than the average fly of the population on the wild host--primarily in that they carried genes for earlier emergence. The genetic changes necessarily accompanying adaptation to a new host would have reduced the probability of encountering members of the parental strain during the critical mating period. The poor dispersal ability of the flies, and the difference in fruiting time of the wild and domestic cherries may have resulted in a large degree of reproductive isolation between the two populations. While the population on wild cherries should be considered in any area-wide eradication program, it is not an important factor in normal control measures.

B. Conventional Control

Control methods -- Control of the cherry fruit flies has varied over the years in both strategy and technique. Control measures have been dictated by the nature of the damage by the maggots. Injury is directly done to the salable product and any infestation causes a calculable loss. First and second instar maggots are hard to detect during the grading process, so under the stimulation of FDA requirements, canneries have set very low thresholds

of infestation, above which they will not accept cherries (Shipman 1951, Phillips 1952, Banham 1972). Such thresholds have varied with the size of the crop and the degree of control available (Parrott 1927).

The control strategies have been preventative for the most part, with control measures being applied whether or not the flies were currently known to be in the orchard. Control methods have most commonly consisted of chemical sprays or dusts directed against the pre-oviposition adults; but control efforts have also been directed against pupae in the soil or emerging adults, eggs or larvae in the cherries, and against larvae as they enter the soil (Bernard 1956). Cultural control measures (see below) and parasite release (Clausen 1956) have been tried with little success. Release of sterile males has progressed to the stage of small field trials against R. cerasi (Boller 1974).

At the turn of the century, when the cherry fruit flies were new pests, there were virtually no useful control measures (Moore 1910). Beach, Lowe, and Stewart (1899) recommended sanitation of packing houses and "good cultivation'. However, the puparia are too small for many to be broken or cracked by cultivation. Frick et al. (1954) found that mortality increased by only 11 percentage points following cultivation. Normal plowing

or cultivation will bring some pupae up to the surface where they will be exposed to weather and predators. Deep plowing may place some pupae too deep for flies to emerge, but Frick et al. (1954) found this effect to be a minor one.

Caesar and Spencer (1915) believed that cultivation was "useless", and that harder soil would retard entry of maggots ready to form puparia, enhancing the effects of predaceous ants and brids, including poultry. Chittenden (1904) and Sanderson and Peairs (1921) recommended fencing hens in around a backyard tree and raking the soil lightly to expose pupae. Perhaps the most effective early control measure was to destroy infected fruit as soon as the injury was noticed (Moore 1910, Hewitt 1911). Beach, Lowe and Steward (1899) recommended that the entire part of the orchard that was infested be destroyed. Prevention of a build-up in population by inspection has continued to be the mainstay of area-wide control programs (Hufford 1939, Figy 1950).

Lead arsenate -- For many years lead arsenate was synonymous with chemical control of cherry fruit fly. The early recommendation was to include a feeding bait with lead arsenate in a spray; this was the common control practice worldwide for Tephritidae at this time (Severin 1914). For instance, Caesar and Spencer (1915)

recommended 2 to 3 pounds of lead arsenate paste to 40 gallons of water and 1 gallon of cheap (black strap) molasses added immediately before spraying (to prevent fermentation of the molasses). The use of more expensive molasses (with sugar added) would have attracted and killed bees. Spraying twice for late varieties and once for early varieties was the usual recommendation.

Most recommendations for several years differed only slightly in the relative amounts of the ingredients (Coulter 1917, Quaintance and Siegler 1918, and Lovett 1923). Caesar and Spencer (1915) found that lead arsenate without molasses gave as good control as the mixture. Ten years later most recommendations were to omit the bait (Herrick 1925, Parrott 1926, Quaintance and Siegler 1931). In Oregon the recommendation to include the bait was made for many years (Jones 1939, Burtner 1943).

Lead arsenate has always been an effective chemical against cherry fruit flies (Illingworth 1912b, Porter 1958, Neilson 1976), although it was recognized that it was unsatisfactory in situations where untreated trees were in close proximity (Cox 1952). Middlekauff and Hansberry (1941) noted that it took 4 days for arsenicals to kill cherry fruit flies in laboratory tests. Generally, no ill effects on fruit or established trees have

been noted due to lead arsenate, which is the least phytotoxic of the arsenical insecticides (Matsumura 1975). However, stem and fruit injury from this chemical has been noted on some tender varieties such as Morello (Hedrick 1932).

Early authors did not recognize a residue problem on the fruit, although Caesar and Spencer (1915) and others suggested that the last spray might be eliminated on the early varieties to eliminate visible residues. The residue on cherries for fresh market (which were not washed) was recognized as undesirable (Hedrick 1932, Eide 1947) and research toward finding other compounds was spurred by this fact and the problem of legal residue tolerances on fresh market cherries (Ladd 1933, Glasgow and Gambrell 1947).

Robinson (1932) estimated that in dry years (in Oregon) approximately 50 per cent of the cherries would have arsenical residues above the tolerance level of 0.01 grain arsenous oxide per pound of fruit (= 1.4 mg/kg). He also reported on several experimental washing treatments. Hamilton and Pearce (1938) suggested lower dosages of lead arsenate be used, and Hamilton (1940) substituted other arsenicals late in the season to reduce residues.

Arsenical residues have been a problem not only on

the fruit but in the soil as well (Boswell 1952, Rudd 1964). All arsenicals leave water-insoluble residues in the top soil layers (Matsumura 1975). These residues do not affect established trees; but cover crops, replantings, or plantings of field or vegetable crops where an orchard was taken out have been adversely affected (Boswell 1952). Beegle (1975) cited the problem of arsenic residues in the soil of Pacific Northwest orchards as the one example of "irreparable harm" done by insecticides.

Non-arsenical chemical control -- The search for a substitute for lead arsenate was pursued throughout the 1930's, but it remained the best chemical control for cherry fruit fly until the mid-1940's (Porter 1958). Manis and Portman (1950) strongly recommended it as a post harvest spray as late as 1950. Hedrick (1932) found the fluorosilicates promising. Cryolite was a very promising chemical for several years (Ladd 1933, Glasgow and Gambrell 1947, Eide 1947), but lost favor due to its incompatability with some fungicides (Cox 1952). Eichman (1936) used Dutox (barium fluorosilicate) for the last spray to reduce residues.

Rotenone was the second non-arsenical insecticide to be widely tried as a substitute for lead arsenate. Ladd (1934) and Glasgow and Gambrell (1947) recommended

rotenone for fresh market cherries. Hamilton (1940) and Parrott (1942) found that only phenothiazine or rotenone could be substituted for lead arsenate, and the latter was preferred due to the cost and irritating nature of phenothiazine. Eide (1947) found that phenothiazine gave better control than lead arsenate. He believed that rotenone retarded the growth of maggots and gave poorer control of adults than was generally believed; he found sprays and dusts of rotenone that were applied by air to be satisfactory, however. Phenothiazine was not entirely compatiabe with fungicides (Cox 1952) and left a heavy residue (Webster and Eide 1945). Rotenone became the standard treatment on fresh market cherries, although it was more costly and somewhat less effective than lead arsenate (Porter 1958). Rotenone has been used recently in some areas during cherry harvest (Johansen 1971), or where "organically grown" cherries are desired.

Glasgow and Gambrell (1947) reported that DDT and benzene hexachloride were unsatisfactory as sprays against adults. Cox (1952) found DDT to be effective and regarded BHC as a rather good control agent, but noted that the former resulted in excessive residues after normal washing, and the latter gave cherries a disagreeable odor. Eide (1947) found that BHC gave 100 per cent control when applied to the soil before mature

larvae were added. It was the DDT analog methoxychlor which first joined rotenone as a standard substitute for lead arsenate sprays or dusts (Frick 1950, Jones 1950, Porter 1958).

Many organophosphates are effective against cherry fruit fly. Parathion was one of the first and most effective organophosphates, acting against larvae in the fruits as well as against adults (Sherman 1951, Cox 1952, Frick and Simkover 1953b). It has a 14-day pre-harvest limitation, however (AliNiazee and Capizzi 1976) and has been used post-harvest to help reduce fruit fly populations for the following season (Johansen 1971).

TEPP has been used just before harvest because its residues dissipate rapidly (Frick and Johansen 1953), but it is highly toxic to mammals; Frick (1957a) suggested that DDVP (dichlorvos) might be able to replace it. Malathion ULV at 12-16 ounces per acre (0.9-1.2 liters/hectare) has been found to be effective and satisfactory (Zwick et al. 1970, AliNiazee and Capizzi 1976), and its use has become widespread in the Dalles and the Willamette Valley (AliNiazee 1973b).

Azinphosmethyl has been found effective against cherry fruit flies (Frick 1959, Wooley and Mills 1960). Diazinon is much less toxic to mammals than parathion, but Frick (1957a) found it slightly superior for control

of western cherry fruit fly. Johansen (1971) briefly reviewed the control measures available at the start of the 1970's and concluded that diazinon was the most nearly perfect cherry fruit fly control chemical available at that time.

Eradication effort in California -- The planning for any area wide eradication program for cherry fruit flies should include consideration of the strategy and techniques employed in the northern California eradication effort of the 1950's. It was a multi-faceted effort and was described by Robinson (1951, 1952) and Armitage (1953). It was basically a four-pronged attack against the flies, including (1) the removal of as many host trees as possible, (2) removal of fruit from trees prior to infestation, (3) application of soil insecticides, and (4) weekly application of foliage sprays (methoxychlor) to host trees. Effectiveness of the program was monitored with sticky ammonium carbonate traps and per cent infestatation checks at harvest. The program was dropped because it was not eradicating the pest (Harper 1966). With the additional tool of sterile insects, such a program might be effective.

C. Induced Sterility in Insects

Effects of irradiation -- Soon after their discovery,

X- and gamma rays were found to penetrate and affect or kill living tissue. In 1906 Bergonie and Tribondeau enunciated what is perhaps the most basic law of radiobiology: the radiosensitivity of cells is directly proportional to their proliferative activity and future, and inversely proportional to their degree of differentiation. Lethally irradiated cells tend to die at division, primarily because of damage to chromosomes which results in the daughter cells receiving a deficient genetic complement (Davies and Evans 1966, Lawrence 1971).

Germ cells are actively dividing cells and are radiosensitive. Exposure of germ cells to radiation can result in mutated offspring or a reduced ability of the irradiated adult to produce viable offspring. The latter effect, following irradiation of an insect, is commonly referred to as radiation-induced sterility, regardless of the pathway by which it was obtained. Such sterility can result from infecundity, aspermy, sperm inactivation, altered mating behavior, as well as genetic effects (LaChance 1967). Point mutations are not an important part of radiation-induced insect sterility (Lawrence 1971), and sterility due to aspermy and differences in mating behavior are usually unacceptable for a sterile insect technique (SIT) program because they do not

prevent normal males from fertilizing eggs.

The most desirable type of genetic damage in insects for SIT programs is 'dominant lethality'. Muller (1927) first used this term to describe damage to germ cells that caused death to the embryo after fertilization. Mandl (1964) noted that this term may actually cover a wide variety of changes whose effects are all expressed as death in the embryonic stage. Most commonly, acentric or dicentric chromosomal abberations cause a maldistribution of genetic material during mitosis. Eggs that die due to dominant lethality are commonly said to be 'infertile' even though a union of gametes has taken place so that the term is technically incorrect (Bushland 1960).

In the lepidoptera and other insects with holokinetic chromosomes (with diffuse centromeres), the doses of radiation necessary to induce sterility are higher than in other insects. In these insects chromosome fragments are not lost during mitosis because each fragment has its own spindle attachment. Translocations occur, however, and F_1 sterility follows due to the effects of aneuploid segregation at meiosis in the translocation heterozygote (North and Holt 1968, Curtis 1971). North (1975) discussed the problems of irradiation of lepidoptera and the "inherited sterility"

modification of SIT. See also LaChance (1975).

The effects of radiation on insect germ cells depend on the stages (of spermato- or oogenesis) present at the time of irradiation (Mandl 1964, Curtis 1971). Insects are most often irradiated in the late pupal stage or sometimes as young adults. At these times there are spermatids and spermatozoa present (LaChance 1967, Englemann 1970, Grosch 1974) and the irradiation of these stages usually results in viable sperm with dominant lethals. LaChance (1962) found in Cochliomyia hominivorax (the screwworm) that pupae were sterilized at a somewhat lower dose than adults, presumably due to the greater number of spermatids which are more sensitive than spermatozoa. After utilization of spermatids and spermatozoa that were present at the time of irradiation, a period of aspermy may result because irradiated spermatocytes produce few mature sperm, even after low doses (Riemann 1967).

At low doses some primary spermatogonia will survive and repopulate the gonads with the various stages of germ cells, which will eventually result in the production of viable sperm capable of fertilizing ova. Riemann and Thorson (1969) investigated by cytological techniques the doses necessary to prevent the regaining of fertility in three species of Diptera and found that a dose that

induced 90 per cent dominant lethality was sufficient for most flies. Steiner and Christenson (1956) studied Dacus dorsalis Hendel, D. cucurbitae Coquillett, and Ceratitis capitata (Wiedemann), and found that a substantial loss of sterility in males occurred 30-50 days after sterilizing with 8.4 krad or less.

In the case of irradiated females, the most common effect of radiation is infecundity, caused by death of the eggs due to genetic damage to either the eggs or to the trophocytes (LaChance and Leverich 1962, LaChance and Bruns 1963, Bacetti and de Dominicis 1963). As with other Hymenoptera, Habrobracon juglandis (Ashmead) exhibits facultative arrhenotoky, that is, unfertilized eggs produce males: Whiting (1946, 1955) found that females produced eggs for five days after irradiation, and that irradiated females mated to males with genetic markers produced all male progeny showing markers. The fact that all progeny were male showed that only the haploid number of chromosomes were present (or operative). The genetic markers showed that the genetic information had come from the male parent, and therefore the genetic material contributed by the female had been rendered inoperative by exposure to irradiation. These experiments demonstrated that the damage to the egg was genetic and not cellular in nature. Grosch (1971) reviewed the

response of female arthropods to sterilizing agents.

The dosages of radiation necessary to sterilize higher Diptera have been in the range of 3-10 krad. For two economically important species a dose of only 3 krad has been found sufficient: the onion fly Hylemya antiqua (Meigen) (Noordink 1971), and the house fly Musca domestica L. (Smittle et al. 1971). Furthermore, Noordink (1971) reported that female onion flies were infecund at a dose of 2 krad; Shepard et al. (1972) reported sterility in the house fly at 2 krad and infecundity of females at 7 krad.

Doses of 6-10 krad have induced sterility in tephritids. Steiner and Christenson (1956) reported a radiation dose of 6.7 to 8.4 krad was required in three species of tropical fruit flies. However, a dose of 9.5 krad was used in the eradication of one of the three, Dacus cucurbitae, from the island of Rota (Steiner et al. 1965). Hooper (1971) found that 7 krad produced 99.5 per cent sterility in male Mediterranean fruit flies, Ceratitis capitata, and 3 krad produced infecundity. Burditt et al. (1975) reported that exposure of adults or pupae to 5-8 krad caused sterility in male Caribbean fruit flies, Anastrepha suspensa Loew; the females were rendered infecund by these dosages.

While tropical fruit flies are almost always

irradiated as pupae, temperate fruit flies are most often irradiated as adults becuase of the extended period for adult emergence (Haisch and Boller 1971, Boller et al. 1975). Boller et al. (1975) found a 99 per cent reduction in egg hatch after irradiating male R. cerasi with about 9.5 krad. Females were less sensitive than males: 99 per cent reduction in the hatch of eggs laid by irradiated females did not occur until after a dose of about 14 krad. Fecundity was still about 30 per cent of controls after doses as high as 20 krad.

The biometry of radiobiology is presented and discussed by Fabrikant (1972). Curtis (1971) and Lawrence (1971) also discuss methods of representing radiobiological data.

Ducoff (1972) and Grosch (1974) discussed the causes of death in irradiated insects. The short life span of most (adult) insects makes it difficult to divide radiation-induced insect mortality into the bimodal distribution of acute and delayed death that can be seen in mammals.

An increase in post-radiation mortality should be attributable to a specific mode-of-death, associated with damage to a particular sensitive tissue. The 2-week or hemopoetic syndrome in insects (as well as the 4-day death in rodents) is believed to be caused by intestinal

damage (Ducoff 1972). Riemann and Flint (1967) clearly demonstrated that midgut damage was the main cause of increased mortality following irradiation of adult boll weevils, Anthomus grandis Boheman. This mortality can be decreased by fractionation of the dose (Hayes et al. 1977). However, for most insects the causes of irradiation-induced increases in mortality are not clear-cut. Little (1967) found that damage to the midguts of an earwig, Chelisoches morio (F.), and the Mediterranean fruit fly, was insignificant following lethal irradiation.

In Diptera, somatic cell division is generally lacking in adults, and irradiation of adults apparently accelerates natural mortality patterns. At any rate, the damage done and consequent lethality are more dose dependent than in most other insects (Ducoff 1972). Baxter and Blair (1967) have done extensive radiation studies on Drosophila and found a clear dose-longevity relationship.

Increased mortality may be due, at least in part, to impairment of phagocytic and other humoral components involved in an insect's disease resistance (Elbrady 1964, Mortimore et al. 1970). Damage to the mid-gut by radiation and the consequent loss of phagocytes and invasion of microbes into the hemocoel may be important in insects

as in mammals (Grosch 1974). Jafri (1965) demonstrated that pathogens can depress the radiation dose required for increased mortality in Tribolium castaneum (Herbst)--however, see comments by Ducoff (1972).

Irradiation of insects sometimes has the unexpected effect of increasing longevity in insects. In many cases, such as Drosophila spp. (Lamb 1964, Sacher 1963) and the house cricket, Acheta domesticus (L.) (Hunter and Krithayakiern 1971), the life span of the female is markedly increased, and it has been suggested that this is due to the reduction of energy put into reproduction. In other cases, for instance the codling moth, Laspeyresia pomonella (L.) (White and Hutt 1970), longevity increased for both sexes after irradiation. In the house fly, Musca domestica, (Pockstein et al. 1967) doses of 10 or 15 krad increased the longevity of the males; this is believed to be due to retardation of physiological processes and lowering of activity levels--wing abrasion in males was reduced (see Ducoff 1972, for further references). Boller et al. (1975) reported increased longevity after 10 krad, but decreased longevity after 12.5 krad and higher doses for male R. cerasi.

Chemosterilants -- Sterility can be induced by chemical agents as well as gamma irradiation and X-rays. Agents such as juvenile hormone analogs may affect insect

fertility or fecundity (Riddiford 1972, Rens 1975, Moreno et al. 1976). The monogamy-inducing hormone of the accessory gland could be used to prevent mating (Leopold 1976). Some organo-metalic fungicides have insect-sterilizing properties, although they have not been expressely used in that way (Davidson 1974). Antimetabolites most often act by producing infecundity in the female by inhibiting the production of gametes. L-asparaginase is the only known enzyme with insect-sterilizing effects (Chang et al. 1974).

The most widely used chemosterilants--the alkylating agents--induce dominant-lethal mutations, as does irradiation. Most modern chemosterilants--such as tepa, metepa, thiotepa, tretamine, and apholate--are aziridines (Boŕkovec and Woods 1963, Boŕkovec et al. 1968).

Chemosterilants are cheap, and may be applied orally or topically by many different means. They do not require an expensive apparatus, as irradiation methods do, but the dosage is more difficult to control with chemosterilants (Curtis 1971). The possibility of attracting insects to a chemosterilant in the field and thus directly sterilizing part of the wild population has been an attractive potential advantage; Knipling (1968) calculated the extra advantage of this method. Furthermore, it has been suggested that in some cases

insects might carry enough of the chemosterilant with them to also sterilize individuals with whom they mate ("boobytrapping": Morgan 1967, Whitten and Norris 1967). Unlike radiation-sterilized males, chemosterilized males commonly show hypercompetitiveness. Boŕkovec (1966) suggested that this effect was due to the chemosterilant from released males sterilizing the females or sterilizing the sperm from previous or subsequent matings.

However, the sterilizing, mutagenic and generally toxic properties of alkylating agents and most other chemosterilants also extend to vertebrates; and these agents may be carcinogenic also (Hayes 1968). Hence the use of non-persistent chemosterilants has been favored, and their use will probably be restricted to use in programs involving the release of mass reared insects (McDonald 1974). Because of their high toxicity, chemosterilants are looked at with generally less favor than gamma irradiation unless the latter is unacceptable for some reason--e.g. gamma irradiation damaged the gut lining of adult boll weevils (Riemann and Flint 1967), so chemosterilants were used to supplement irradiation (Klassen et al. 1969).

The subject of chemosterilants has been reviewed by a number of authors, including Smith (1963), Boŕkovec (1966), LaBrecque and Smith (1968), Campion (1972), and

Davidson (1974). Campion (1972) lists 640 references dealing with chemosterilants, and in an appendix lists the references by insect or mite species studied. McDonald (1974) discusses the future of chemosterilants and reviewed their hazard to vertebrates.

D. Sterile-insect Technique

The screwworm -- The sterile insect release method (SIRM), or sterile insect technique (SIT) was conceived in the late 1930's (NAS 1969). The screwworm, Cochliomyia hominovorax (Coquerel), was selected as the target pest. The female of this species only mates once, and it was reasoned (Knipling 1955) that if the one mating was to a sterile male, then no progeny could result. In addition, the screwworm was restricted to very small overwintering areas in the U. S., and a method for rearing on an artificial medium was known. After it was determined that females and males could be sterilized by a dose of 5 krad (Baumhover et al. 1955), and that irradiated males were reasonably competitive, the technique was applied in samll scale trials.

Suppression of a population of screwworms by SIT was first demonstrated on Sanibel Island, two miles off the Florida coast in 1952. Eradication of the insect was first achieved from the island of Curaçao after 13

weeks of releasing less than two sterile males per hectare (435 per sq. mile) per week (Bushland 1960).

The screwworm had been introduced into the southeastern U. S. in 1933; it overwintered in part of southern Florida only, and expanded northward annually. It was eradicated from this area by releasing over two billion sterile insects (mostly in Florida) over a period of 18 months. Both sexes were released because of difficulties involved in separating them. The eradication of the screwworm from the southeastern U. S. remains the only successful eradication of a species from a large area, and was described in detail by Bushland (1960).

The continuing release of millions of sterile adult screwworms in the southwestern U. S. and northern Mexico must be considered to be a suppressive rather than an eradicative measure. Except for 1972, when nearly 100,000 cases of screwworm infestation occurred in the U. S. (Davidson 1974), this release has kept the fly at very low levels (LaChance 1974, Bushland 1975). An effort to extend this sterile-insect barrier further south to a narrower section of the Central-American isthmus (as was first suggested by Hightower and Graham, 1968) is currently underway.

Requirements for SIT -- The biological and ecological

attributes of C. hominovorax have sometimes been considered as guidelines for selecting candidates suitable for SIT--especially the traits of monogamy and extremely low population density. However, the peculiarities of each insect species will determine whether it can be suppressed by SIT, and it cannot be predicted with assurance ahead of time which species are amenable to this technique. There are a number of factors that must affect the feasibility of SIT, however, and these must be considered in order to try to predict the liklihood for success, even if they are not all requirements in every case:

1) First of all, some method of inducing sterility without undesirable behavioral changes or undue loss of competitiveness must be available. The point is discussed elsewhere.

A nitrogen atmosphere during radiation has a protective effect on biological material, primarily because it produces anoxia (Arena 1971, Coggle 1973). Studies with the Mediterranean fruit fly have shown that competitiveness is improved by irradiation in a nitrogen atmosphere (Hooper 1971b, Langley and Maly 1971, Wakid 1973). Ohinata et al. (1977) reported that atmospheres of carbon dioxide, helium, partial vacuum, or nitrogen during radiation of pupae each resulted in better competitiveness than air.

The reduction of competitiveness following induced sterility has prompted some scientists to emphasize alternate sources of sterile insects (Denell 1973, Whitten and Pal 1974). For a number of insects these alternate methods have been promising--e.g. cytoplasmic incompatability in mosquitos (Pal 1974, Grover et al. 1976).

2) The female must be monogamous, or the sperm must be competitive. LaChance (1975) noted that in lepidoptera, eupyrene sperm must be transferred to affect the female, while in many Diptera the transfer of secretions from the male (without sperm) will elicit changes in mating behavior and stimulate oviposition.

Polygamy may actually be more advantageous than monogamy in some cases. In several species sperm from the last mating take precedence: R. cerasi (Boller et al. 1975), the red cotton bug, Dysdereus koenigii F. (Harwalkar and Rahalkar 1973), the tobacco budworm, Heliothis virescens (F.) (Flint and Kressin 1968), and several species of beetles (Henneberry et al. 1964, Ladd 1966, Lindquist and House 1967). This is in contrast to insects such as the cowpea weevil, Callosobruchus maculatus (F.) where sperm from the first mating have some precedence (Tilton and Browder 1973). In Ceratitis capitata, Causse (1970) found initial precedence by

sperm from the last mating was followed by a mixing of the sperm. If sperm from the last mating has precedence, immigrating polygamous females that have already been fertilized could still be affected by SIT.

3) A method of mass rearing the insect should be available: a look at the huge numbers released in the screwworm eradication and suppression projects would seem to make this point an absolute requirement, but this is not necessarily so. Autocidal methods may be so much more efficient at very low population densities than other available methods that even SIT utilizing field-collected material may become economically feasible. As Knipling (1964) has said:

> As a general working hypothesis, it is submitted by the writer that where the complete elimination of a bisexual insect population is the final objective, and is feasible with current control procedures, there will be circumstances where final elimination can be brought about more effectively by the release of sterile insects, regardless of the cost of producing them.

Horber (1963) demonstrated suppression in the cockchafer, Melolontha vulgaris F., using field collected material. This insect has a three year life cycle and could not very well be mass reared. Furthermore, the tsetse sly, Glossina spp. is considered a very good candidate for SIT (Knipling 1967) in spite of its very

low reproductive potential. This insect only produces one offspring every 6-11 days, for a total of 8-9 pupae per female (Offori and Dorner 1975). This facet of its biology works both ways, however, and the lack of increase potential, plus the efficiency of SIT at the very low population densities common for this group of insects outweigh the production problems. Mass rearing techniques have been developed for this insect (Nash et al. 1971, Offori and Dorner 1975) and suppression of a population of G. morsitans Westwood had been demonstrated (LaChance 1974).

4) The presence of a low population level at some point in the insect's life cycle might also be considered a necessity. However, the more efficient mass-rearing techniques are, the higher the populations that can be suppressed. (If the chemosterilant-bait combination is being used, populations need not be very low, unless the adult form is injurious at the unreduced levels.)

When the field population is not reduced to low levels by natural factors before SIT is used, it is necessary to have other good methods of reducing the population. This is the situation with the cherry fruit flies. Commercial practices regularly bring the fly population down to the very low level where the SIT can be expected to be efficient--but because of the extremely

low economic threshold for this insect, further diminution (eradication) is desirable.

5) Information on the rate of increase, as well as the population density at the time of release, are needed. Both of these parameters may be difficult to measure under commercial crop conditions, and the information obtained from uncontrolled situations (e.g. abandoned orchards) may not be applicable to agricultural situations (Bogyo 1974).

Knipling (1964, 1966) assumed a rate of increase (r) of 9x in the numerical tables he developed to explain the principles of SIT. Bogyo (1974) emphasized that this parameter greatly affects the chances for success of SIT. He noted that the time (generations) until eradication would vary depending on the value of r.

The measurement or calculation of density and rate of increase are somewhat simplified for a univoltine insect, which has only one chance to increase during the year. In the case of cherry fruit fly, the population level may be measured by sifting soil samples containing overwintering pupae, by emergence traps, by baited yellow sticky traps to catch adults, or the level may be estimated from infestation levels from the previous year. The yellow sticky traps would be most useful in a SIT program because (a) in a high density situation,

the population would be reduced prior to SIT by chemicals, so only the post-chemical density would then be of interest; and (b) in a low population situation, the assessment of migration into the orchard would not be assessed by other methods.

Determining the point at which an insect has been eradicated is usually more difficult. The index for the screwworm eradication was the absence of infested livestock (Bushland 1960). It was assumed that a reservoir in wild animals did not exist after livestock showed no infestation for a period of time. This assumption would not be safe where different strains of an insect existed on different hosts. For the western cherry fruit fly, movement from the wild host is so difficult that it may be considered as a separate problem after the population on domestic cherries is eradicated.

The bait and other traps available for cherry fruit flies are not attractive enough to depend on them for determining if eradication has been achieved. Steiner (1969a) found that even with the very good sex lures available for tropical fruit flies, populations could exist at very low levels for 1-2 generations without detection. (The low dispersal capability and monophagous habit of the cherry fruit flies will make trapping

easier, however.)

Determination of eradication may require examination of a large volume of fruit. However, this would only be necessary if the cessation of all control measures was contemplated. In a cherry growing area such as the Willamette Valley, the question will be for a long time, not whether to continue to release, but whether to spray or to release the sterile flies.

6) The costs of SIT must be less than current control costs plus losses. Alternatively, the cost of a SIT program might be partly or wholly underwritten by a governmental agency which might figure in the benefit of a social or environmental nature, rather than just the cost-benefit economics that a grower would be concerned with. The achievement of eradication would, of course, greatly lower pest control costs in future years. Lever (1971) discusses the economic factors affecting the decision of whether to include SIT as part of a control program.

The SIT would be most practical for those insects with a restricted host range and a crop of high economic value--particularly if concentrated in a small area (Knipling 1964). The intensive use of chemicals during the short cherry fruiting season to achieve very low population levels, the restricted host range of cherry

fruit flies, and the high value of cherry fruit, are all favorable indicators for the economic feasibility of SIT against western cherry fruit fly.

7) The released insects must not cause annoyance or undue losses. The release of only male mosquitos, which cannot vector disease, is the classic illustration of this point. Similarly, female fruit flies may cause damage by ovipunctures in fruit (Steiner and Christenson 1956, de Murtas et al. 1970). Female cherry fruit flies may inoculate the brown rot disease organism, Sclerotinia fructicola (Winter) Rehm into cherries at the time of ovipuncture.

An economical method for separating males and females must be available if it is necessary. The size and weight differences between sexes in the pupal stage may be sufficient to serve as a basis for doing this in cherry fruit flies. Whitten and Taylor (1970) and Grosch (1971) have advocated increased use of females in SIT, for example, the release of sterilized females in separate areas.

8) Good air or ground release methods for distribution of the pupae or adults without injury and with adequate coverage must be available or developed.

SIT, tephritids, and orchard pests -- Although mention of the sterile insect technique automatically brings the

screwworm to mind, the effects of gamma radiation and/or chemosterilants have been investigated for a great many other species (Davidson 1974). LaChance (1974) listed 18 species in which population suppression by SIT had been demonstrated. Of these, five were tropical fruit flies: Ceratitis capitata (Wiedemann), Dacus dorsalis (Hendel), Dacus cucurbitae Coquillet, Dacus tryoni (Froggart), and Anastrepha ludens (Loew). The suppression of C. capitata in Costa Rica (Rhode et al. 1971) and Tunesia (Cheikh et al. 1975) was particularly significant because of the size and practicality of the programs.

Field trials with the European cherry fruit fly have since been reported (Boller 1974, Boller and Remund 1974). In addition to this cherry-infesting species and the tropical fruit flies that infest citrus and other tree fruits, one other orchard pest, the codling moth, Laspeyresia pomonella (L.), is being studied in a SIT research program, which has progressed as far as field releases (Proverbs et al. 1969, Butt et al. 1970, Proverbs 1971).

The radiation biologies of the various tephritids are fairly similar, but the ecology of the tropical tephritids is so different from temperate species that the problems involved in the application of SIT will be

much different. For instance, the great dispersal capabilities, and the polyphagous habits of tropical fruit flies (they are not even limited to orchard crops) necessitate a program over a wide area. On the other hand, temperate tephritids, such as the western cherry fruit fly, are restricted both by their narrow host range and their limited powers of dispersal (Bateman 1972, 1976). Although an area-wide strategy could be used against these insects, the SIT could be used on a more limited scale: to achieve eradication (for the season) and guard against immigration from nearby areas. Although wild fruit is not a common source of infestation due to differences in fruiting time (see section IA), and the western cherry fruit fly is otherwise monophagous, immigration from abandoned domestic and mahaleb trees is a very serious problem.

Recent reviews of the sterile insect technique have been done by Proverbs (1974), Pal and LaChance (1974), and Whitten and Foster (1975).

II. MATERIALS AND METHODS

A. Source of Insect Material

The adult flies used in these experiments were reared from maggots, or from pupae, collected in a heavily-infested, abandoned cherry orchard located in northwest Benton County, Oregon. This orchard contained mostly sweet cherry varieties, but there were also several sour and mahaleb trees.

Soil samples were taken from two to twelve cm deep and kept in an unheated building until pupal collection. Overwintering pupae were separated from the soil with a Salt-Hollick wet sieve apparatus in which the soil was forced through two different mesh screens with a pressurized stream of water from a garden-hose nozzle. Floating pupae were collected onto paper towels, and later counted into Petri dishes. This method was used exclusively in 1973, and to a minor extent in 1974-76.

Soil was collected from beneath sweet cherry trees on several dates in 1973, and pupae from these samples were transferred to 3° C. Soil samples were collected on August 17 and pupae were refrigerated on August 20; similarly on August 20 and 22; on August 23 and 29; and on August 30 and September 25. Pupae from each collection date were split into groups of 25 and kept under

refrigeration for 30, 60, 90, 120, or 150 days to determine the minimum chilling requirements.

In 1974-76 nearly all pupae were obtained by collecting maggot-infested cherries in July. In the laboratory, these cherries were piled two deep over hardware cloth which was supported 3.8 cm high over the floor of a container with about 0.5 cm of dirt in the bottom. The cherries-over-dirt were kept at 26.7° C in 1974 (for emergence in 1975) and at 21° C in 1975 and 1976.

Two weeks or more after the cherries were set over the hardware cloth (when the maggots were no longer to be seen crawling over the surface of the soil) the soil was sifted with 6.3 mesh per cm screen (equivalent to U. S. series 18). Containers of pupae (100 pupae per Petri dish or 3/4 oz. (22 ml) condiment cup with plastic lid) were put into a walk-in refrigerator for 30-340 days at a temperature of 3° ± 1° C (except for one hour per day when the unit self-defrosted and the temperature would rise to 7° C). A few dishes were kept at 6° or 10° C for part or all of their chilling period.

In referring to the amount of insect material obtained from a lot of cherries, two terms are used. The per cent infestation refers to (number of infested cherries/total number of cherries), and the per cent

yield refers to (number of maggots and pupae/number of cherries).

After the desired period of chilling, the pupae were removed from refrigeration and held at 26.7° C for emergence. In 1975 pupae were removed from refrigeration and held at 26.7° C for emergence. In 1975 pupae were removed from refrigeration in lots of 400 after 99, 150, 201, 240 and 263 days to determine emergence curves. Emergence from pupae removed at other times, as needed for other experiments, was also recorded (Figure 1). All flies emerged in Petri dishes, and before they began to emerge a drop of honey was put on the lid of the Petri dish to supply food to the flies immediately upon emergence.

Eight lots of 200 pupae were sifted with a screen with 10 mesh per linear inch (= ca. 4 per linear cm) to see if pupae could be sexed on the basis of size.

B. Irradiation of flies

Flies were irradiated in the Co-60 gamma radiation facility at the Radiation Center, Oregon State University. The irradiator is a custom built machine designed to give high gamma dose rates. The source is in the form of 12 rods which are arranged in a circle to form a cylinder which can be raised to surround the lower part

of the irradiator sample chamber (see illustration in Appendix D). All irradiation work with western cherry fruit fly was done in this lower part of the chamber.

The irradiator was loaded with a 3300 curie Co-60 source in February 1963. During the course of the experiments reported herein, the dose rate varied from 2000 to 1600 rads per minute (decreasing with time). The dose rate for any particular day was calculated by interpolating between values for the first day of each month. These values were available for two positions within the chamber. I calculated such values for the position which was used to irradiate the fruit flies (see Appendix D).

Radiation intensity varies inversely with the square of the distance between the source and the point of measurement (Arena 1971). The dose rate at the center of the irradiator was about 0.7 times as great as at the edge (position E vs. position D of P. A. Harmon[5]) where the flies were placed for irradiation. The use of small irradiation containers for the flies minimized the variation in dosage due to distance effects: flies were irradiated in small plastic containers, 5.1 cm high and 1.9 cm dia.; or 10.2 cm high and 3.2 cm dia., if many flies were being irradiated together. Control flies

[4]Thermoluminescent dosimeter calibration of the Oregon State University Radiation Center Cobalt-60 Irradiator, unpublished. 1976. 32 pp.

were taken to the irradiator room, but were not placed in the irradiator. Flies were irradiated as adults 1-3 days old, or as pupae 1-4 days before emergence.

C. Laboratory Cages

Flies were collected daily and put into holding cages or directly into experimental cages. All cages were kept at 26.7° C. Holding cages were one pint ice cream cartons (9 cm high and 9 cm dia.) from which the tops were removed and replaced with cheesecloth. Experimental cages were made from clear plastic shoeboxes (inverted, 29 x 15 x 9 cm). A rectangular ventilation hole (2.5 x 5 cm) was cut in one end; and access holes (1.6 cm dia.), cut at each end of the top, were plugged with cotton. Cages were stacked two high on a shelf just below the ceiling lights of the experimental chambers. Light intensity was about 1500-3000 lux, and the cages were rotated both vertically and horizontally daily to eliminate any differences in light intensity among the cages.

A few preliminary experiments were done in krisper-sized, clear plastic cages (23 x 30 x 10 cm). These cages had a small ventilation hole (2.5 x 3.8 cm) at one end, and an access hole (2.5 cm dia.) in the center of the top.

D. Food and Water

Food for the adult flies consisted of a liquid diet (U. S. Biochemical Corp., Cleveland) containing agar (18% by weight), brewer's yeast (31%), and sucrose (51%), plus propionic acid and water. This diet was absorbed by cotton in a 3/4 oz. (22 ml) condiment cup (No. 1-ST Dixie, American Can Co., Easton, Pa.). Two drops of honey were put on the outside of the cup. One of these cups was put in each cage. All except the holding cages also had a cup of water-soaked cotton. These water cups kept the relative humidity in the shoebox cages at about 35 per cent. The sleevecages also contained a 9 cm Petri dish lid with two sheets of filter paper and wet cotton, which kept the relative humidity at about 45 per cent.

E. Artificial Cherries

In laboratory experiments in which the per cent egg hatch was measured, artificial cherries were supplied to serve as a substrate for egg laying and to stimulate oviposition (AliNiazee and Brown 1977). These artificial cherries were made of soft ceresin wax (Deutsche Texaco Wax MP 121) to allow ovipositor penetration. The wax was colored with oranage candle wax dye (10 per cent by weight). The cherries were thin

hollow hemispheres, 1.1 x 1.3 cm dia. They were made by dipping the end of a small test tube (Pyrex No. 9800) first into hot soapy water (about 50° C) and then into molten wax (about 80° C). The test tube was quickly removed from the wax, turned upright, and the dribble of wax that formed was blown down the side of the test tube with hot air from a hair dryer. Wax and water were known to be just the proper temperatures when the artificial cherry was translucent when first removed from the beaker of molten wax, and then turned opaque within seconds. The cherry was cut to proper size by rolling the test tube against a razor blade mounted on a board at the proper height. After use the cherries were melted down and the wax reused.

A circle (9 cm dia.) of five cherries was centered on the floor of each shoebox cage. Because the flies are attracted to light and spend much time on the ceiling of a cage, cherries were also hung from the cage ceiling. A rectangular hole (4 x 18 cm) was cut between the two access holes on the cage ceiling. A piece of acetate was taped over this hole. The acetate had a row of five round holes (cut with a No. 5 cork borer) with centers 3.8 cm apart. Five artificial cherries were attached over these holes by heating until the base of the cherries just started to melt; then the acetate was

taped in place so that the cherries hung downward. This design was adopted with the intention of minimizing the handling of the flies. In later experiments the large hole in the top of the cage was covered with saran, and all the cherries (10) were put on the floor of the cage in two parallel rows 3.8 cm apart.

In one experiment cherries of other colors were used. All were made using 10 per cent candle dye (by weight) except black cherries were 15 per cent dye (AliNiazee and Brown 1977). One cherry of each color was put on the ceiling, and on the floor of each cage. Position for each color was randomly determined for each cage. In this experiment the number of eggs laid on the outside vs. inside of the cherries was recorded.

Krisper cages had 16 cherries (4 square) on the floor of the cage, with centers 3.2 cm apart.

Two pieces of clear plexiglass 1/8 in. (0.32 cm) thick and 22 x 5 cm long and wide were placed on top of each of the smaller sized sleevecages, under the inverted clear plastic box. Each piece of plexiglass had a row of five artificial cherries with centers 3.8 cm apart. A third set of five cherries was put on the floor of the cage.

In one experiment, only the ten cherries at the top of these sleevecages were used. A drop of solution

containing 20 per cent honey and 10 per cent sucrose was deposited on 5 of the 10 cherries (every other one), and its effect on egg laying was determined.

Only real cherries were used in the larger sleeve-cages. These were tied by the stem and suspended, five on each of two strings, strung just below the glass top, and five more were set on the floor. Alternatively, a whole twig with cherries on it was set in the cage in a vial of water. Freshly-picked cherries were replaced daily.

F. Egg Gathering

Eggs were removed from the inside or outside of the artificial cherries with a fine brush. The eggs were placed in a drop of water for 30 seconds to one minute before moving them to moist filter paper, upon which they were kept for eight days at 26.7° C, and scored for hatching. Eggs were collected once a day and artificial cherries were changed every third or fourth day in shoe-box cages; in sleevecages the eggs were collected once or twice daily, and the artificial cherries were changed every other day.

G. Laboratory Studies

The number of eggs laid, the per cent hatch, and the

longevity of adults were observed daily. Escapees and insects that were inadvertently crushed were omitted from calculations of longevity. The number of pairs mating was observed several times (usually three) daily.

Dose-sterility data was obtained for flies irradiated as adults. Males were irradiated with 0, 1.2, 2.5, 5.2, 8.0, 10.8, 13.5, and 16.3 krad; they were put into shoebox cages (with cherries on ceiling and floor) with unirradiated females. For most dosages there were two cages with four pairs each and eight cages with one pair each, for a total of 16 pairs of flies (see Table 22).

Females were irradiated with 2.5, 5.2, 8.0, and 13.5 krad, and put with unirradiated males. There were four pairs in each cage and two or three cages per dosage (see Table 23). In a separate experiment, two sets of four females each were irradiated with 8.0 and 13.5 krad and were put with equal numbers of males in krisper cages.

Other females were irradiated with 8 krad as pupae, and six were put with two unirradiated males in each of four cages. There were two control cages.

To test whether sperm from the first or last mating has precedence, females were mated to normal males and then to males irradiated as adults with 8 krad (and vice versa). Flies were kept in shoebox cages (all cherries

on the floor), and the flies were observed three or more times daily for mating.

In a preliminary experiment to test for competitiveness, males were irradiated with 13.5 krad and put into two krisper cages with sterile-to-normal male ratios of 1:1 and 4:1; there were four pairs of unirradiated flies in each cage, including the controls.

The effects of sterilizing males in the pupal stage, and competitiveness (with sterile-to-normal male ratios of 1:1, 4:1, and 8:1) were assessed in experiments carried out in sleevecages. Competitiveness was assessed by calculating the value e (Haisch 1970), an index of competitiveness which may vary from 1 (perfect competitiveness) to 0 (total lack of competitiveness). The formula is given and discussed in Appendix E.

An experiment was carried out in the larger sleevecages in which equal numbers of freshly-picked cherries were supplied to the treatment and control cage each day, and the old ones were removed and kept for subsequent determination of per cent infestation (by dissection). Seventeen females and four unirradiated males were put into each cage, and twelve males irradiated with 13.5 krad were put into the treatment cage, to make a sterile-to-normal male ratio of 3:1.

Two normal males and five females were released

into each of the smaller sleevecages. Irradiated males (8 krad) were added to treatment cages to make sterile-to-normal male ratios of 1:1, 4:1 and 8:1. Incandescent lighting supplemented the fluorescent lighting in the chamber to bring the light intensity up to 2300-2600 lux at the top of the cages, and 1100-1700 lux at the floor of the cages.

To test for the presence of a male pheromone, two identical shoebox cages were prepared and six males were added to one cage. At the beginning of the experimental period each day, three males were removed from the 6-male cage (without removing the top of the cage) and put into the control cage. Three females were added to each cage, and for one hour the cages were observed and scored for attempted (unsuccessful) and for successful matings.

H. Field Cages

Limb cages for use in the field were constructed using "one inch" chickenwire, formed into a cylinder 91 cm in height and 51 cm dia. for support. Fiberglass screening (6.3 mesh per linear cm) covered the chicken-wire skeleton. Cheesecloth (11 mesh per linear cm) was sewn to the screening to make a sleeve on each end of the cylinder. The sleeve was wired around the limb. The chickenwire frame was wired at two or more points

to the limb so that the cage would rest in position without the cheesecloth supporting any of the cage's weight. The cages each had a volume of 185 liters.

I. Field Studies

Eight limb cages were placed in cherry trees at the Entomology Farm, Oregon State University. Four cages were placed in one Royal Anne tree and four others were placed in two adjacent Bing trees. Four were treatment cages; two were control cages, into which only unirradiated flies were introduced. Two were "uninfested control" cages into which no flies were introduced, and which served to check whether or not any infestation had occurred before the cages were set in place.

Four unirradiated female flies and one unirradiated male fly were released into each of six cages. The four treatment cages received, in addition, 20 male flies that had received 8 krad of gamma irradiation on June 25. Flies were placed in the cages on June 29. Female flies had emerged on June 23 and 24. Male flies had emerged on June 23-25. Male and female flies were held separately before release into the cages.

Cages were inspected on the second and fourth days, and every third day thereafter, for holes in the cages, for spiders and other predators, and for any dead flies,

all of which were removed as soon as they were noticed.

Evaluation of the effect of the 20:1 sterile-to-normal male ratios was conducted in two parts. Twenty-five cherries were removed from each cage on July 11, 17, 24, and 27. These cherries were closely examined under a microscope at low magnification. The cherry skin was peeled back wherever there was a puncture that might have been made by the ovipositor of a fly. If an egg was found it was dissected out and kept on moist filter paper in a Petri dish and scored for hatching. These cherries were then held for five days and dissected and scored for infestation with maggots.

All cherries remaining in the cages were picked on July 27. These cherries were held for six days to allow the eggs to hatch; then they were dissected and scored for infestation. The first 25 cherries from each cage on July 27 were kept separately and dissected for eggs as above; their infestation was added to the others to determine the total infestation on July 27.

III. RESULTS

A. Per cent Yield from Field-collected Cherries

This study was done to obtain data that could be useful in evaluating the suitability of SIT for control of the western cherry fruit fly, Rhagoletis indifferens Curran. Determination of a suitable means of obtaining large numbers of insects is one of the prerequisites of a SIT program. Mass laboratory rearing is the usual way of obtaining large numbers of insects. AliNiazee and Brown (1977) developed an artificial diet for maggots, which gives a moderate yield of pupae. The other alternative is field collection of material, by sifting pupae from the soil or collecting infested cherries. The optimum time for either method of field collection was unknown.

In 1974, 1975, and 1976, infested cherries were picked in an abandoned orchard as a source of insect material for the next year. In 1974, small samples were taken periodically, beginning June 28, and dissected. When the per cent yield (number of maggots/number of cherries) determined by this method exceeded 50 per cent (on July 15), I began to harvest cherries and put them over soil.

Table 1 shows the per cent yield data for the most

heavily bearing tree for 1974. The per cent infestation had already peaked by July 15. The per cent yield determined by the soil method was much higher than for dissection. Eggs and very small maggots that had not yet reached the pit would not get counted with the dissection method, and it is possible that other small maggots that had just begun to work around the pit might have been overlooked. Infestation on sour cherry trees was somewhat lower than on sweet cherry trees.

In 1975, samples to be put over dirt were taken at the same times that samples were dissected (Table 2). Again the yield by the latter method was much lower. The per cent yield peaked on about July 23, in 1975, but varied from tree to tree. On July 17 one tree showed a per cent yield of 31 per cent by dissection of cherries, so the harvest of cherries for obtaining pupae by the soil method began after this date.

In 1976, the levels of infestation never rose as high as they did in the previous years. Table 3 presents data from one of the most heavily-bearing trees, the same one as in Table 2. The yield had peaked at 101 per cent on July 17, and by July 23, many maggots had left the cherries, so that the per cent yield was reduced to 44 per cent on that date.

The harvesting of infested cherries for the purpose

Table 1. Per cent yield of pupae--1974.

Date	No. of cherries	No. of pupae	Per cent yield	Tree
July 15	500	719	143.8	Sweet
" 18	600	809	134.8	"
" 23	250	270	108.0	"
July 18	300	327	109.0	Sour
" 23	250	207	82.8	"

Table 2. Per cent yield of maggots[a] or pupae[b] from a sweet cherry tree--1975.

Date	No. of cherries	No. maggots	No. pupae	Per cent yield
July 10	100	15		15
	100		56	56
July 17	400	48		12
	400		279	70
July 23	100	60		60
	400		606	151
July 26	360		410	114

[a]Per cent yield of maggots was determined by dissection.

[b]Per cent yield of pupae was determined by the soil method.

Table 3. Per cent yield of pupae from a sweet cherry tree--1976.

Date	No. of cherries	No. pupae	Per cent yield
July 12	750	689	91.9
" 14	750	701	93.5
" 17	1156	1165	100.8
" 23	770	339	44.0

of obtaining pupae by the soil method should begin shortly after a figure of 25 per cent yield is obtained by the dissection method. If all the cherries are to be picked within a few days, picking should commence after a 50 per cent yield is obtained by dissection.

B. Emergence in the Laboratory

Emergence from field-collected pupae -- Pupae from soil samples collected in August 1973 did not yield any adult flies after 30 days of refrigeration. Emergence after 60, 90, 120, and 150 days of chilling was 6.7, 13.4, 16.0, and 8.0 per cent respectively (Table 4). Comparing only those groups kept at 3° C for the whole period of chilling, the emergence was 6.7, 14.0, 20.0, and 8.0 per cent for 60, 90, 120, and 150 days respectively. Per cent emergence was greatest after 90-120 days of chilling.

Average time to emergence at 26.7° C was 48.6 days (after 60 days of chilling), and decreased to 36.7, 32.7, and 31.8 days after 90, 120, and 150 days of chilling respectively. Temperatures in the orchard, and in the unheated building before sifting may have affected the per cent emergence and time to emergence (especially for the 60 day group) so the date of refrigeration is included in Table 4.

Table 4. Cherry fruit fly emergence from soil-sifted pupae.

Days under refrigeration	Group No.	Date refrigerated	Temp.	No. and percentage flies emerged[a]	Ave. No. days in 26.7° C	n
60 days	5	a Aug. 22	+3°C	0		25
	6	b Aug. 29	+3°C	1	6.7%	48.6 ± 7.4	25
	7	c Sept 10	+3°C	4		25
90 days	8	a Aug. 22	+3°C	4		25
	9	b Aug. 29	+3°C	3		25
	10	c Sept 10	+3°C[b]	3	13.4%	36.7 ± 4.0	22
	11	d Sept 25	+3°C[c]	3		25
120 days	12	a Aug. 22	+3°C	6		25
	13	c Sept 10	+3°C	4		25
	14	a Aug. 22	+3°C[d]	1	16.0%	32.7 ± 5.3	25
	15	c Sept 10	+3°C[e]	4		25
	16	d Sept 25	+3°C[f]	5		25
150 days	17	a Aug. 22	+3°C	1	8.0%	31.8 ± 5.2	25
	18	d Sept 25	+3°C	3		25

[a]Groups 1-5 had 30 days chilling and no emergence occurred. Groups 8 and 9 had 14.0 per cent emergence with an average of 35.6 ± 4.5 days. Groups 10 and 11 had 12.8 per cent emergence with an average of 38.0 ± 3.1 days. Groups 12 and 13 had 20.0 per cent emergence with an average of 35.3 ± 3.0 days. Groups 14-16 had 13.3 per cent emergence with an average of 30.0 ± 5.9 days.

[b]Group 10 had +3°C for 60 days, then +10°C for 30 days.

[c]Group 11 had +3°C for 70 days, then -16°C for 24 days.

[d]Group 14 had +3°C for 100 days, then -6°C for 24 days.

[e]Group 15 had +3°C for 105 days, then 15°C for 15 days.

[f]Group 16 had +3°C for 90 days, 6°C for 15 days, and 10°C for 15 days.

Puparia from dishes 1, 2, 4, 6, 9-12, 14-16, and 18 were dissected in March and April 1974. The contents were classified as (live or dead) parasites, live pupae, dead nearly-adult pupae, and dead undeveloped pupae (Table 5). Dishes 1, 3-5, 7, 8, 13, and 17 were rechilled for five months; emergence was observed, and then the puparia were dissected in January 1975.

A few flies emerged after rechilling (Tables 5 and 6). A relatively large number of parasites emerged after rechilling from pupae that had originally been chilled for 30 to 60 days. There were still live pupae in dishes 1, 4, 5, 8, 13, and 17 after rechilling. The greatest percentage of live pupae (11.8%) were in the group originally chilled only 30 days (Table 6). In the 60, 90, and 120-day groups, live pupae were in the range of 6-9 per cent. After 150 days chilling, live pupae made up only 2 per cent of the total; in this group the total dead or parasitized was 84 per cent--very nearly as high as in the 30 and 60-day groups (86.1 and 84.1 per cent respectively). The dead and parasitized pupae after 90 or 120 days totaled only 67.8 and 71.0 per cent respecitvely. In every group the number of dead pupae was over 50 per cent.

A total of 33 parasites emerged: 61 per cent were a small black diapriid parasite, Psilus sp.; and 29

Table 5. Emergence and pupal dissections of field-collected pupae after various periods of chilling.

Days in cold	Dish No.	Emergence[a]		Dissections				
						Dead pupae		
		Flies	Parasites	Parasites	Live pupae	Near adult	Undeveloped	Total
30	1[b]		(2)	2	2	1	12	19
	2			2	4	8	10	24
	3[b]	(2)	(2)	1	0	10	10	25
	4[b]		1+(1)	2	5	7	9	25
60	5[b]	(1)	(1)	2	2	2	17	25
	6	1		0	3	5	16	25
	7[b]	4+(1)	2+(2)	4	0	4	8	25
90	8[b]	4	1	0	3	8	9	25
	9	3	1	1	3	6	10	24
	10	3	3	2	0	4	9	21
	11	3	1	1	0	6	12	23
120[c]	12	6	3	1[d]	3	4	8	25
	13[b]	4+(1)	4	1	4	2	9	25
	15	4	1	5	0	5	10	25
	16	5	3	2	2	1	12	25
150	17[b]	1+(1)	(1)	1	1	6	14	25
	18	3	4	2	0	4	12	25

[a]Emergence indicated in parentheses occurred after rechilling.
[b]Rechilled (see text).
[c]Dish No. 14 was not dissected.
[d]Live parasite; other parasites dissected were dead.

Table 6. Summary of emergence and pupal dissections of field-collected pupae of the western cherry fruit fly.

Days in cold	Flies							
	Em-erged	Unem-erged	Emerged[a] 1	Emerged[a] 2	Live pupae	Dead pupae: Near adult	Dead pupae: Unde-veloped	Total
30	6	7	0	2	11	26	41	93
	6.5%	7.5%		2.2%	11.8%	28.0%	44.1%	100%
60	5	6	5	2	5	11	41	75
	6.7%	8.0%	6.7%	2.7%	6.7%	14.7%	54.7%	100%
90	6	4	13	0	6	24	40	93
	6.5%	4.3%	14.0%		6.5%	25.8%	43.0%	100%
120	11	9	19	1	9	12	39	100
	11%	9%	19%	1%	9%	12%	39%	100%
150	5	3	4	1	1	9	27	50
	10.0%	6.0%	8.0%	2.0%	2.0%	18.0%	54.0%	100%

[a]Flies emerged: 1, after first chilling; 2, after rechilling.

per cent were a larger red braconid parasite Opius muliebris Mues. The identifications were made by P. M. Marsh.

The per cent emergence from pupae collected and wet-sieved in the spring at a site 14 km south of Junction City, Oregon, was 79-91 per cent in April, 77 per cent in May and 41-73 per cent in June (Table 7). The days-to-emergence was about 24 days in April, but was less than 10 days in June. The synchronization of emergence was not as good as from pupae kept at 3° C for 200 days (Tables 11 and 15, Figure 4): the minimum consecutive days for 80 per cent emergence was 5-7 days. These pupae were taken from a sprayed orchard with problems due to nearby unsprayed trees. Pupae obtained from an unsprayed orchard would be expected to have a considerable degree of parasitization (as in Table 6).

Four other lots of 100 pupae were wet-sieved on April 15 and then kept at 6° C for 35 and 50 days (Table 8). This treatment did not hurt the per cent emergence (82-89%), which corresponded closely to that for pupae sifted in April and brought directly to 27° C (Table 7). The synchronization of emergence was improved by holding at 6° C: standard deviations and CV's ($s/\bar{x}$) and minimum days for 80 per cent emergence were lower.

Table 7. Per cent emergence from pupae collected and wet-sieved in the spring.

Date[a]	No. pupae	Days until emergence	Per cent emergence	Min. days for 80% emergence	$s/\bar{x}$
22 Apr.	100	24.6 ± 2.4	85.0	6	0.10
22 Apr.	100	24.1 ± 3.4	91.0	5	0.14
28 Apr.	91	23.8 ± 3.0	79.1[b]	6	0.13
11 May	95	18.7 ± 2.8	76.8	7	0.15
16 June	77	8.4 ± 2.5	71.4	6	0.30
17 June	85	6.3 ± 2.2	72.9	6	0.35
18 June	109	6.9 ± 2.1	41.3	6	0.30

[a]collected, wet-sieved, and placed in 26.7°C.
[b]2.2% parasitization: 1 Psilus sp., and 1 tachinid

Table 8. Per cent emergence from pupae kept at 6° C for 35 and 50 days following wet-sieving on April 15.

Days at 6° C	Days until emergence	Per cent emergence[a]	Min. days for 80% emergence	$s/\bar{x}$
35	20.3 ± 1.6	89	4	0.08
35	20.0 ± 2.1	84	6	0.11
50	18.6 ± 2.0	88	4	0.11
50	18.3 ± 1.6	82	5	0.09

[a]100 pupae per replicate

Pupae could be sifted in the spring before many day-degrees had been accumulated by the presumably post-diapause pupae, and held at 6° C. Any wet-sieving or sifting method of obtaining pupae must include a means for concentrating pupae in a volume of soil, or it will not be economically feasible.

Per cent emergence -- The per cent emergence from pupae

collected in the field and then chilled at 3° C was highest after 90 or 120 days of chilling. In 1975 emergence from pupae obtained from infested cherries (by the soil method) was 32.8 ± 12.9 per cent, and did not vary with the duration of chilling ($r = 0.03$, Figure 1). In 1976, per cent emergence increased with longer periods of chilling ($r = 0.91$). Per cent emergence was 0 after 60 or fewer days of chilling; it was 2-3 per cent after 75 days, and rose to approximately 60 per cent emergence after 300 days chilling. Emergence in 1977 was similar to that in 1976 and is included in Figure 1.

Flies that emerged in 1975 came from maggots that were kept at 27° C, but in 1976 flies emerged from cherries held at 21° C. The increased temperature, or the greater decrease in temperature for the 1975 flies may have been responsible for the change in emergence pattern. I am aware of no other differences in handling or treatment for the two years. It is possible that some unnoticed malfunction in the cooling unit occurred; but any large aberration is unlikely. An important point is that there is some treatment that will increase the per cent emergence at only 100 days or less chilling. It may be that greater temperature change stimulates the flies to begin reacting to the lowered temperatures immediately.

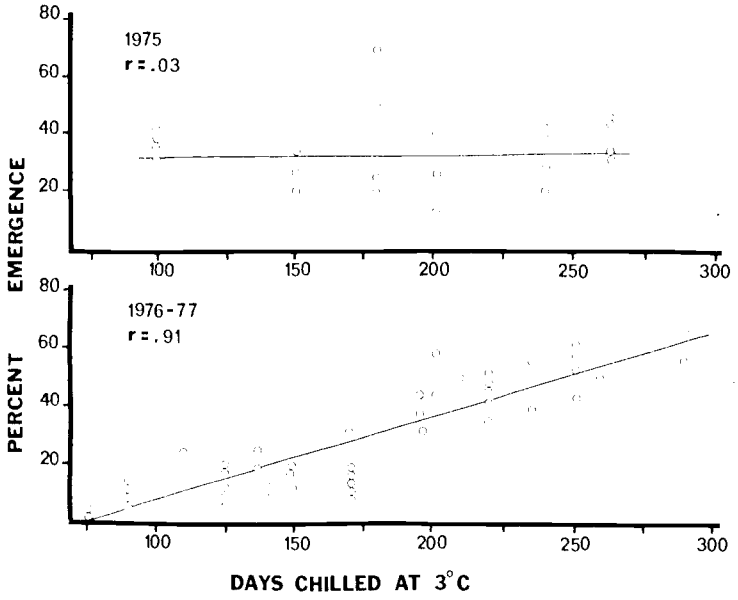

Figure 1. Per cent emergence of adult western cherry fruit flies after various periods of chilling at 3° C.

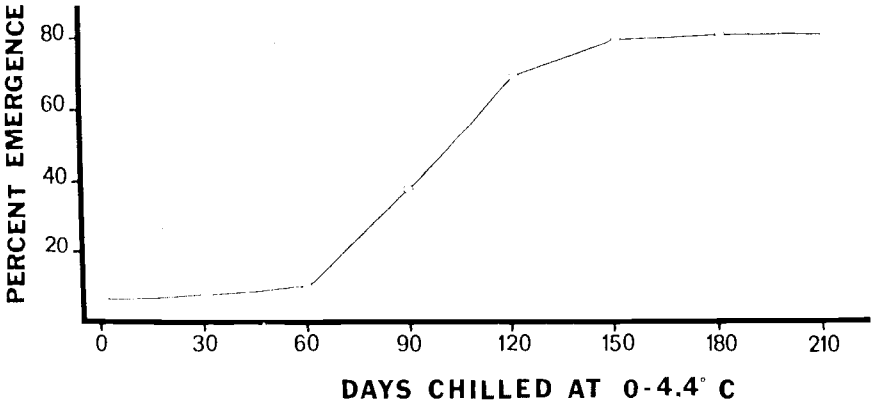

Figure 2. Per cent emergence for an eastern Washington population of R. indifferens (Frick et al. 1954).

Frick et al. (1954), who worked with a Washington population of western cherry fruit fly, found that per cent emergence rose from minimal levels after 60 or fewer days of chilling, to 37 per cent after 90 days at 0-4.4° C. Emergence continued to rise to 69 per cent after 120 days chilling, and levelled off at 80-81 per cent for 150 days or more chilling (Figure 2).

The differences between Frick and co-workers' and my results may be due to either genetic differences in the population, or to differences in handling procedures. As was noted in the introduction, the average winter temperatures in the Willamette Valley are milder than those for the Yakima Valley, so the flies in the two areas would be under somewhat different selective pressures. On the other hand, Frick and his collegues kept pupae in moistened soil, while I kept pupae in Petri dishes without soil. Frick et al. (1954) kept different batches of pupae at temperatures from 0° to 4.4° C and stated that temperatures within this range had the same effect as far as the final per cent emergence was concerned, so temperature during the period of chilling is probably not the cause of the differences in response.

Groups that had originally been chilled for 99, 150, 179, 201, and 263 days were rechilled (for 150+

Table 9. Per cent emergence after rechilling--400 pupae in each group (1975).

Days chilled first time	Per cent emergence	Days chilled second time	Additional per cent emergence	Total emergence
99	36.2	223	24.8	61.0
150	29.5	212	2.8	32.3
179	40.5	236	1.8	42.3
201	21.5	150	1.0	32.5
263	38.8	150	0	38.8

days, Table 9). An additional 25 per cent emergence (99 flies out of the original 400 pupae) occurred in the group that had originally been chilled only 99 days. There was 2.8, 1.8, 1.0, and 0 per cent additional emergence in the 150, 179, 201, and 263 days groups, respectively. The last two groups were only chilled for 150 additional days, but the other three were all rechilled for 212-236 days. It is obvious that for a great many pupae, 99 days of chilling is not sufficient to break diapause. (In the pupae sifted from soil, the 30 day group also showed high emergence after rechilling --none had emerged after the first chilling period.) It would appear that at the longer chilling periods, all but a few individuals terminated diapause.

The per cent emergence after rechilling in 1976 (Table 11) was greater than in 1975 (Table 9), except for those originally chilled for 99 days. Emergence

after rechilling in 1976 was 10-24 per cent, compared to 1-3 per cent for comparable groups in 1975.

Time-to-emergence -- The average number of days until emergence (after removal from chilling) was nearly 40 days (after 100 days of chilling). This value steadily decreased as the period of chilling was increased, until it levelled off at about 26 days after 200 or more days of chilling at 3° C (Figure 3).

The sloping part of the curve in Figure 3 is a linear regression, $Y = -0.144 X + 53.7$, of points between 75 and 192 days ($r = 0.94$). The horizontal part of the curve is at about 26 days; the average of points between 201 and 316 days was 26.2 ± 1.10 days. With this information one can determine when it is necessary to remove pupae from refrigeration to have flies by a certain date.

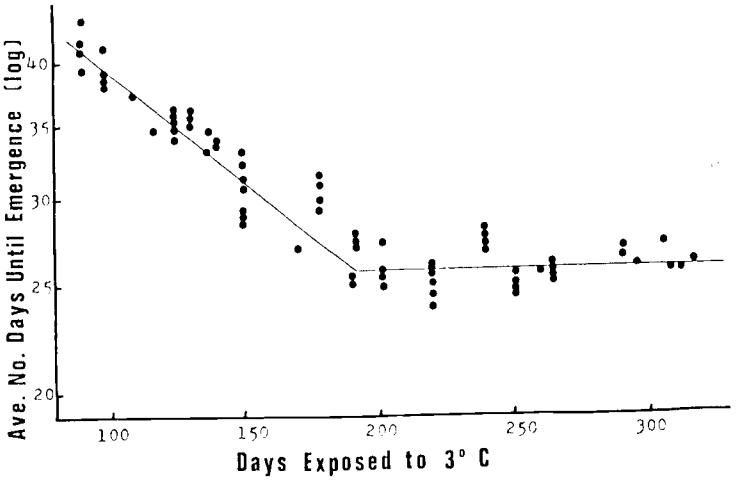

Figure 3. The effect of duration of chilling on days to emergence.

Table 10. Emergence of adults from pupae--1975.

Days in +3° C	Days until emergence[a]	$s/\bar{x}$	Days for 80 % emergence[b]	Number of flies[c]
99	39.5 ± 5.0 a	0.13	12	147
150	30.0 ± 4.1 b	0.13	10	118
179	30.3 ± 4.1 b	0.13	9	162
201	25.5 ± 3.2 d	0.13	4	86
240	27.4 ± 2.9 c	0.10	4	129
263	25.8 ± 1.4 d	0.05	4	155

[a]Values for days until emergence sharing a letter are not significantly different at the 0.05 level.
[b]Minimum number of consecutive days necessary to include 80% of the flies that emerged.
[c]Number of flies that emerged from 400 pupae.

Table 10 shows the time-to-emergence for six lots of 400 pupae chilled for various lengths of time in 1975. The values for average days until emergence varied from 40 down to 26 days, and are similar to those obtained by Frick et al. (1954). However, they held their pupae at room temperature after chilling and reported time to first fly. They did not extend their refrigeration time long enough for their data to indicate a levelling off. For a few groups of pupae held at 27° C after refrigeration, they did report 24-30 days to first fly.

Four groups of pupae that had originally been chilled at 3° C for various lengths of time were rechilled for 220 days (Table 11). The average days to emergence was 30-31 days in all groups indicating that the reaction to temperature was basically the same as

Table 11. Per cent emergence after rechilling (1976).

Days chilled at 3° C first time	Ave. days to emergence	Per cent emergence	Days chilled at 3° C second time	Ave. days to emergence	Per cent emergence	Total per cent emergence	No. of pupae
99[a]	33.7 ± 6.0	40.5	220	31.2 ± 2.8	8.0	48.5	200
161[b]	29.4 ± 5.8	33.0	220	31.1 ± 3.7	24.0	57.0	200
184[b]	27.3 ± 3.9	31.5	220	30.5 ± 3.7	14.8	46.3	400
190	25.3 ± 2.5	40.3	265	27.6 ± 3.4	11.0	51.3	300
220	24.4 ± 2.0	40.5	220	30.2 ± 3.6	19.3	61.3	300

[a]Put in 3° C after 90 days at 10-12° C.
[b]Put in 3° C after 30 days at 10-12° C.

with the first chilling. Additional chilling (265 instead of 220 days) in a fifth group resulted in a shorter average days-to-emergence (27 days). However, these values are all longer than that found for days-to-emergence following a first chilling of 200 days or more.

The timing of emergence from holdover pupae in comparison to first-year pupae differs in two other tephritid species. Boyce (1934) found that for Rhagoletis completa Cresson, flies from two-year-old pupae emerged before those from one-year-old pupae under field conditions. Allen and Fluke (1933) found that emergence from two-year-old pupae of the apple maggot occurred 8-10 days later than for first year pupae.

Emergence of males vs. females -- Under laboratory conditions female flies emerged earlier than males after pupae were chilled at 3° C (Table 12). A signed rank test (Snedecor and Cochran 1967) showed that this difference was significant ($P < 0.01$).

After pupae were chilled at 3° C for 90-290 days, males comprised 48.4 per cent of 1628 flies that emerged from 8800 pupae. The linear regression of per cent males on days-at-3° C was found to be $Y = -0.0607 X + 58.32$ (see Appendix F). The correlation coeficient ($r = -0.29$, $n = 67$) was significantly different from 0 ($P < 0.05$, Clarke 1969). Similarly, Boyce (1934) found

Table 12. Per cent males and days to emergence for male and female flies in the laboratory.

Days at 3° C	Days to emergence		Per cent Males	No. of Flies
	Males	Females		
90	43.6 ± 5.5	39.9 ± 4.8	44.1	34
99	39.6 ± 4.4	38.6 ± 4.5	58.0	143
125	36.2 ± 5.0	35.6 ± 3.1	50.0	36
125	36.0 ± 3.9	33.8 ± 4.4	61.1	54
137	34.6 ± 5.9	33.2 ± 3.8	50.0	40
150	31.2 ± 3.9	28.9 ± 4.1	48.3	118
150	29.9 ± 3.6	30.7 ± 3.8	34.8	46
165	30.5 ± 5.3	30.0 ± 4.2	44.6	83
179	30.0 ± 3.5	30.2 ± 3.7	49.7	161
190	25.4 ± 2.5	24.8 ± 1.8	55.0	120
192	29.2 ± 3.5	27.3 ± 2.9	41.7	151
201	25.7 ± 3.2	24.8 ± 1.4	60.0	85
210	25.8 ± 1.6	25.5 ± 1.7	36.4	99
220	25.0 ± 2.4	24.1 ± 1.6	47.5	127
240	27.4 ± 3.1	27.5 ± 2.8	48.5	130
250	24.9 ± 1.3	25.1 ± 1.6	49.3	223
260	26.2 ± 1.3	25.6 ± 1.4	36.8	95
263	25.7 ± 1.3	25.9 ± 1.4	43.9	155
290	27.0 ± 2.0	26.9 ± 1.8	40.8	179

that for walnut husk fly, the percentage of males was lower after cold winters, while the opposite was true after mild winters.

For pupae kept at 10-12° C for 30-150 days before chilling at 3° C, females emerged later than males on the average (Table 13). There was a tendency for an increased percentage of males when long periods (90, 120, 150 days) at 10-12° C preceeded chilling at 3° C.

While there was some variation in the comparative emergence of males and females following different chilling regimens, the overall emergence was close to 50:50 (males:females). The deviation tended to be smaller after longer periods of chilling, and was not sufficient to be of practical significance.

Table 13. Days-to-emergence for male and female flies from pupae held at 10-12° C before chilling at 3° C.

Days at 10-12 °C	Days at 3° C	Days to emergence		Per cent males	No. of flies
		Males	Females		
90	99	33.6 ± 6.6	33.8 ± 5.2	58.0	81[a]
30	161	28.5 ± 5.3	30.2 ± 6.2	45.5	66[a]
150	165	27.1 ± 1.9	27.7 ± 2.2	56.3	39[b]
30	184	27.3 ± 3.7	27.3 ± 4.0	45.2	126[c]
120	184	27.0 ± 1.5	27.2 ± 1.8	63.6	107[a]

[a]Emerged from 200 pupae.
[b]Emerged from 100 pupae.
[c]Emerged from 490 pupae.

Sexing of pupae -- Pupae that went through a 4 mesh per linear cm screen were 66-81 per cent males, while pupae that did not were 85-95 per cent females (Table 14). Over-all, 74 per cent males were obtained in the first group, and 91 per cent females in the second group.

This method of sexing pupae is far from perfect, but it is easy and may be useful. By separating those pupae that did not go through the screen, about 4/5 (77%) of females can be removed from the population with only a small loss (10.7%) of males.

Synchronization of emergence -- Flies emerged more synchronously as well as earlier when the number of days of chilling was increased (Tables 9 and 15). The standard deviation for days-to-emergence was 5.0 after 99 days at 3° C, but declined to 1.4 days after 263 days of chilling.

Examination of the coefficient of variation, $C = s/\bar{x}$, indicates that reduction in the size of the standard deviation may be due entirely to the concomitant reduction in the mean that occurred between 100 and 200 days of chilling. However, the standard deviations and the coefficient of variation continued to decline after periods of chilling longer than 200 days.

Regardless of whether the reduction in variance is associated with a reduction in the mean, it is important.

Table 14. Sexing of western cherry fruit fly pupae by size. Small pupae went through a screen with 4 mesh per linear cm; large pupae did not.

Lot No.[a]	No. small pupae	No. flies emerged	Per cent male	No. large pupae	No. flies emerged	Per cent male
1	99	34	73.5	101	54	15.1
2	131	41	65.9	69	22	9.1
3	113	47	78.7	87	42	4.8
4	98	51	76.5	102	66	7.6
5	119	56	67.9	81	46	10.9
6	114	53	81.1	86	40	5.0
Total	674	282	73.9 ± 6.0	526	270	8.8 ± 3.9

[a]200 pupae per lot. Lots 1 & 2 were chilled at 3°C for 192 days, lots 3 & 4 for 201 days, and lots 5 & 6 for 220 days.

Table 15. Emergence of flies from pupae.

Days in +3° C	Days until emergence	Days for 80 % emergence[a]	No. of flies
90	41.5 ± 5.4	14	34
99	39.5 ± 4.9	12	145
125	35.5 ± 4.2	10	90
137-140	33.8 ± 6.1	12	62
150	30.1 ± 4.0	10	164
165	30.2 ± 4.7	12	83
179	30.3 ± 3.9	9	162
190	25.2 ± 3.1	6	121
201	25.5 ± 3.1	4	86
220	25.1 ± 2.1	4	322
240	27.4 ± 2.9	4	129
260-263	25.7 ± 2.0	4	205
290	27.1 ± 2.0	4	121

[a]Minimum consecutive days necessary to include 80% of the flies that emerged.

It is more convenient and efficient to work with the flies in the laboratory if they are emerging over a shorter period of time. As will be discussed later, it is necessary to have well-synchronized emergence if one is to irradiate the flies in the pupal stage.

The effect and importance of the synchronization of emergence can perhaps be more clearly realized by examining the column in Table 15 which lists the minimum number of consecutive days necessary for 80 per cent of the total number of flies to emerge. After 99 and 150 days chilling, this value was 12 and 10 days respectively; it further decreased to 9 days after 179 days chilling. After 200 or more days of chilling, the days necessary for 80 per cent emergence was only 4.

The progressive synchronization of emergence with longer periods of chilling is illustrated in Figure 4 for four selected periods of chilling. After 99 days chilling, the first fly emerged 28 days after removal from refrigeration. Emergence peaked on day 41 with 14 flies emerging. Emergence continued until day 52, with one additional fly emerging on day 59.

In contrast, after 150 days of chilling, the bulk of emergence occurred between days 24 and 31, and a small (1-2 per day) but steady emergence continued through day 39. After 201 days of chilling, all except

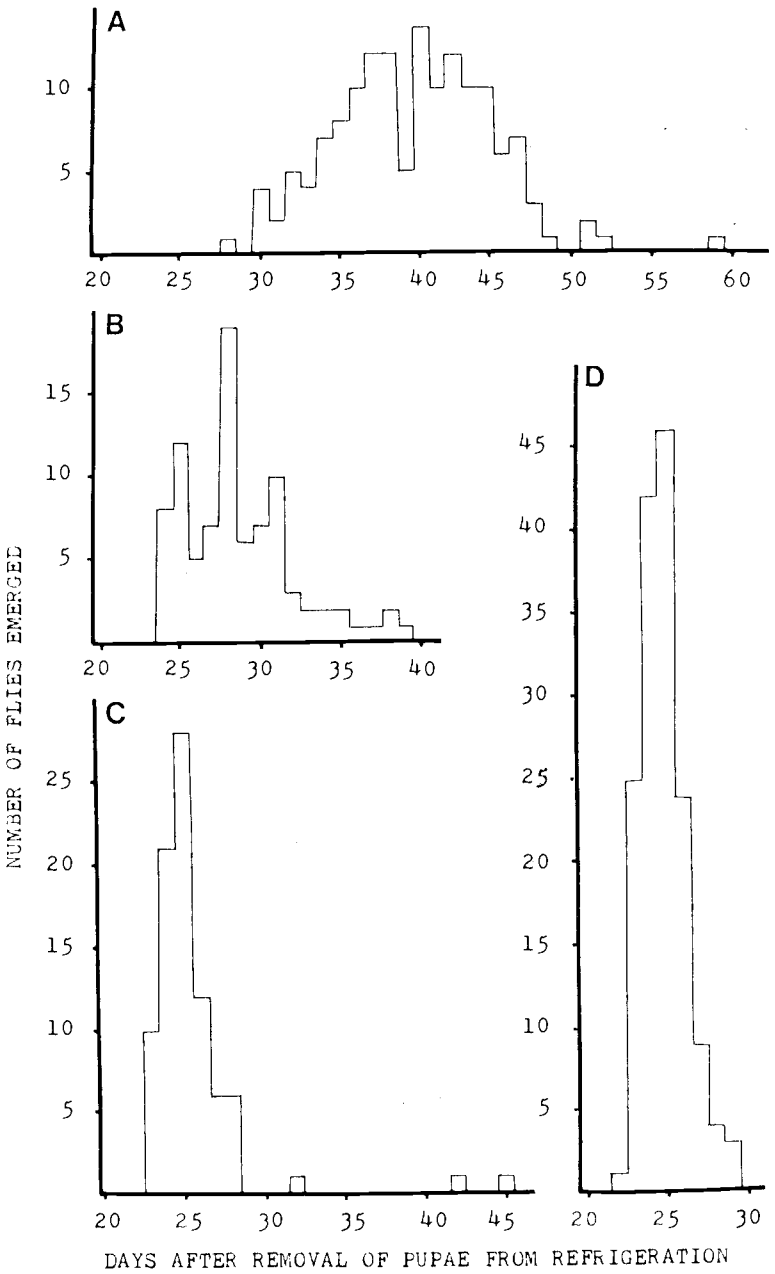

Figure 4. Synchronization of emergence of western cherry fruit fly after (A) 99, (B) 150, (C) 201, and (D) 263 days of chilling.

three straggler flies emerged during a six day period (days 23-28) with the peak at day 25.

After 263 days of chilling, emergence was very similar, but there were no stragglers, and the emergence on day 26 was slightly higher than on day 25. One fly emerged on day 22 and three on day 29, so that emergence occurred over a total of 8 days. The larger number of total flies that emerged made the per cent emergence within a six day period (97.4%) and within a four day period (88.4%) greater than the figures for 201 days of chilling (96.5% and 82.6%). One can also easily see from these graphs (Figure 4) that the time to emergence decreased with the longer chilling times, and that there was little change between 201 and 263 days.

Table 15 is similar to Table 11, but includes data for 1976. It can be seen that the variation in per cent emergence that occurred in 1976 (see Figure 1) did not affect the patterns for time-to-emergence and synchronization that were noted in the 1975 data.

Effect of 6° C -- Two-hundred pupae, collected by the soil method in 1974, were chilled at 6° C for 250 days. Flies emerged after an average of 19.6 ± 2.7 days (CV = 0.14). It took eight days for 80 per cent emergence to occur; flies emerged from 57 per cent of all pupae.

The per cent emergence is only slightly higher

than what would be expected for pupae chilled for 250 days at 3° C (Figure 1, 1976-77 data). The days-to-emergence value of about 20 days is less than the plateau value of about 26 days (Figure 3) obtained after chilling at 3°C, and the synchronization was poor. In fact, a batch of 300 pupae collected at the same time and treated identically until chilling, but kept at 3° C for 220 days exhibited 80 per cent emergence over a period of only three days! (These pupae kept at 3° C had 42 per cent emergence and days-to-emergence was 24.6 ± 2.6 days).

The poor synchronization of these insects chilled at 6° C means that this temperature is not acceptable for chilling, even though per cent emergence was good and time-to-emergence was reduced. It is possible that synchronization might be further improved by lowering the holding temperature to 0, 1, or 2° C. Furthermore, the possibility is suggested that synchronization and earlier emergence might both be obtained by following several months of 1-3° by a month of 6° C or even 10° C.

Females emerged slightly earlier than males after treatment at 6° C (19.4 ± 2.7 days vs. 19.9 ± 2.8 days). Males comprised 58.8 per cent of the flies that emerged.

Non-diapause pupae -- In 1974, 1000 pupae were kept at 26.7° C and photoperiod of 19L:5D rather than

refrigerating them. Eleven flies emerged (8 males and 3 females), which was 1.1 per cent emergence. Emergence occurred within 18-36 days after the cherries had been picked and put over dirt.

Of the 11 flies that emerged, two males were mated to each female in each of three cages. These females laid a total of 108 eggs of which 46 hatched (Table 16). These 46 maggots were placed on artificial medium (AliNiazee and Brown 1977) and yielded 26 pupae. The last pupa was formed on September 30. No flies had emerged by January 17, 1975, and the pupae were put into 3° C and left there for 166 days. Only one female fly emerged from these pupae. I was unable to start a non-diapausing strain of flies.

Frick et al. (1954) reported a second generation (in the field) amounting to 0.3 to 1.1 per cent of the pupae formed that year. They placed emergence cages in

Table 16. Eggs laid and hatched, and longevity of non-diapausing females.

Female No.	No. eggs laid	No. eggs hatched	Per cent hatch	Days lived
1	47	19	40.4	28
2	60	27	45.0	70
3	1	0	0	27
Total	108	46	42.6	-

the orchard on July 30, after emergence was presumed to be over. However, S. C. Jones[6] reported emergence as late as August 18 following disturbance of the soil under an emergence cage. Second generation emergence reported by Frick et al. could have been due to late emergence of pupae formed the previous year. The results reported in this section do not indicate whether or not there would be a second generation under field conditions.

C. Egg Laying

Number of eggs laid per female -- The number of eggs laid per female in shoebox cages was 65.2 ± 90.1 (Table 22). There was a very great variation in the number of eggs laid by females kept individually with one male: the range was 0-325 eggs.

The average age of females when they laid their first egg in shoebox cages was 14.8 ± 5.0 days (n = 40). The range was 6-33 days; all but two of the observations fell in the range 8-23 days. Only females that laid over 10 eggs were included in this calculation.

Location of eggs laid -- For shoebox cages with five cherries mounted on the ceiling (as well as five on the floor), the number of eggs laid in each position was recorded (Table 17). The radiation dose (krad given to

[6]Annual report on cherry fruit fly for the Agricultural Experiment Station, Oregon State University, unpublished. 1945:10, 15-16.

Table 17. Percentage of eggs laid on the top and bottom cherries of shoebox cages.

Dose in krad	No. laid top	No. laid bottom	Total	Per cent laid on top
0	174	233	407	42.8
2.5	268	417	685	39.1
5.2	183	256	439	41.7
8.0	170	191	361	47.1
10.8	80	100	180	44.4
13.5	117	105	222	52.7
16.3	233	453	686	34.0
Total	1225	1755	2980	41.0

males) is included only as a convenient way of dividing the data into replicates. The correlation coefficient, r, for (dose/per cent laid on top) was only 0.04, so the dose did not affect the location of egg laying.

The results indicate that only 41 per cent of the eggs were laid on (or in) the ceiling cherries. Due to the extremely time-consuming problems of attaching the top cherries to the acetate, and collecting the eggs, the design of the cages was changed following the main dose-sterility study. In the new set-up, all ten cherries were placed on the floor.

Eggs laid in and on different-colored cherries -- Orange cherries were significantly preferred over the second-highest color, dark green, when the flies were given the choice of five colors (Table 18). In an earlier study,

Table 18. Eggs laid on the inside and outside of artificial wax cherries of five different colors.

Color	Number of eggs laid[a]		Total
	Outside	Inside	
Orange	103 (43)	24 (5)	127 (48)
Dark green	46 (16)	11 (3)	57 (19)
Red	48 (14)	6 (4)	54 (18)
Black	26 (12)	4 (3)	30 (15)
Light yellow	8 (1)	2 (0)	10 (1)
Total	231 (86)	47 (15)	278 (101)

[a]Number eggs hatched in parentheses.

orange cherries were preferred to black, dark green and red cherries, although the differences were not significant (AliNiazee and Brown 1977).

In this experiment the number of eggs laid on the outside of cherries was nearly five times as great as those laid inside. In some cases, particularly involving young flies, large numbers of eggs will be laid inside the cherries; the 17 per cent laid inside in this experiment was quite low. More eggs are laid inside thinner cherries.

Two different types of behavior have been noticed that result in an egg being laid on the outside of a cherry. In the first type, the female is unable to insert her ovipositor in a too-thick cherry. After much attempted boring, an egg comes out while the ovipositor is in the air, and the egg sticks to the cherry when the

ovipositor is brought down again. In one case, the egg stuck to the cherry by its tip only, and then was flattened to the cherry prior to ovipositor-dragging.

In the second type, the female has the ovipositor inserted (at least part way) into the cherry and makes a vigorous pumping action. The egg does not go through to the inside, however, but is laid on the surface as the fly removes her ovipositor from the cherry. This type of oviposition is otherwise identical to the action when the egg is laid inside the cherry.

Eggs laid on cherries with sucrose/honey -- When five out of ten cherries at the top of a sleevecage had drops of sucrose/honey solution, 25 eggs were laid on cherries with the solution and 41 were laid on cherries without. This difference is significant: Chi^2, $P < 0.05$). Other studies have indicated that Rhagoletis flies are not primarily attracted to fruit for purposes of feeding (Prokopy 1968b, Prokopy and Bush 1973), although feeding on juices exuding from a fresh ovipuncture occurs. The drop of liquid on the wax cherry apparently had a deterrent effect for egg laying.

Time necessary for eggs to hatch -- A batch of 201 eggs collected over a two week period were observed twice daily for egg hatch. Eighteen eggs hatched in 3 days, 156 hatched in 4 days, and 27 took 5 days to hatch. The

average number of days-to-hatch was 4.04 ± 0.48 days. At other times a very few eggs have been noticed to hatch on the sixth day.

D. Mating Behavior

Mating age and pre-oviposition period -- The age at first mating for flies in shoebox cages was 14.8 ± 5.9 days for males and 14.3 ± 5.8 days for females (n = 20 pairs). The males and females put into a given shoebox were approximately the same age, so it is not surprising that values calculated from this data are very similar for the two sexes. A small number (6) of females caged with older, previously mated males mated at an average age of 10.8 ± 2.4 days.

These values, plus the figure of 14.8 days for the first egg, indicate that mating and oviposition may proceed more slowly in the laboratory than in the field, where the pre-oviposition period is considered to be 7-10 days (Johansen 1971). This figure for the field is more of a minimum than an average, however. The ranges for day of first mating in the laboratory were 6-25 days for males, and 5-24 days for females, so it is very debatable whether or not the average periods to first mating and oviposition are shorter in the field. Also, laboratory data were generated by making (at least)

three observations per day. It is certain that some flies mated without being observed, so the true values are somewhat lower than the estimates reported here.

In a separate experiment, male and female flies were put together in shoebox cages for one hour per day and their behavior in regard to the artificial cherries and each other was monitored. Time spent on cherries hanging from the ceiling (top) and on the bottom of the cage was timed with a stopwatch. When only one or two males and females were put in the cage, there was a marked period when the flies were 5-10 days old, during which they were not attracted to the artificial cherries (Figures 5-8). Following this period, the flies (especially males) began to spend more time on the cherries, and mating occurred within several days of this change in behavior. The male/male and male/female interactions (facing each other and fluttering wings) largely disappeared at this time also. Mating was initiated while flies were on the floor, ceiling, or on cherries.

When four pairs of flies were put into each cage, the initial period in which cherries were unattractive was not as well-defined. The time spent on cherries was more erratic, and in one cage no mating occurred. The density of flies in the cages affected their behavior.

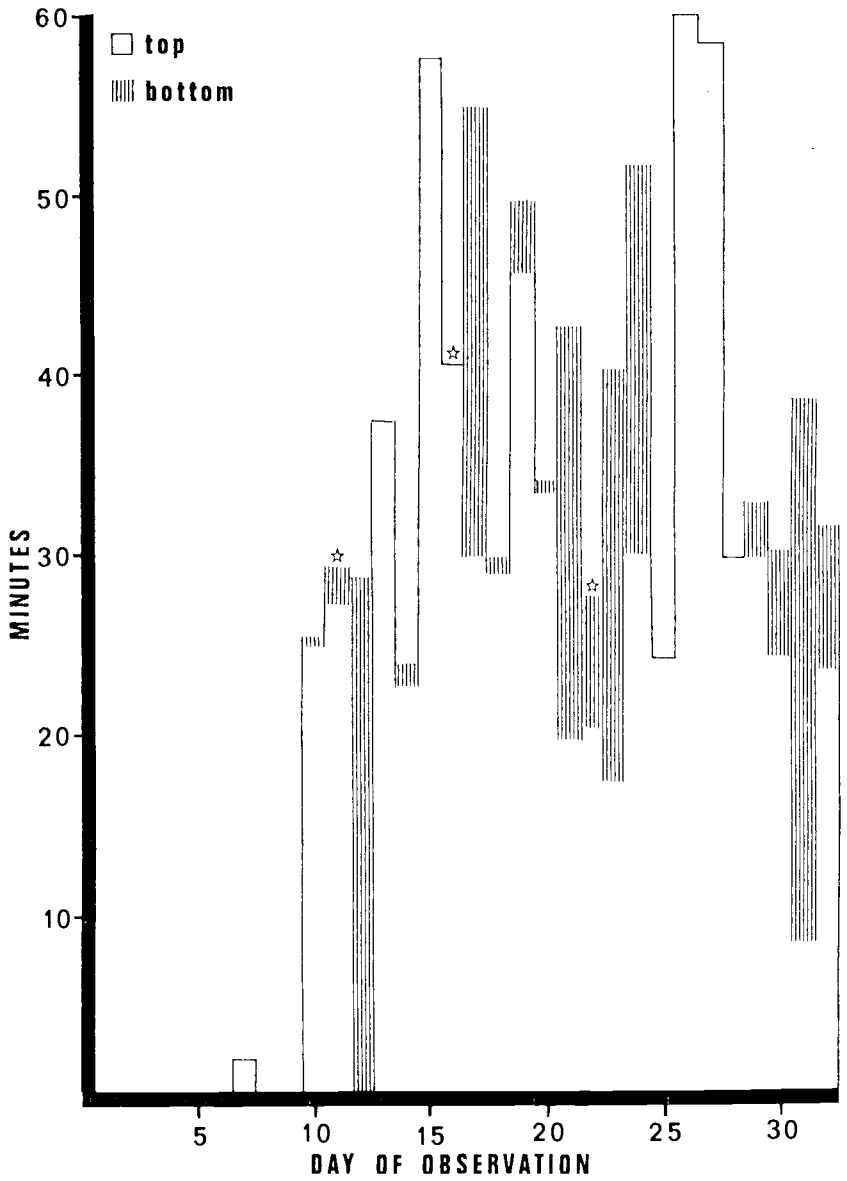

Figure 5. Average time male flies spent on cherries on the top and bottom of the cage during one hour of observation per day. Stars indicate that mating occurred (cage No. 1).

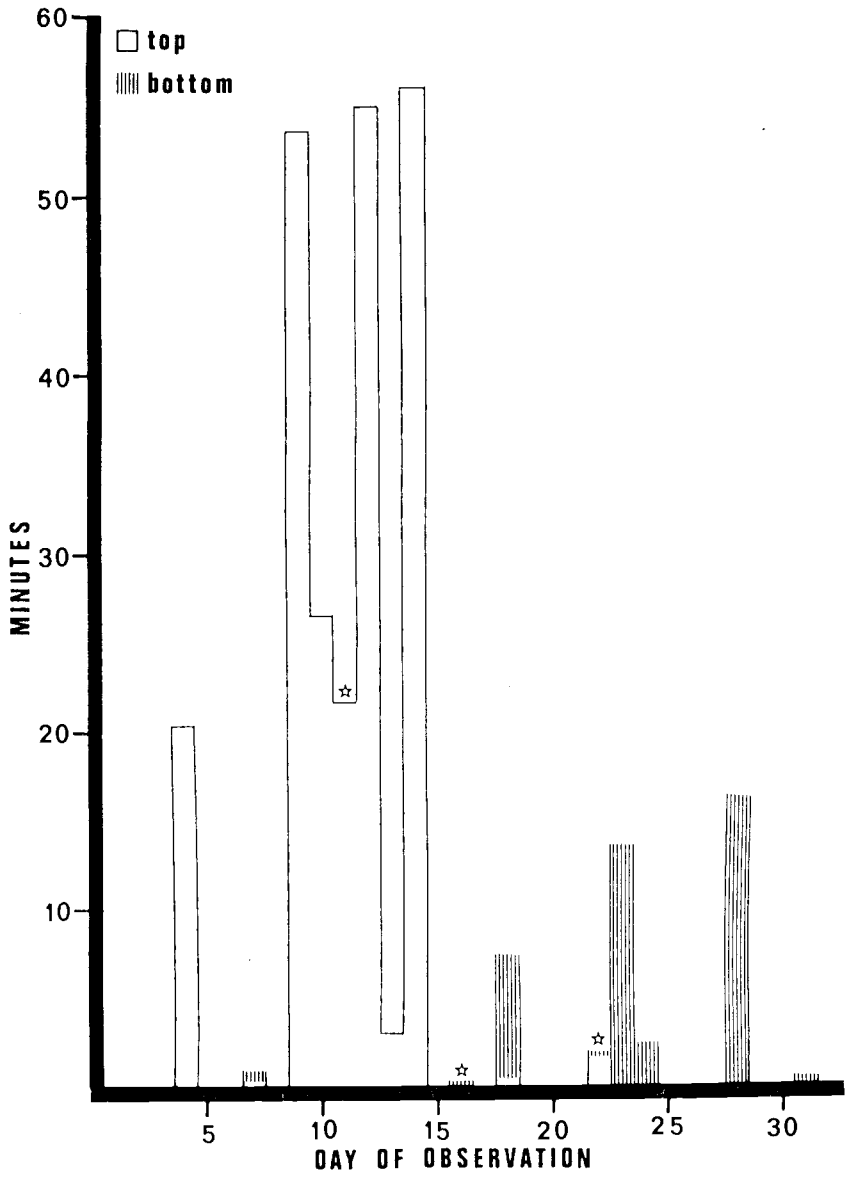

Figure 6. Time spent on cherries on the top and bottom of the cage by one female during one hour of observation per day. Stars indicate that mating occurred (cage No. 1).

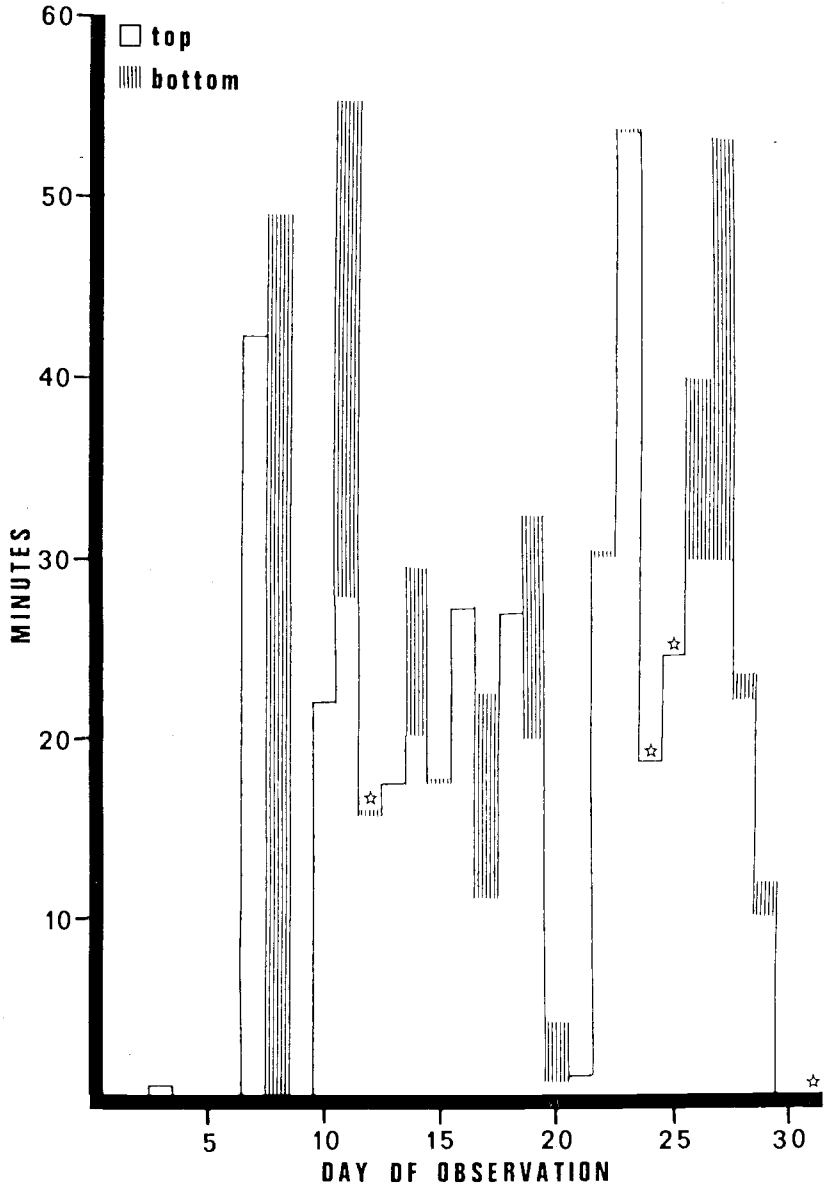

Figure 7. Time spent on cherries on the top and bottom of the cage by a male during one hour of observation per day. Stars indicate that mating occurred (cage No. 2).

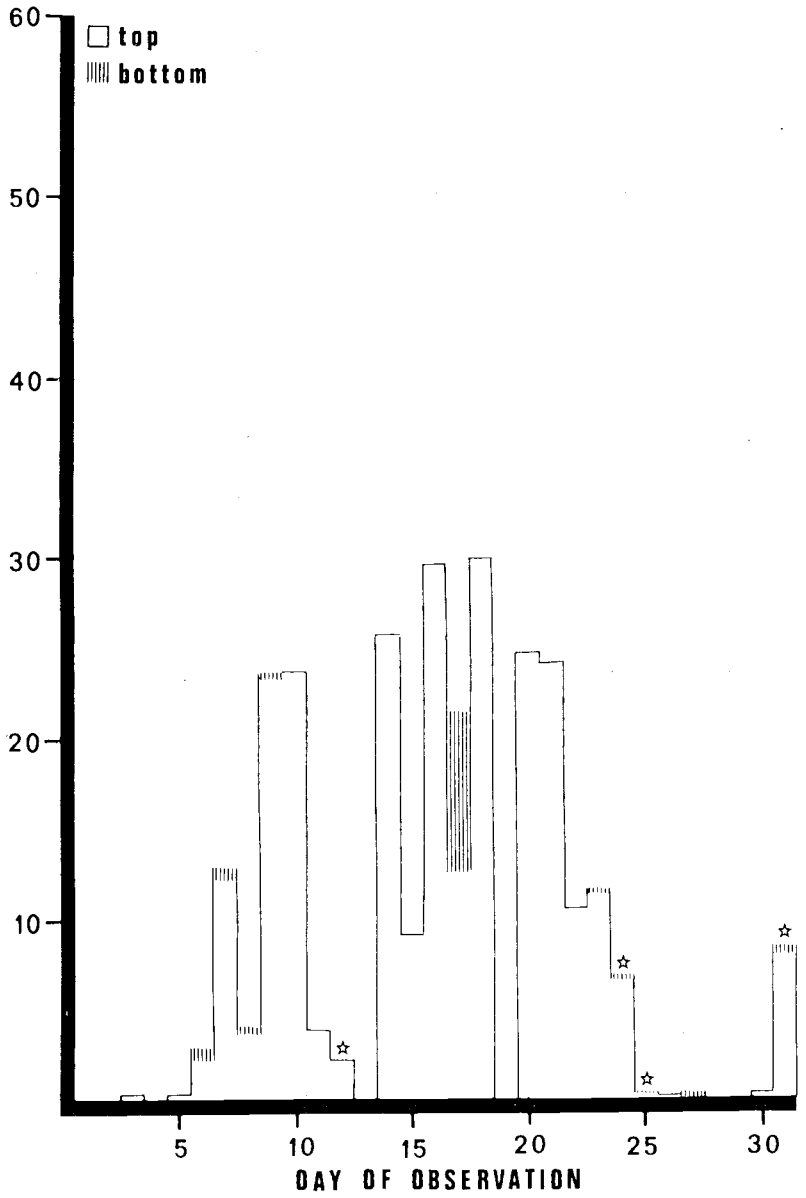

Figure 8. Average time female flies spent on cherries on the top and bottom of the cage during one hour of observation per day. Stars indicate that mating occurred (cage No. 2).

Mating of normal and irradiated males -- Normal males remained in copula for an average of 70.3 ± 33.9 min. (n = 38), while the time for males irradiated with 8 krad as adults was 58.9 ± 24.5 min. (n = 18). This is not a significant difference ($t_{.05}$ = 0.21).

The differences in the number of observations (n) in the above calculations is not significant: the data was drawn from several sources, including observations of normal flies without concurrent tests of irradiated males. Included above is data from an experiment with equal numbers of flies for both groups that was carried out in inverted baby food jars for 1-2 hours a day. The values for time in copula for this experiment were: normal males, 69.4 ± 25.2 min. (n = 9), and irradiated males, 56.8 ± 23.6 min. (n = 10).

In two sets of sleevecage experiments with 4:1 sterile-to-normal male ratios, and in one with a 1:1 ratio, the normal males were painted (with a small dot of tempera paint on the thorax) so that they could be separated from males irradiated as adults (Table 19). In the first set (4:1 ratio), irradiated males were observed mating 2.2 times per male, compared to 2.5 times per normal male in the same cage. Normal males in the control cage mated 5.5 times. In the second set, irradiated males mated 2.1 times per male, and normal

Table 19. Number of matings observed per male in cages with sterile and normal males.

Ratio	Control cages	Treatment cages	
		Normal males	Irradiated males
1:1	8.0	6.3	4.8
4:1a	5.5	2.5	2.2
4:1b	5.0	3.0	2.1

males mated 3.0 times per male. Normal males in the control cage mated 5 times per male. With a 1:1 ratio, irradiated males mated 4.8 times per male compared to 6.3 times per normal male. Control males mated 8.0 times per normal male. The presence of sterile males reduced the frequency of mating by normal males in the treatment cages.

The irradiated males mated nearly as often as the normal males when they were together in the same cage; the number of times the normal males mated was reduced by 40-50 per cent when 4:1 ratios of sterile to normal males were present (compared to controls). The presence of sterile males in a 1:1 ratio had a lesser effect. The total number of matings in the 4:1 cages were about twice that in the control cages: 23/11 and 23/10. Total matings in the 1:1 cages were about 1.4 times that in the control cage.

In three other cages with 4:1 ratios, the normal

males were not painted, but the total number of matings in these 4:1 cages was again about twice the total of the control cages: 15/8, 17/8, and 43/24. The total number of matings in the 8:1 cages, with nearly twice as many total males, was about the same as in the 4:1 cages. The 8:1/control ratios for matings was again about two: 15/8, 40/24, and 37/24. It appears that an upper limit to the number of times a female is willing to male may have been reached.

Male pheromone -- In tests to detect the presence of a male pheromone, control flies had 22 unsuccessful mounts and 1 successful mating, while flies where six males had been kept in the cage had 7 unsuccessful attempts and 9 successful matings (Table 20). (There was no difficulty in determining these two categories. Successful matings lasted at least 31 min., while unsuccessful mounts were generally less than 10 seconds.) The data strongly suggest that there is a type of male pheromone present in western cherry fruit fly. For the pooled data from the three replicates Chi^2 is significant ($P < 0.005$).

E. Dose-sterility Studies

Irradiated males -- When irradiated males were mated to normal females in shoebox cages in a 1:1 ratio, the percentage of fertile eggs was reduced with increased

Table 20. Tests to determine the presence of a male pheromone: number of successful matings and unsuccessful attempts in "six-male" and control cages.

Rep. No.	Mating	6-male	control
1	Successful	5	0
	Unsuccessful	2	1
2	Successful	0	0
	Unsuccessful	2	6
3	Successful	4	1
	Unsuccessful	3	15
Total	Successful	9	1
	Unsuccessful	7	22

Table 21. Per cent hatch of cherry fruit fly eggs after irradiation of males with several Co-60 dosages.

Dose in krad	No. eggs laid	No. eggs hatch	Per cent egg hatch	Corrected per cent egg hatch	No. pairs of flies
0	1699	242	14.2	100	22
1.2	274	15	5.47	39	12
2.5	1798	8	0.44	3.1	16
5.2	721	3	0.41	2.9	16
8.0	809	2	0.24	1.7	16
10.8	269	0	0	0	12
13.5	324	0	0	0	8
16.3	1013	0	0	0	8

dosage (Table 21). At a dose of 1.2 krad, the per cent egg hatch was about 39 per cent that of the control, while at 2.5 and 5.2 krad, it was about 3 per cent. A reduction in egg hatch of over 98 per cent was obtained when males were irradiated at 8 krad. No eggs hatched at a dose of 10.8 krad or above. The extrapolation of results on a log scale indicates that a 99 per cent reduction in egg hatch can be obtained by exposure to a dose of about 7 krad, and a 99.9 per cent reduction by a dose of about 9 krad. The line in Figure 9 is drawn to give more weight to those points supported by greater numbers. A linear regression put the 99 per cent reduction at 8 krad, and the 99.9 per cent reduction at about 13 krad. The biometry of radiobiology is discussed by Fabrikant (1972).

The number of eggs laid by females in this study was highly variable, ranging from 0 to 325. The average per female was 65.2 ± 90.1 eggs for the 46 females caged with males as individual pairs (Table 22). When the eggs from cages with four pairs of flies were added, the average stayed exactly the same at 65.2 eggs per female ($n = 106$). The values for each group changed, however. The group in which males were given 16.3 krad changed most drastically--from 12.0 eggs per female to 126.6 eggs per female. (The cage with four pairs of flies for

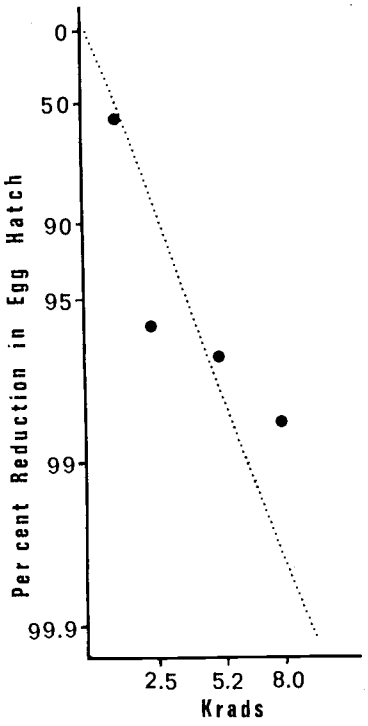

Figure 9. Extrapolation of per cent reduction in egg hatch.

this group had an average of 244 eggs per female!)

The value of the correlation coefficient (average number of eggs/radiation dose) for the 46 individual pairs was -0.73; this is significantly different from 0 at the 0.05 level. When the larger number of insects was considered, the correlation coefficient, r = 0.10, was not significant. With the extreme variability of the number of eggs laid per female, the results from the larger number of insects msut be considered to be more likely correct. The irradiation dose given to males

Table 22. Average number of eggs per female, for females mated to males exposed to various radiation dosages.

Dose in krad	Ave. No. eggs laid (individuals)	No. of females	Ave. No. eggs laid (all flies)	No. of females
0	65.8 ± 104.6	10	77.2	22
1.2	78.7 ± 23.1	4	34.2	12
2.5	102.0 ± 118.5	8	112.3	16
5.2	71.3 ± 127.8	8	45.0	16
8.0	97.3 ± 117.0	8	50.6	16
10.8	63.0 ± 65.8	4	22.4	12
13.5	40.0 ± 18.1	4	40.5	8
16.3	12.0 ± 15.9	4	126.6	8
Total	65.2 ± 90.1	46	65.2	106
	r = -0.73		r = 0.10	

does not appear to affect the number of eggs laid by the females.

Irradiated females -- A smaller number of females were irradiated at several dosages (Table 23) and tested for fertility by releasing them with equal numbers of normal males. At dosages of 5 krad or higher, no eggs were laid. At 2.5 krad only about three eggs per female were laid (34 total) and none of these hatched. Control females averaged 52 eggs per female (622 total) of which 26 per cent hatched.

Two sets of four females each were irradiated with 8.0 and 13.5 krad and put with equal numbers of males in

Table 23. Eggs laid and per cent hatch, and longevity for irradiated female flies and their mates.

Dose in krad	No. eggs laid	Per cent hatch	Longevity (days) Males	n	Females	n
0	622	26.0	40.7 ± 23.3	11	26.1 ± 11.5	8
2.5	34	0	30.9 ± 10.8	7	34.7 ± 23.8	8
5.2	0	-	26.5 ± 22.0	6	25.6 ± 15.3	7
8.0	0	-	23.3 ± 23.8	8	28.6 ± 15.6	8
13.5	0	-	34.5 ± 25.6	6	21.8 ± 14.4	6

krisper cages. Control females laid 156 eggs (39 each, of which 25% hatched). Treatment females laid no eggs.

Twenty-four females irradiated as pupae with 8 krad also laid no eggs, while twelve control females laid 207 eggs of which 38 per cent hatched. In two of the four treatment cages, no mating was observed, and in a third cage only one mating was observed. In the control cages 2 and 4 matings were observed. In the fourth treatment cage, 7 matings were observed, and in this cage only did irradiated females make ovipunctures in the cherries. Even in this cage, over one month elapsed before any punctures in the cherries were made. It was noted above that release of female fruit flies may be a problem due to damage of fruit by ovipunctures. The lack of ovipunctures by irradiated females is encouraging. The lower tendency toward mating would be advantageous if females are released in the same areas as males. They

would not use up the released males' sperm. If females are to be released in a separate area, however, they must mate with the wild males to have any effect.

Longevity -- The longevity of irradiated males was affected by the amount of radiation received. In general, longevity decreased with increasing dose. For instance, a reduction in longevity of about 25 per cent occurred after exposure to 5.2 krad, and a 50 per cent reduction in longevity followed exposure to 8.0 krad. (Table 24). However, the dose-longevity curve (Figure 10) is not a straight line, but is rather erratic--at 10.8 krad the reduction in longevity was only 32 per cent. The linear regression line, $Y = -1.39 X + 44.7$, puts the 25 and 50 per cent reductions in longevity at 8 and 16 krad respectively (Figure 11). The correlation coefficient for dose/longevity for males ($r = -0.84$) was significantly different from 0 ($P < 0.01$).

Unirradiated female flies caged with the above irradiated males showed a less dramatic reduction in longevity with increasing doses of irradiation given to males (Figure 11 and Table 24). At 2.5 and 5.2 krad, the reduction was about 20 per cent, and at 8.0 and 13.5 krad it was about 30 per cent. The linear regression line, $Y = -0.92 + 52.4$ gives the 25 per cent reduction in longevity at 14.2 krad. The correlation coefficient

Table 24. Longevity of irradiated males and of normal females caged together.

Dose in krad	Irradiated males					Normal females				
	Longevity		Per cent reduction in longevity	Range (in days)	No. of flies	Longevity		Per cent reduction in longevity	Range (in days)	No. of flies
	Ave. days	S.D.				Ave. days	S.D.			
0	51.7	± 14.7		28-84	14	56.4	± 19.5		18-94	16
1.2	43.4	± 17.4	16.1	18-75	9	53.9	± 9.2	4.4	44-81	12
2.5	35.4	± 19.0	31.5	18.59	8	45.8	± 22.0	18.8	14-76	11
5.2	37.9	± 15.9	26.7	11-58	7	44.4	± 23.8	21.3	24-90	9
8.0	26.3	± 18.5	49.1	10-63	11	38.7	± 22.3	31.4	10-63	9
10.8	35.3	± 15.6	31.7	7-53	8	49.7	± 24.1	11.9	8-79	6
13.5	22.2	± 10.0	57.1	12-39	6	40.2	± 27.6	28.7	12-71	6
16.3	26.0	± 10.9	49.7	13-40	6	37.0	± 21.2	34.4	18-62	4

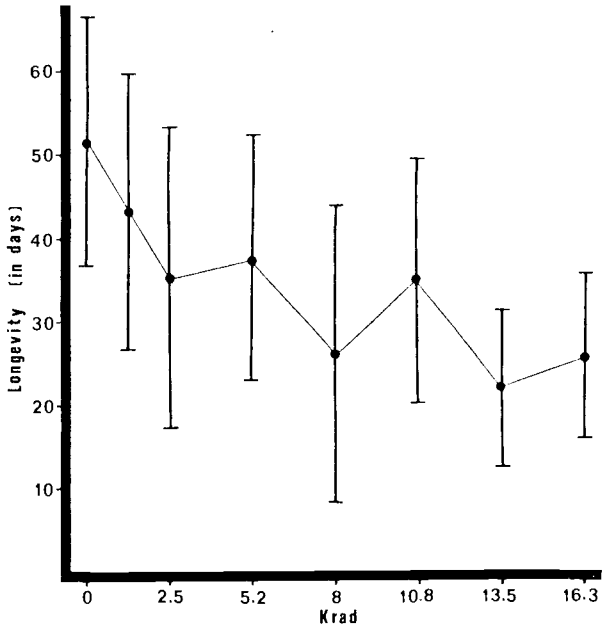

Figure 10. Longevity of male flies given various doses of gamma radiation, with indication of standard deviations.

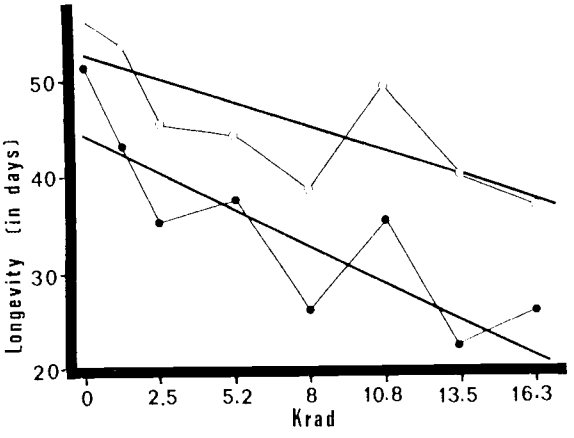

Figure 11. Longevity of irradiated male flies (solid) and of female flies caged with them (open circles). Linear regression lines are indicated.

for these females ($r = -0.77$) was also significant ($P < 0.05$). A comparison of the regression lines (Snedecor and Cochran 1967) for males and females indicates that the slopes are not significantly different ($P > 0.25$), but the elevations of the lines differ significantly ($P < 0.005$). (The residual variances are homogeneous.)

Longevity of irradiated females was not significantly lower than control females, whether irradiated as adults (Table 23) or pupae (Table 25). The correlation coefficient for dose/longevity for females irradiated as adults was -0.51; the value for males caged with them was -0.30.

The decrease of longevity in response to increasing doses of radiation that occurred in the male flies is not unusual for Diptera (see section I-C). The fact that unirradiated females caged with males also showed a significant decrease in longevity supports the hypothesis that disease was involved. An increase in early deaths (Figure 12) was the main factor in reducing longevity; this was associated in some cases with the development of a swollen abdomen. The increased mortality in the irradiated males may have been due to lowered disease resistance, and in the females due to the constant exposure to sick males.

Table 25. Longevity of female flies exposed to 8 krad as pupae, and of their mates.

Dosage	Rep. No.	Female (days)	Male (days)
8.0 krad	1	50.7 ± 10.3	69.5 ± 6.4
"	2	46.5 ± 12.4	36.5 ± 17.6
"	3	54.3 ± 11.1	80.5 ± 50.2
"	4	44.5 ± 13.4	72.5 ± 7.7
"	Total	49.0 ± 11.7	64.8 ± 27.3
Control	1	50.8 ± 20.4	80.0 ± 0
"	2	58.7 ± 14.1	63.5 ± 2.1
"	Total	54.8 ± 17.2	71.8 ± 9.6

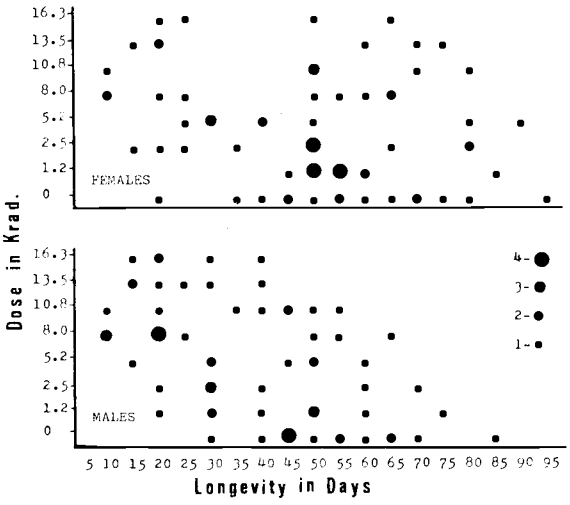

Figure 12. Number of flies dying during five day intervals. Unirradiated females were caged with irradiated males.

As was mentioned in the Introduction, some insects, especially females may show increased longevity at low or moderate doses of irradiation (Ducoff 1972). The

lack of a significant decrease in longevity in females in this experiment may be due to a combination of factors: some that are acting to increase longevity and others that are acting to decrease it (as in the males). The decreased egg-laying and even the absence of boring with the ovipositor by irradiated females indicates that reproductive energy is being conserved, and this may have helped to counterbalance other effects (lowered disease resistance) that increase early deaths.

The finding by Boller et al. (1975) that longevity of male R. cerasi increased at 10 krad, but not at higher dosages, was based on three cages of 10 pairs at each dosage. If lessened disease resistance was the major factor in decreased longevity, there was a greater chance of an epizootic occurring after the first fly became sick than in my experiment with only 1-4 pairs per cage. Moderate doses of radiation may have a small positive effect on longevity of males (and a somewhat larger positive effect on females) which is usually cancelled out by lessened disease resistance.

F. Competitiveness

Preliminary trial -- An unreplicated preliminary experiment with 1:1 and 4:1 sterile (13.5 krad) to normal male ratios was made in krisper cages. The 1:1 ratio yielded

a 12.2 per cent egg hatch and the 4:1 yielded 15.5 per cent. Both of these were below the control value of 25.0 per cent. The higher ratio of 4:1 had no increased effect over the 1:1 ratio in this cage.

1:1, 4:1, and 8:1 sterile-to-normal male ratios -- Further experiments were conducted with males sterilized with 8 krad, in sleevecages. In the first and second experiments there were a total of three replicates of each ratio (4:1 and 8:1) and two control cages (Table 26). In the third experiment there were three cages with 1:1 ratios and a control cage (Table 27).

In the first experiment, the cage with a 4:1 sterile to normal male ratio had 13.5 per cent egg hatch, compared to the expected value (assuming perfect competitiveness) of 12.5 per cent. Per cent egg hatch values for the 8:1 ratio cages, on the other hand, were considerably above their expected values. Consequently, the values for competitiveness were poor (e[7] = 0.16 and 0.39) for the 8:1 cages, and excellent for the 4:1 cage (e = 0.89).

In the second experiment, none of the observed values for per cent egg hatch were over twice their expected values. The 8:1 cage had a good competitiveness value of 0.72, while the 4:1 cages had fair values of

[7] e is an index of competitiveness that varies between 0 and 1. A value of 1 indicates perfect competitiveness. See Appendix E for the formula and discussion.

Table 26. Percentage egg hatch and number of eggs laid for Rhagoletis indifferens with sterile to normal male ratios of 4:1 and 8:1 and control groups.

FIRST EXPERIMENT

Group	No. eggs	No. hatch	Observed % hatch	Expected % hatch[a]	E/O[b]	Competitiveness
Control	405	249	61.5			
4:1	616	83	13.5	12.6	0.93	0.89
8:1a	239	64	26.8	7.1	0.27	0.16
8:1b	645	97	15.0	7.1	0.47	0.39

SECOND EXPERIMENT

Group	No. eggs	No. hatch	Observed % hatch	Expected % hatch[a]	E/O[b]	Competitiveness
Control	444	269	60.6			
4:1a	137	31	22.6	12.4	0.55	0.42
4:1b	364	67	18.4	12.4	0.67	0.57
8:1	578	52	9.0	7.0	0.75	0.72

SUMMARY

Group	No. eggs	Per cent hatch	E/O[b]	Competitiveness[c]
Control	849	61.1 ± 0.6		
4:1	1117	18.2 ± 4.5	0.77	0.69
8:1	1462	16.9 ± 9.1	0.48	0.40

[a]The formula for expected per cent egg hatch is in Appendix E.

[b]E/O = expected/observed per cent egg hatch.

[c]Competitiveness in the summary section was calculated on the basis of total number of eggs laid and hatched, not the average of three replicates.

0.42 and 0.57. The per cent hatch in the two control cages was nearly identical: over 60 per cent in both cages.

In the third experiment (1:1 ratio), two of the three cages showed very good competitiveness (e = 0.80 and 0.91), while in the third, the expected per cent hatch was only about 2/3 of the observed (e = 0.31). The per cent hatch in the control was 46.5 per cent.

Figures 13 and 14 show the variation over time for the treatment and control groups in the first two experiments (each point is an average of five days data). Egg hatch in the first control cage remained close to 60 per cent throughout the duration of the experiment, while the second peaked at 70 per cent for one five-day period and then tapered off. In the third experiment (Figure 15), each point is an average of four days data. Control values ranged from 38.5 to 55 per cent. In all three figures the curves for the treatment groups are much more erratic than those for the controls, as might be expected where the chance of mating to either sterile or normal males was possible.

In summary, good competitiveness was obtained with 1:1 and 4:1 sterile to normal ratios under laboratory conditions (e = 0.62 and 0.69 respectively). The competitiveness for the 8:1 group was less satisfactory (e =

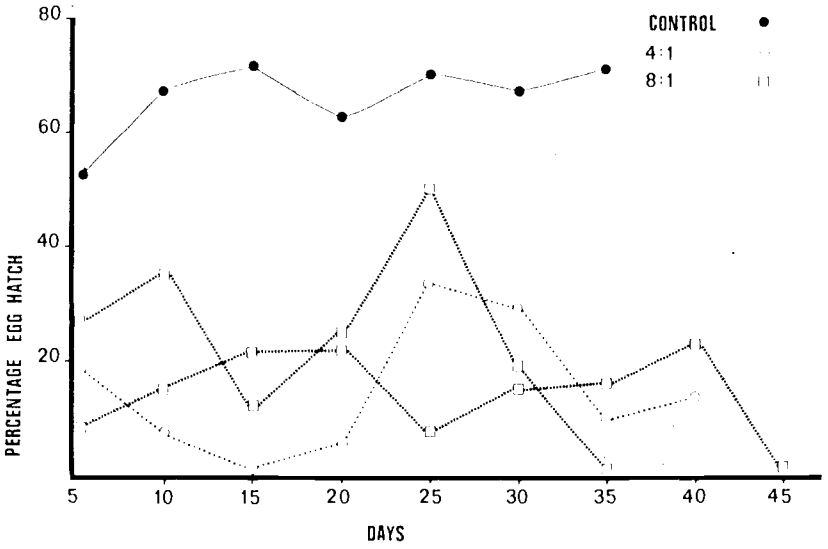

Figure 13. Per cent egg hatch with sterile to normal male ratios of 4:1 and 8:1, average over five day periods (first experiment).

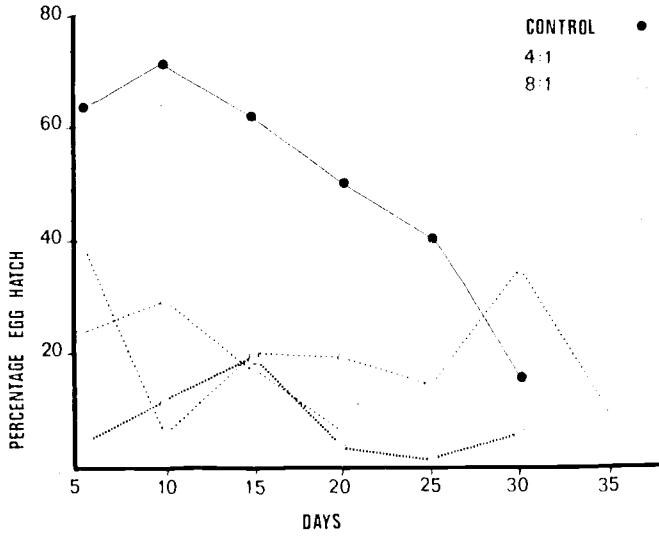

Figure 14. Per cent egg hatch with sterile to normal male ratios of 4:1 and 8:1, average over five day periods (second experiment).

Table 27. Percentage egg hatch and number of eggs laid with sterile to normal male ratio of 1:1.

Group	No. eggs	No. hatch	Observed % hatch	Expected % hatch[a]	E/O[b]	Competitiveness
Control	114	52	46.5			
1	138	49	35.5	23.0	0.65	0.31
2	141	36	25.5	23.0	0.90	0.80
3	145	35	24.1	23.0	0.95	0.91
Total	424	120	28.4 ± 6.2	23.0	0.81	0.62

[a]The formula for expected egg hatch is given in Appendix E.

[b]E/O = expected

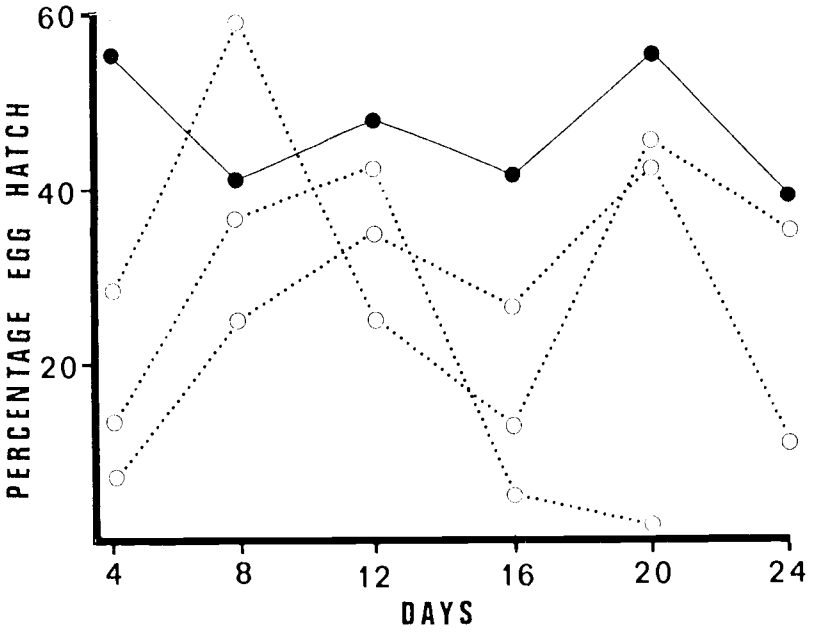

Figure 15. Per cent egg hatch with sterile to normal male ratios of 1:1, average over four day periods.

0.40). The per cent egg hatch for these groups was 28.4 ± 6.2 ($s/\bar{x}$ = 0.22) for the 1:1 ratio, 18.2 ± 4.5 ($s/\bar{x}$ = 0.25) for the 4:1 ratio, and 16.9 ± 9.1 ($s/\bar{x}$ = 0.54) for the 8:1 ratio. The variance in the 8:1 situation was greater, and the difference in competitiveness may be due to chance. However, with the larger total number of males in the 8:1 cages, a pair of flies would be more likely to be disturbed during mating. Sterilized flies might be less likely to remain in copula in the face of disturbance, and the lower value for competitiveness for males in the 8:1 cage may be due to this factor.

Flies irradiated as pupae and adults -- To determine if flies could be irradiated as pupae, male flies were irradiated with 8 krad as adults or pupae, and put into sleevecages with 4:1 sterile to normal ratios, and a comparison of their competitiveness and longevity was made. The experiment was replicated twice, and in each case (Table 28) the males irradiated as pupae were less than half as competitive as those irradiated as adults: e = 0.24 compared to 0.61, and e = 0.17 compared to 0.38.

Longevity of male flies irradiated as pupae was not significantly shorter than longevity of those irradiated as adults (Table 29). In one cage of the first replicate, the males irradiated as pupae lived slightly longer than those irradiated as adults; these flies also

Table 28. Percentage egg hatch and competitiveness with males irradiated as adults and pupae, with sterile to normal male ratios of 4:1 and control groups.

FIRST REPLICATE

Irradiated as	No. eggs laid	Observed % hatch	Expected % hatch[a]	Competitiveness
Control	85	15.3		
Adults	198	4.5	3.1	0.61
Pupae	355	7.9	3.1	0.24

SECOND REPLICATE

Irradiated as	No. eggs laid	Observed % hatch	Expected % hatch[a]	Competitiveness
Control	193	32.1		
Adults	62	12.9	6.5	0.38
Pupae	89	19.1	6.5	0.17

[a]Per cent egg hatch assuming perfect competitiveness.

lived longer than the average for the two normal male flies in this cage. Irradiated male flies were somewhat less long-lived than females in the same cages in most cases. Longevity in replicate 2 was less for both males and females than in replicate 1. The number of flies involved in these experiments were too small to draw any definite conclusions about longevity, but the results are consistent with the hypothesis that lowered disease resistance is an important factor in the increased early mortality in these flies.

Irradiated pupae were kept at 3° C for 260 days and

Table 29. Longevity (days) of male flies irradiated with 8 krad as pupae and adults. Females and control males were not irradiated.

Irradiated as	FIRST REPLICATE		SECOND REPLICATE	
	Males		Males	
	Normal	Irradiated	Normal	Irradiated
Adults	53.5 ± 24.8	52.4 ± 16.9	27.0 ± 0.0	22.8 ± 8.4
Pupae(a)	34.0 ± 36.8	52.8 ± 28.6	40.0 ± 14.1	23.0 ± 13.5
Pupae(b)	40.0 ± 7.1	30.3 ± 17.1	43.0 ± 22.6	30.3 ± 18.8
Control	42.0 ± 11.3		30.5 ± 0.7	
	Females		Females	
Adults	49.8 ± 26.8		26.8 ± 0.4	
Pupae(a)	57.8 ± 26.3		30.3 ± 4.8	
Pupae(b)	39.3 ± 39.1		43.8 ± 16.5	
Control	55.8 ± 27.6		30.2 ± 0.4	

irradiated on day 23 (after one female had emerged from the control dishes on this day). Emergence was 34 per cent (after an average of 25.8 ± 0.9 days), and 56 per cent (26.3 ± 1.7 days) for the irradiated insects; and 44 per cent (25.9 ± 2.3 days) and 56 per cent (25.4 ± 1.6 days) for the controls.

For the second replicate, pupae were kept at 3° C for 290 days and irradiated on day 24 (after one female emerged from the dish that was to be irradiated). Emergence was 58 per cent (after an avarage of 26.5 ± 1.0 days) for the irradiated insects; and 56 per cent (26.9 ± 1.7 days) and 65 per cent (27.3 ± 2.3 days) for two control dishes.

Irradiation of pupae just before flies commenced to emerge did not significantly depress the per cent emergence or affect the average days to emergence. Thomou (1963) found that irradiation of olive fruit fly pupae, Dacus oleae (Gmelin), lowered the per cent emergence of flies from younger pupae, compared to pupae that were eight days old when irradiated. In this experiment, 88 per cent of control flies and 87 per cent of those irradiated as pupae emerged within the first four days after irradiation. The number of pupae at an early stage of development would have been too small to show a significant difference.

Sequential mating of sterile and normal males -- Sequential mating of females to normal and irradiated males indicated that sperm from the last mating has precedence in the western cherry fruit fly (Table 30). Per cent hatch of eggs from females mated first to irradiated and then to normal males was lower (26.7%) than for controls (36.3%). However, the deviation was not significant ($0.4 > P < 0.2$). In two out of five cases the per cent egg hatch was below the range for the controls (25-56%).

The hatch of eggs from females mated first to normal and then to irradiated males was 0 per cent in four out of five cases. The value of 16.8 per cent obtained in the fifth case was below the value of any of the controls. The deviation of this group from the expected value for egg hatch was highly significant ($P < 0.001$, $Chi^2 = 62.5$).

The results may be interpreted as showing that while sperm from the last mating has precedence, some mixing may occur. However, in the one case that gave egg hatch where the last-mated male was irradiated, nine matings with normal males took place before the switch was made, and only one mating to the irradiated males occurred afterward. The spermatheca may have been full of sperm from previous matings, or perhaps the single

Table 30. Per cent hatch of eggs laid by females mated sequentially to normal and irradiated males, and vice versa.

Group	Rep.	Per cent hatch	Matings[a] observed	Eggs laid
Controls	1	38.9	2 N	36
	2	25.0	5 N	56
	3	33.3	10 N	54
	4	27.8	5 N	36
	5	56.3	9 N	32
		36.3 ± 12.4		
Normal then irradiated males	1	0	1 N--2 I	30
	2	0	1 N--2 I	18
	3	0	1 N--1 I	51
	4	0	5 N--3 I	75
	5	16.8	9 N--1 I	131
		3.4 ± 7.5		
Irradiated then normal males	1	49.4	2 I--2 N	85
	2	27.4	3 I--3 N	135
	3	7.3	1 I--1 N	96
	4	39.8	3 I--3 N	103
	5	9.8	2 I--10N	41
		26.7 ± 18.4		

[a]N = number of matings to normal males; I = number of matings to irradiated males.

mating with the irradiated male was unsuccessful for other reasons.

As was discussed in section I-D, it is advantageous if the sperm from the last mating has precedence if there is the possibility of immigration of fertilized females. Furthermore, precedence (by sperm from either

the first or the last mating) simplifies the calculation of the theoretical effect of releasing sterile insects (Berryman 1967, Bogyo et al. 1970).

Per cent infestation of real cherries in sleevecages -- The per cent infestation of real cherries in sleevecages with 3:1 sterile (13.5 krad) to normal male ratios was only 9 per cent, compared to 61 per cent for controls. This reduction of 85 per cent is even greater than the expected reduction of 75 per cent (assuming perfect competitiveness). Results presented in Table 31 are divided into three time periods and indicate that reduction was maintained over a period of 20 days. There was a greater per cent infestation in both treatment and controls during the first six days.

A possible explanation for the better-than-expected results in this experiment is the large number of females used in the experiment. With a male: female ratio of 1:1 in the treatment cage, the females would have mated fewer times than where the males greatly outnumbered them. It can be inferred that these females were more receptive to males, and any deficiency in mating ability in irradiated males may be masked when females are receptive.

Only 10-15 fresh cherries were introduced into each cage each day. With 17 females in each cage, the number of cherries without oviposition-deterrrent pheromone

Table 31. Reduction in per cent infestation of real cherries with a sterile to normal male ratio of 3:1.

Dates	No. of cherries	Infested cherries	Per cent infested	$s/\bar{x}$
TREATMENT				
July 9-14	94	11	11.7	
July 15-24	92	6	6.5	
July 25-31	96	9	9.4	
Total/Ave.	282	26	9.2 ± 2.6	0.28
CONTROL				
July 9-14	94	68	72.3	
July 15-24	92	55	59.8	
July 25-31	96	50	52.1	
Total/Ave.	282	173	61.4 ± 10.2	0.17

would have been quickly reduced to zero each day. The excellent results in this experiment are largely due to the effect of the oviposition-deterrent pheromone and the large number of females, rather than supercompetitiveness of males.

G. Field Studies

Eggs collected -- A total of 229 eggs were obtained from the four 25-cherry samples from the field cages. Fifteen per cent were collected on July 11, 20 per cent on July 17, 31 per cent on July 24, and 34 per cent on July 27: the total number of eggs increased on each sampling date (Figure 16). There was a minimum of 12

and a maximum of 61 eggs in the cages. No eggs from the treatment cages hatched, but 10 out of 23 eggs (43.5%) from the Royal Anne control cage, and 18 out of 59 eggs (30.5%) from the Bing control cage hatched. The number of eggs that hatched in the controls declined with the passage of time because infertile eggs laid at any time previously remained under the cherry skin, while fertile eggs hatched after several days and no longer remained to be sampled.

Infestation in 25-cherry samples -- As can be seen from Figure 17, maggots were found in the infested control cages on all four sampling dates. Out of the total of 100 cherries taken from each cage, 31 were infested in the Royal Anne control, and 79 in the Bing control. One of the treatment cages for each variety contained some infestation: a total of 7 maggots were found in cage No. 4 on the last three sampling dates, and a single maggot was found in cage No. 2 on the final sampling date. The other two treatment cages had no infestation in these 100 cherries.

Infestation on the final sampling date -- On July 27 percentage infestation (Figure 18 and Table 32) on Royal Anne trees was 0 per cent (cage No. 1), 3.2 per cent (cage No. 2), and 49.2 per cent for the infested control (cage No. 3). On Bing trees the infestation

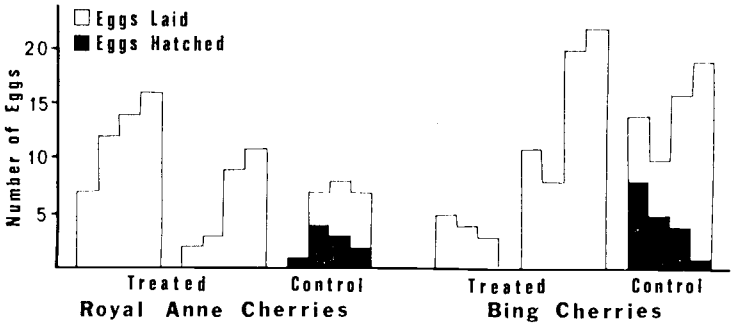

Figure 16. Number of eggs laid and hatched on four sampling dates, from cherries in field cages.

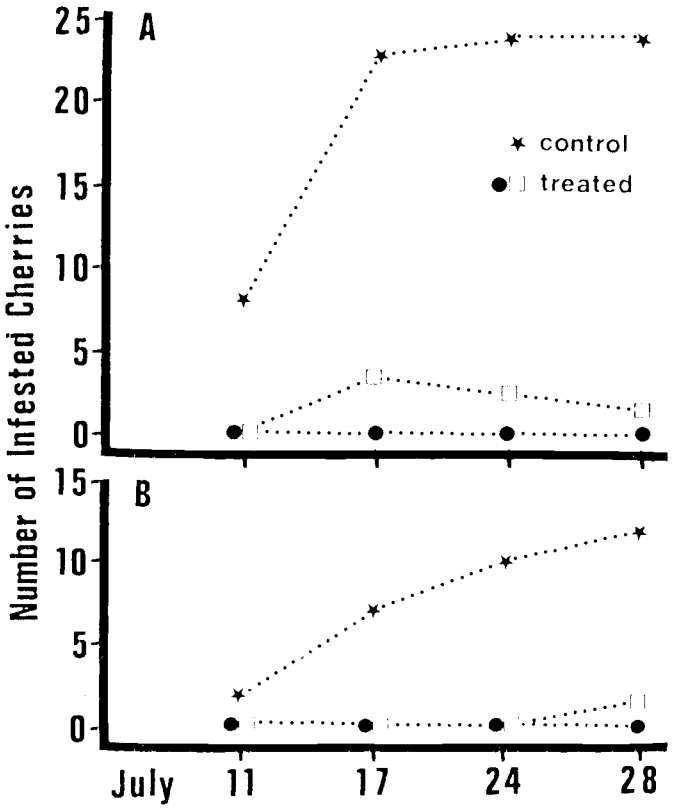

Figure 17. No. of infested cherries in 25-cherry samples from field cages on four sampling dates. A: Bing, B: Royal Anne.

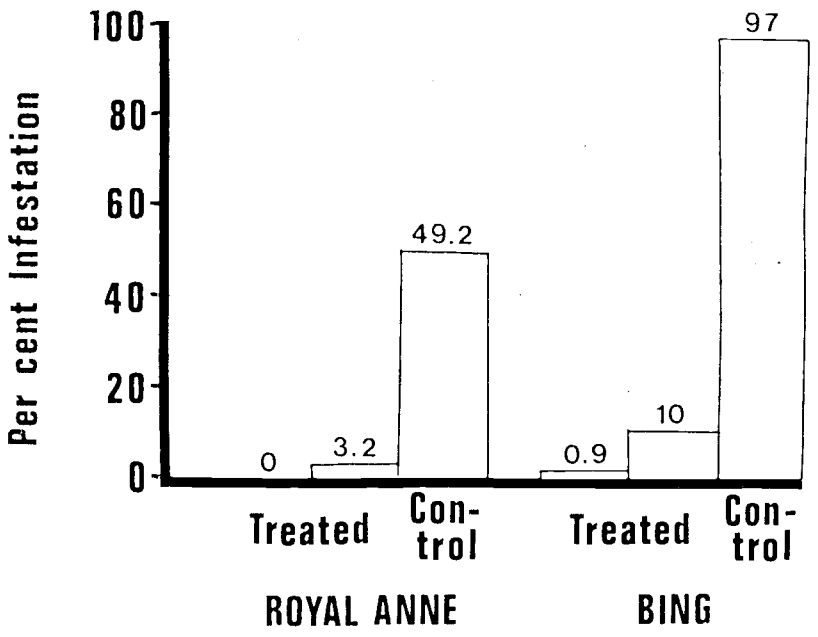

Figure 18. Per cent infestation in field cages on the final sampling date (harvest).

Table 32. Infestation of sweet cherries in field cages containing 20:1 sterile to normal male ratios.

Cage No.	Tree variety	Treatment	Number of cherries	Number cherries infested	Per cent infestation
1	Royal Anne	20:1 Ratio	107	0	0
2	"	"	124	4	3.2
3	"	Control	120	59	49.2
4	Bing	20:1 Ratio	110	11	10.0
5	"	"	117	1	0.9
6	"	Control	100	97	97.0

was 10.0 per cent (cage No. 4), 0.9 per cent (cage No. 5), and 97.0 per cent for the infested control (cage No. 6). Cages 7 and 8 ("uninfested controls") had no infestation. All cages had 100 or more cherries on July 27 except No. 7 and No. 8 which had 92 and 84 respectively.

The per cent reduction in infestation on the Royal Annes was 93 per cent, and on the Bings 95 per cent. This is very close to the 96 per cent reduction expected for a 20:1 ratio assuming perfect competitiveness. The great reduction of per cent infestation was in part due to an effect from the oviposition deterrent pheromone from females that mated with sterile males. This factor lessened the number of eggs laid by fertile females. Thus the reduction in infestation had two components: the reduction in fertility due to dominant lethals in the sperm of the sterile males, and the marking of cherries by infertile females.

Mortality of flies in field cages -- There was little mortality during the first half of the experiment, and five males and one female were still alive in cage No. 2 on July 27 (Table 33). There were a number of flies that were unaccounted for in each cage. Dead or escaped male flies would have changed the sterile to normal male ratio. It is noteworthy that the greatest

number of missing flies was in cage No. 4 which had the highest per cent infestation of any of the treatment cages. It is possible that the comparatively poor results in this cage were due to a changing of the sterile to normal male ratio.

Table 33. Mortality of flies in field cages.

Date		Cage number 1	2	4	5	3	6
July 1		----	----	----	----	----	----
5		----	----	----	----	----	----
8		----	----	1♂	----	----	----
11		1♂	1♂	----	----	----	----
14		2♂	----	2♂1♀	1♂	----	----
17		1♂	2♂1♀	----	3♂	----	----
20		1♂1♀,	1♂1♀	----	7♂1♀	1♀	1♀
24		2♂	1♂	1♀	3♀	1♂	3♀
27		2♂	1♂[a]	----	----	3♀	----
TOTAL DEAD	♂♂	9	6	3	11	1	0
	♀♀	1	2	2	4	4	4
MISSING	♂♂	12	10	18	10	0	1
	♀♀	3	1	2	0	0	0
TOTAL	♂♂	21	21	21	21	1	1
	♀♀	4	4	4	4	4	4

[a] 5 males and one female alive in cage No. 2 on July 27.

IV. DISCUSSION

A. Diapause and Emergence

Diapause -- Diapause is a state of arrested development that is resistant to environmental extremes. It is an adaptive strategy: the physiological condition of diapause is initiated in response to token stimuli in advance of seasonally adverse conditions (e.g. cold winters, or hot, dry summers). In multivoltine insects diapause is facultative and occurs in only one generation per season. In univoltine insects such as the western cherry fruit fly, diapause is obligatory and no mechanism is needed to insure induction of diapause at one time and its prevention at another. While the diapause of a usually univoltine insect may sometimes be prevented under laboratory conditions (e.g. the apple maggot), the study of the control of diapause in a univoltine insect is largely a matter of termination.

Western cherry fruit flies form puparia as early as the end of June, and thus have as much as three months of temperatures favorable to the development of most insects before cold temperatures begin. The chilling requirement of diapause insures that the pupae do not respond during this time, but instead emerge in the next season when fruit is again available. At room

temperatures and short photoperiods, Frick et al. (1954) did not obtain any emergence until 188 days of favorable temperatures had passed. Such spontaneous termination of diapause occurs only after an extended period of time has passed under unchanging conditions (Tauber and Tauber 1972). With long photoperiods, I obtained only 1.1 per cent emergence (within about a month after pupation). For cherry fruit flies, the spontaneous termination of diapause is a laboratory artifact.

The emergence pattern of Rhagoletis lycopersella Smyth, the Peruvian tomato fly, whose life cycle is not adapted to a seasonally extreme environment, but rather to a more or less constantly harsh desert environment (Smyth 1960), is interesting in that what may be spontaneous termination of diapause occurs under field conditions. A peak of adult emergence occurs about a month after pupation; but then low level emergence continues from 80 to 240 days (and maybe longer) after pupation. (This latter emergence is increased somewhat if moisture is increased.) This life cycle contrasts very sharply with that of the western cherry fruit fly which is adapted to the short fruiting season of its host. The emergence pattern of R. lycopersella is somewhat comparable to that of the western cherry fruit fly when it has not received a clear cut stimulus from

the environment and is insufficiently chilled (Figure 4, and Frick et al. 1954).

In contrast with the complete asychrony of spontaneous termination of diapause, the synchronization of emergence of R. indifferens improved steadily with longer periods of chilling at 3° C. Per cent emergence also increased with longer periods of chilling (1976-77 data, and Frick et al. 1954). Time-to-emergence (after removal from chilling) was minimized by 200 or more days of chilling at 3° C. These findings emphasize the importance of "diapause development" (Andrewartha 1952, Tauber and Tauber 1973) or "reactivation" (Danilevskii 1965). During diapause development changes occur that allow development to resume under subsequent higher temperatures. Williams (1956, 1969) showed that in Hyalophora cecropia L. the cold acts directly on the insect brain, rendering it able to resume its neurosecretory function. The prothorocotropic hormone secreted by the brain in turn causes the prothoracic gland (or its equivalent) to produce ecdysone (Highnam and Hill 1969), so development can occur.

The variation of time-to-emergence (as well as per cent emergence and synchronization) with increased periods of chilling indicates that diapause development was not completed during the shorter periods of chilling

in all flies. With longer periods of chilling it is completed in a greater percentage of the population.

Response to temperature is not necessarily uniform throughout the duration of diapause. Insects that do not complete diapause development during the period of cold temperatures may do so at elevated temperatures that would be unsuitable for initiation of diapause development. Tauber and Tauber (1976) reviewed the evidence for changing responses to temperature during diapause. In the western cherry fruit fly, nearly all insects have completed diapause development after 200 (or more) days of chilling and so are able to begin development as soon as exposures to favorable temperatures occur, which then results in synchronized emergence

Emergence -- The laboratory data showing additional emergence after rechilling, and the finding by Frick et al. (1954) and Jones (Appendix B) that some flies wait until the second or third season to emerge as adults indicate that all pupae do not complete diapause development while overwintering. This phenomenon occurs in most Rhagoletis species (Boller and Prokopy 1976). For western cherry fruit fly, the greatest percentage hold-over was in groups chilled for the shortest periods (Tables 6 and 9).

Whether or not any particular fly emerges would depend upon whether its own threshold of chilling was exceeded. If overwintering one or more years has adaptive value, the genetic make-up of a population could be expected to include individuals whose thresholds were such that they would not receive enough chilling during any winter their area was likely to receive. The per cent emergence and number of hold-over pupae will depend on both environmental and genetic factors and their interaction.

In addition to those insects that do not complete diapause development and do not emerge, it was noted above that (in the laboratory) others apparently completed diapause development at elevated temperatures. It is possible, particularly after mild winters that the degree of diapause development of a population at the end of winter could contribute to the timing and synchronization of emergence in the field. This factor, in addition to variations in the environment that cause variations in the heat units received by members of the same population, may account for the emergence of flies being spread out over a period of a month or more in the field.

Sifting of pupae from soil in the fall and chilling for several months resulted in much higher mortality

than sifting pupae in the spring and bringing them directly to the rearing room (26.7° C). Low parasitization was due to use of pesticides in the orchard from which spring-collected pupae were taken. Emergence from non-parasitized pupae was 25 per cent at best for fall-collected pupae (groups 12 and 13, chilled 120 days--see Tables 4 and 5); while spring-collected pupae averaged 78 per cent emergence. Clearly some aspect of the chilling/storage period was more favorable in the field. The spring-collected pupae did not have as good synchronization as pupae kept at 3° C for 200 days. This may have resulted from inadequate chilling, or from uneven accumulation of heat units resulting in some pupae being further along in development when they were taken from the field. Holding spring-collected pupae at 6° C for 1-2 months improved synchronization (Table 8), which points to inadequate chilling as a reason for the lack of synchrony in emergence.

Pupae that were collected by the soil method gave different results for per cent emergence in 1975 and 1976-77 (Figure 1). In 1975 the maggots were held at 27° C rather than 21° C, and it appears that the temperature during puparium formation may affect how the pupae respond during diapause development. The abrupt drop from 27° C to 3° C may somehow cause the pupae to react

to the cold more immediately than is true with a smaller change in temperature.

In 1976-77 a relationship between number of days chilled and per cent emergence was established, but differed from that found by Frick et al. (1954)--Figure 2. They found a levelling off at 80 per cent emergence after 150 days of chilling. The difference could be genetic, but it seems unlikely that flies from the Willamette Valley--which experiences milder winters than the Yakima Valley--would have greater chilling requirements. The differences may be at least in part due to the method of storing pupae: Frick et al. (1954) stored pupae in moist soil at 0° - 4.4° C, and then removed them to room temperatures. I kept pupae in Petri dishes without soil at 3° ± 1° C and 80-95 per cent relative humidity. This treatment might have a different effect than being in contact with moist soil. Another possibility is the effect of temperature or humidity after removal from chilling. Neilson (1964) found that pupae of the apple maggot held at 25° C had the greatest per cent emergence at 80 per cent relative humidity (81% emergence compared with 4% at 60% R. H. and 70% at 100% R. H.). The relative humidity was 45 per cent in my sleevecages where Petri dishes of pupae were kept for emergence in 1976-77; it may have been slightly lower

in 1975.

All four replicates that received 99 days chilling in 1975 had over 30 per cent emergence (Figure 1 and Appendix G). This result would not be expected from the 1976-77 curve. For laboratory purposes it is important to note that it is possible to obtain a fairly high per cent emergence after a relatively small number of days of chilling under some circumstances. Otherwise, unless pupae are held over a second year, rechilled, or reared on artificial diet (all of which are unreliable or give low yield) a supply of flies for laboratory use during October-December will be unavailable.

Presently, a supply of western cherry fruit fly pupae in numbers suitable for a SIT program could only be obtained by rearing them in an isolated cherry orchard. Such an orchard could be within about five miles of commercial cherry-growing orchards with safety. To remove any possible contamination it might be better to have the control area and the rearing orchard farther apart: for instance, for a SIT program in Lane Co., Oregon, flies might be reared in Benton Co., where there is not such a heavy concentration of orchards. Flies for release in the Dalles would probably have to be reared in another part of the state.

A generally overlooked advantage offered by mass

rearing is to select for desirable attributes in the insects. For instance, selecting for higher mating frequency by males could be done, which would obviously improve a SIT program. It should be possible to select for this trait and release flies with the trait into the isolated orchard that is to be used for rearing western cherry fruit fly.

B. Biology of R. indifferens and its Suitability for SIT.

Biology -- Considerable variation was apparent in the age at first mating and oviposition. In laboratory cages some females never laid any eggs and other laid very few. This may have been due in part to less than perfect stimuli provided by artificial cherries; however, there is no evidence that there is not a similarly wide variation in the field.

Cages with 1-2 male and female flies showed a change in the flies' behavior similar to that known to occur in the field. For 5-10 days after emergence the flies are not attracted to cherries. Mating and then oviposition begin after the change in behavior in regard to cherries has occurred.

The relatively long pre-oviposition period of the cherry fruit fly has permitted very good control to be

achieved with chemicals in most situations. Similarly, the pre-mating period may be very advantageous for the success of SIT against cherry fruit fly. Wild females will fly about the tree where they emerged, and perhaps to nearby trees, before mating occurs, so that panmixia with regard to released and native flies is at least theoretically possible. The pre-mating period also removes one objection to release of females as well as males. Donnelly (1965) noted that if females are released with males, it may lessen dispersal. However, if released flies are of such an age that they are not yet ready to mate, they will ignore each other at first and disperse. Whitten and Pal (1974) cited selection for individuals which mate soon after adult eclosion (in mosquitos) as a possible means of resistance to SIT (and one which could not be overcome by going back to the wild population to get new breeding stock). This problem would not arise in cherry fruit flies and other insects with long pre-oviposition periods.

The number of flies in a cage appears to have some effect on behavior. Some of the effect may be due to the presence of the male pheromone: if more males are present the females may be more receptive. With sterile and normal males present in a cage in numbers greater than those for females, the total number of matings was

higher than for control cages with smaller numbers of males. This could have been due to the male pheromone, or simply to a greater number of mating attempts by the greater number of males (relative to the number of females).

The effect of the male pheromone to make the females more receptive was seen in the laboratory. It would presumably act in the field to attract females from distances greater than the range of visual contact. If sterilized males were to produce less pheromone, this could contribute to lowered competitiveness in the field.

The presence of large numbers of sterile males (in the 4:1 and 8:1 ratio cages) reduced the frequency of mating by normal males. In these tests the number of females was five per cage (or 2.5 times the number of normal males). If irradiated females were not released in a field program, so that only wild females were present, the reduction in the number of times a normal male could mate (due to low receptivity of the females which had mated with sterilized males) should be even greater.

Causse (1974) found that more matings occurred in Ceratitis capitata when the females outnumbered the males. Similarly, in western cherry fruit fly, males

can be expected to mate repeatedly if there is an excess of females. If irradiated females were released in a separate area from males and had not lost their propensity to mate, the normal males would mate with them instead of with normal females. In this case, the loss of receptivity of females after several matings would not be a factor.

The successful suppression of a cherry fruit fly population might also depend on the deposition of oviposition-deterrent pheromone by normal females that had mated sterilized males. (Any releleased sterilized females would not deposit the pheromone because they would not lay any eggs. However, females irradiated at an advanced age--e.g. 10 days old--might lay some eggs and deposit pheromone.) A normal, fertile female would be deterred from laying eggs in many cherries, and would lay a smaller total number of eggs if a high percentage of cherries were coated. If the population of flies were very low, this factor would have no effect, however, because there would be many cherries without a coating of pheromone.

Suitability of SIT for R. indifferens -- The western cherry fruit fly is a candidate for the sterile-insect technique for a number of reasons. (1) It is a tephritid, and the radiation biologies of this family are favorable

for the technique. Specifically, in R. indifferens I found that sterility (ca. 99.5%) could be induced in males by a dose of 8 krad. Females were rendered infecund by this dosage, while the competitiveness of males was at an acceptable level. It is possible that nitrogen or other atmosphere during radiation of the flies could result in increased competitiveness such that irradiation in the pupal stage would be feasible.

2) Pesticides are currently being used to control populations at levels where the SIT is more efficient. It is generally considered desirable to eradicate this pest (as evidenced by the California effort to do so, and the low economic thresholds), but such attempts are probably doomed to failure without some technique that is efficient at very low population levels.

3) The pre-oviposition (and pre-mating) period that permits good control with pesticides will also allow mixing of released flies with the native population before mating. The finding that sperm from the last-mated male has precedence is also very favorable for a successful SIT program.

4) A major problem in some areas is the immigration of flies from backyard trees or abandoned orchards. If these sources are far enough away (ca. one-half mile) the number of flies immigrating to an orchard would be

few enough so that SIT alone could control this problem.

Ideally, abandoned orchards should be removed, but spraying followed by SIT might be suitable in these areas too. Release of sterile females (or of the fraction separated by screening of pupae that will yield nearly all females) in abandoned orchards would make use of the one-half of the reared insects that would have no additional effect if they were released with the sterile males.

Release of flies into individual backyard trees may be more efficient and would be safer than spraying pesticides. Also, people who might object to spraying their backyard tree might accept release of sterile flies.

5) Use of SIT in an integrated control program rather than relying on frequent applications of pesticides from first emergence to harvest would be an improvement in population management for this pest. The development and general use of mechanical harvesting in the last decade has created a situation that is especially suitable for SIT. Some fruit is left on the tree following mechanical harvesting, and any female fruit flies that were not killed by insecticides, or that immigrated into the orchard after the last spray, can build up the population unhindered in this remnant

of cherries. SIT would be efficient in combating this low density population which offers no immediate threat to the grower, but serves to build up a population for the next year.

SIT could also be used before harvest (after any large numbers of flies from the peak emergence period had been reduced with pesticides). The technique would have the advantage of leaving no chemical residue. Most chemical control agents have a restriction on the minimum time interval between the last application and harvest (AliNiazee and Capizzi 1976).

Sterile to normal male ratios -- With a univoltine population it is desirable to have large sterile to normal male ratios. For instance, if a 20:1 ratio was determined to be the smallest ratio that would achieve eradication in five generations for a multivoltine insect, one would like to have a much higher ratio (50:1 or 100:1) for a univoltine insect. The reason is that time is measured in generations for SIT, and one does not want to wait 4-5 years to determine if the SIT release is working as predicted. If continuous suppression, or protection from invasion/immigration is the purpose of the releases, the ratios could be the same as for multivoltine insects.

Lawson (1967) noted that to cause a very sharp

decrease in the population in the first generation by SIT, the total number of insects released must be sharply increased. (This action would also reduce the number of generations needed for eradication.) The total number of released insects necessary to achieve eradication will be greater if it is done in fewer generations. The ratio selected for release will be a compromise between the desired rate of eradication and the cost of obtaining insects. A 20:1 sterile to normal male ratio would be a reasonable figure for field trials, with separate trials at 40 or 50:1 being desirable.

Berryman (1967) developed a model to describe the effect of sterile males on a wild population, and it can predict the numbers of sterile males necessary under a variety of situations. Bogyo et al. (1971) analysed the effects of varying a number of parameters with the model. They found that the probability of survival from egg to adult is perhaps the most crucial parameter for a SIT program. For instance, with mean number of eggs per female at 100, and competitiveness of males at 0.75, a 0.25 probability of survival would require a 20:1 ratio; while a 0.50 probability would require a 50:1 ratio. Life table type data cited earlier indicate that Rhagoletis flies have high mortality in the last larval instar and in the pupal stage. The incorporation of at

least one chemical spray into a cherry fruit fly eradication program employing SIT would greatly aid in achieving eradication, by greatly lowering the probability of survival to a reproductive adult.

The model indicates that reduction in competitiveness of males following irradiation will not require a much greater sterile to normal male ratio unless competitiveness falls below 40-50 per cent. When sperm from the first or last mated male has prececence, the required sterile to normal male ratio is exactly the same as if the female was monogamous.

The model can be used to estimate whether the number of flies available for release will be sufficient, or if one or more chemical sprays will be necessary, or if the eradication area could be expanded or must be contracted.

Separation and use of females -- The release of sterile females is most often neutral in regard to the success of a SIT program (Whitten 1969, Whitten and Pal 1974). The release of females is detrimental if they are not 100 per cent sterilized. Their release may also be detrimental if they use up most of the sterile males' sperm. If a sterile male has lost all his sperm in mating with sterile females, and is then in the condition of aspermy when he mates with a wild female, it is

just as if no mating had taken place.

Kojima (1971) developed a (stochastic) model in which natural selection was allowed for by varying survival rate and fecundity-fertility by a random percentage. As with the Berryman-Bogyo model, he found that the "population expansion factor" to be a critical one. Kojima also concluded that the release of sterile males alone was more effective than release of sterile males and females. However, in doing this he assumed that if females were not released, the number of males reared could be increased by a like amount. This is not true for the rearing systems of most insects, and certainly not for the western cherry fruit fly at the present time. White et al. (1976) found that in the release of codling moths, males, females, or males and females together were approximately equally effective.

It would not be reasonable to separate the females from the males unless it could be done easily, or unless their presence had some deliterious effect, or unless some other use could be made of them. If females were more radioresistant than males, or in some other way caused damage (e.g. ovipunctures), it would then be advisable to separate the sexes. Whitten (1969) suggested that female insects could be separated and (a) parasitized before release, (b) boobytrapped with a

chemosterilant, or (c) released in a separate area.

Some rather elaborate methods of sexing insects have been suggested and developed in SIT projects. Sexing of house flies with a sex-linked marker can be done by machine (Whitten 1969). A rapid method of sexing mosquito pupae based on a grid or screen and the pupae's own movements has been developed (Sharma et al. 1972, Pal 1974). Whitten and Forster (1975) suggest that for many insects the linking of insecticide resistance genes to the sex chromosome would be an attractive form of conditional-lethal sex killing.

Sexing of adult western cherry fruit flies is easy, but very time consuming. Sexing of pupae is less accurate, but very fast. By sifting with a 4 mesh per linear cm screen, pupae can be separated into two fractions: one that is mostly (ca. 75%) males and one that is mostly (ca. 90%) females. Release of sterile flies with such a 3:1 male:female ratio would be an improvement over release of a 1:1 ratio if it is determined that the release of females with males is detrimental (e.g. as a sperm sink for sterile sperm). Sifting with screens that are slightly larger and smaller would yield two groups of pupae that were very nearly one sex, and a third with both sexes. Remund and Boller (1976) described the size distribution in

R. cerasi adults and pupae.

I suggest that for western cherry fruit fly, females be separated (by screening of pupae) and released in abandoned orchards where suppression is desirable (as a means of reducing sources of infestation) but where fruit would not be harvested so that control is not critical. Irradiated females would act as a sperm sink, and most wild females would never mate if enough sterile females were released. It may be necessary to irradiate older females (ca. 6-10 days old) to obtain optimum mating behavior and so the females will lay eggs and coat the cherries with oviposition-deterring pheromone.

Irradiated females of R. indifferens were found not to make ovipunctures for a period of about a month after irradiation. If, however, ovipunctures by released females were found to occur before harvest, adult females remaining after screening could be separated by hand.

The marked difference between these findings and the situation in the case of the European cherry fruit fly, R. cerasi, is correlated with the short pre-oviposition period of the European species. In that species eggs are laid at relatively high doses, and the female is actually somewhat more radioresistant than

the males (Boller et al. 1975).

Sexing of western cherry fruit fly would not be necessary for post-harvest releases, however, and if releases were started only shortly before harvest as was suggested, the released females should make no ovipunctures before harvest. Where male and female flies are released together, there should be little or no problem with released females if flies are irradiated 1-3 days after emergence. The released female flies would tend not to go to cherries to lay eggs, and so the males would not be able to mate with them.

Initiation of a field program -- The evaluation of the western cherry fruit fly's candidacy for control by SIT has thus far been confined to radiobiological studies, evaluation of methods of obtaining pupae, and cage studies. The field application of SIT will run into problems not encountered in cage studies, but the indications are that these problems will not be insurmountable with the western cherry fruit fly. In a cage study the number of normal and sterile flies is known, and they are confined in a small area so they can be expected to interact. In a field situation, estimation of the absolute field population may be difficult, and without the confines of a cage, it is possible that the flies will not interact as well.

As was discussed earlier, there are several methods for estimating absolute population levels of this fly, of which yellow sticky traps (with feeding attractant) appear to be the most appropriate for SIT. Steiner (1969b) discussed some of the problems in estimating natality (the numbers of new additions to the adult wild population), however his system is more applicable to tropical fruit flies with overlapping generations than to univoltine fruit flies.

The yellow sticky traps used for Rhagoletis flies are much less efficient than the sex lure traps used for tropical fruit flies. Steiner (1969b) stated that 2 or 3 traps per square mile are sufficient for melon and oriental fruit flies, and 10 per square mile for Mediterranean fruit fly (in areas of 25 square miles or more). For western cherry fruit fly, two traps per acre would be necessary (M. T. AliNiazee, personal communication) because of (1) the small areas involved, and (2) trap inefficiency.

With univoltine fruit flies, one has the advantage of estimating populations from (a) the previous year's infestation, or (b) soil samples (overwintering pupae) because generations are discrete. In practice, either of these methods would be limited to situations where the population was very low; otherwise application(s) of

chemicals would be necessary before SIT releases began.

Population levels of western cherry fruit fly might be estimated at nil from lack of infestation the previous year (including hand-picked samples of fruit left on trees after mechanical harvesting). Sticky traps might then be limited to areas where there had been infestations the previous year, and also along orchard edges where immigration might be expected.

The efficiency of the traps should be estimated under the conditions of any given area. Calibration of traps may be done by a mark-release-recapture method (Proverbs 1974), or by correlation with infestation levels. Several methods of marking tephritids are available (e.g. Schroeder et al. 1972).

SIT is most often first tried on an island, or in some defined area that supports a small and more-or-less isolated insect population. The relatively poor dispersal powers of cherry fruit flies means that a test area would not have to be isolated by long distances. Similarly, a SIT program could cover only part of a continuous cherry growing area, or be used on an orchard-by-orchard basis in an integrated control program.

Still, the prospect of initiating a SIT program in a large continuous cropping area is unattractive enough

that Boller and Prokopy (1976) considered species of Rhagoletis on apple and cherry in eastern North America to be poor prospects for SIT. On the other hand, cherry growing areas in the Pacific Northwest are divided into a number of isolated areas (Davis 1968), with the largest concentration of cherries being in the Willamette Valley, followed by the Yakima Valley, and the Dalles, Oregon, area. In the Willamette Valley, the southern cherry-growing area (Lane Co.) is not continuous with the larger cherry-growing area in the northern parts of the valley, and might make a suitable area for an integrated chemical and SIT program against the western cherry fruit fly. The Dalles area has a control district already. In such an area SIT might replace chemicals altogether.

Although longevity of irradiated flies is reduced, both laboratory and field results indicate that the reduction is not large enough to be a major problem. Three or four releases at 10-day intervals, beginning just before harvest if sprays have been applied during peak emergence, would be a reasonable program to start. If no sprays were applied, the timing of the first release might be a matter of some concern. Because the numbers would be very low in situations where the decision was to use SIT alone, and because pupae would

have to be removed from refrigeration long before the first field emergence occurred, the first release date would have to be calculated on the basis of thermal-unit accumulation starting March 1.

Pupae would have to be removed from storage at 3° C 30 days before the anticipated release date. Alternavively, pupae could be moved from 3° C (after ca. 6 months) to 6° - 10° C to shorten the days between removal from refrigeration and emergence.

SUMMARY AND CONCLUSIONS

1. Pupae obtained from soil in August-September had 8-16 per cent emergence after 90-150 days chilling at 3° C. Mortality due to parasitization was 14.8 per cent in these pupae. (For pupae obtained by bringing infested cherries into the laboratory, mortality due to parasites was only 0.17 per cent of fly emergence.) The total parasitization plus dead pupae from other causes ranged from 70-85 per cent. Pupae collected from a commercial orchard in April and May had 79 per cent emergence, which was very satisfactory, but the yield was too low for the effort necessary to sift the soil. If the sifting method is to be used at all, pupae must be concentrated in the soil.
2. Picking infested cherries in July and putting them over hardware cloth and soil in the laboratory is a satisfactory method of obtaining pupae. The infestation at an abandoned orchard in Albany peaked about mid-July, with maximum yields of 1.44, 1.51, and 1.01 maggots per cherry for 1974, 1975, and 1976, respectively. Dissection of cherries is necessary to be sure that picking is done near the time of peak infestation.
3. About 200 days of chilling at 3° C is necessary to

obtain satisfactory synchronization of adult emergence. Chilling pupae for as long as 300 days may be necessary to obtain maximum emergence. Rechilling of pupae may result in additional emergence.

4. The time to emergence decreased from about 40 days after 100 days of chilling until it levelled off at about 26 days after 200 or more days of chilling. Chilling at higher temperatures (6° C) decreased the time to emergence, but also decreased synchronization, so it was unsatisfactory. Adult emergence of 1.1 per cent was obtained without chilling when pupae were held at 26.7° C with a photoperiod of 19L:5D. The report by Frick et al. (1954) of a second generation under field conditions is questioned.

5. Most females can be removed by sifting pupae through a screen with four mesh per linear cm. Two groups of pupae will be obtained: one about 75 per cent male, and the other about 90 per cent female. It is suggested that the latter group be released in abandoned cherry orchards.

6. Female western cherry fruit flies laid an average of 65 eggs per female under laboratory conditions (shoebox cages). When equal numbers of artificial cherries were put on the floor and ceiling of cages,

only 41 per cent were laid on the ceiling cherries. It was concluded that cherries should be placed on the floor only, to increase efficiency of egg collection. The deposition of a sucrose-honey solution on the wax cherries deterred oviposition. Eggs placed on wet filter paper hatched in four days at 26.7° C.

7. Because of problems with per cent emergence and synchronization of emergence after less than 200 days of chilling, and because of problems with rearing methods involving an artificial diet, it is recommended that flies be reared in an isolated orchard.
8. Under laboratory conditions the variability was great for age at first mating (6-25 days for males, 5-24 days for females). First oviposition occurred at age 6-33 days. Response to artificial cherries in the laboratory was similar to behavior reported in the field: after an initial period of 5-10 days during which the flies were not attracted to the cherries, the male (and to a lesser extent the female) flies began to spend a large part of one-hour daily observation periods on the cherries. Mating occurred after the change in behavior.
9. Normal males remained <u>in copula</u> for an average of 70 ± 34 min., while males irradiated as adults with

8 krad had an average of 59 ± 25 min. (n.s.).

10. Data indicates that the sperm from the last mating has precedence, though some mixing may occur.

11. In cages where both normal males and males irradiated with 8 krad as adults were present, the irradiated males mated nearly as often as the normal males. Total number of matings in cages with 4:1 and 8:1 sterile to normal male ratios was about twice that in control cages (which had only 1/5 or 1/9 as many male flies). It was concluded that an upper limit to the number of times a female would mate was reached. The presence of large numbers of sterile males reduced the frequency of mating by normal males.

12. Under laboratory conditions, in several experiments, the number of flies in the cage appeared to affect the results. In separate experiments, the presence of a male pheromone was demonstrated.

13. The dose-response curve indicates that a 99 per cent reduction in per cent egg hatch can be obtained by mating males irradiated as adults with 7 krad to normal females.

14. Under laboratory conditions competitiveness was better with 1:1 or 4:1 sterile to normal male ratios than with 8:1. Irradiated males may be less

competitive where they are likely to be disturbed by other males during mating.

15. Males irradiated as adults were over twice as competitive as males irradiated as pupae.

16. Females did not lay eggs after irradiation with a dose of 5 krad or higher. Females irradiated as pupae with 8 krad did not make ovipunctures during the first month, suggesting that irradiated females might be released without causing ovipuncture damage (or inoculating brown rot) in the field.

17. Longevity of male flies irradiated as adults decreased significantly ($P < 0.01$) with increasing dosage of gamma radiation. This decrease may have been partly or largely due to decreased disease resistance: normal females showed a significant ($P < 0.05$) decrease in longevity with increasing dosage given to the males they were caged with. Longevity of females irradiated as adults or pupae was not significantly less than that for controls.

18. Competitiveness of irradiated flies, as measured by per cent infestation of real cherries (laboratory and field), was very good. The oviposition-deterrent pheromone coated onto cherries by females mated to irradiated males may have lowered the total oviposition of fertile or partly-fertile females, and so

compensated for the lowered competitiveness of males that was seen in the laboratory experiments. Per cent infestation with 20:1 sterile to normal male ratios was reduced 93-95 per cent over the controls in field cage experiments.

19. Laboratory and field data indicate that SIT can be applied to the western cherry fruit fly. Further field studies on small isolated orchards are recommended.

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APPENDICES

APPENDIX A: Effect of winter temperatures on the comparative time to emergence by males and females.

Correlation of the average monthly minimum temperatures (October-March) and the difference in time to emergence for male and female western cherry fruit fly. Data from S. C. Jones[a].

Year	No. cages	Average difference in days to emergence ♂ - ♀	Deviation from Ave. minimum temperature (Oct.-Mar.)[b]
1939	13	0.63 ± 1.04	1.23° C
1940	14	1.13 ± 0.70	2.28° C
1942	7	-0.06 ± 1.13	0.43° C
1944	6	-0.99 ± 1.48	0.17° C

[a]Annual reports on cherry fruit fly for the Agricultural Experiment Station, Oregon State University, unpublished. 1939:15-16, 1940:24-25, 1942:14, 1944:18.

[b]Calculated from information on pages 7, 8, and 15 in Bates, E. M., and W. Calhoun. 1970. Local climatological data for Oregon State University, 1968, with normals, means and extremes. Special report 277, revised July 1970. 42 pp.

Linear regression of the four points in the above table yielded the line $Y = 0.90\ X + (-0.75)$. The correlation coefficient, $r = 0.93$, was significant ($P < 0.05$).

APPENDIX B: Hold-over Emergence

Percentage emergence for 1st, 2nd, and 3rd year emergence of western cherry fruit fly in the Willamette Valley (from S. C. Jones' data[a]).

Year Cages Infested	Per cent emergence			No. of flies
	1st year	2nd year	3rd year	
1933	75.8	23.9	0.3	289
1934	72.9	26.8	0.4	538
1935	98.7	1.3	0	1328
1936	89.9	7.1	3.0	198
1937	52.4	42.9	4.8	21

[a]Annual report on cherry fruit fly for the Agricultural Experiment Station, Oregon State University, unpublished. 1934:8-12; 1935:2, 4, 6-10, 16; 1936:8, 10; 1937:2, 4-5; 1938:22; 1939: 9, 17.

APPENDIX C: X- and Gamma Rays

X- and gamma rays overlap in their electromagnetic wavelengths, and differ in their sources rather than in essentials (Lapp and Andrews 1972). X-ray machines produce polychromatic rays, that is, rays of many wavelengths and photon energies; while radioactive elements produce gamma rays of only one or a few discrete wavelengths and energies (Arena 1971, Ducoff 1971). The choice of which source to use for the irradiation of insects is largely a matter of convenience and cost. For irradiating a small number of insects for a preliminary study, an X-ray machine is often more readily available. For an on-going sterile insect release program, the X-ray technique is not feasible because of the expensive tubes that will burn out with the long exposure periods. There is also a limitation on the volume of insects that can be handled in an X-ray machine (NAS 1969), while special Co-60 source machines have been developed to handle large volumes of insect material. Darden et al. (1954) described a Co-60 source especially designed for sterilizing insects.

Of the radioactive elements, Co-60 is usually preferred over Cs-137 because the former is a more intense source of gamma radiation because it emits two photons for every atom that disintegrates (Arena 1971); and with

a half-life of 5.27 years (Heath 1967), a greater percentage of its atoms disintegrate in a given time than for Cs-137 with a half-life of 30 years. The availability of Co-60 sources was important in making the SIT feasible (NAS 1969).

The unit of exposure dose for X- and gamma rays is the roentgen (R), which is defined in terms of the number of ionizations produced in a standard absorbing substance, air. The rad (an acronym for radiation absorbed dose) is defined as that amount of radiation that deposits 100 ergs of energy per gram of absorbing substance (Lawrence 1971). Different substances exposed to the same exposure will absorb different doses. However, water, muscle, fat and material of similar effective atomic number will absorb approximately the same dose. Insects should be irradiated in containers of low effective atomic number such as plastic, rather than glass.

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APPENDIX D: Dose-rate for the OSU Co-60 Irradiator

The decay constant $\lambda = 0.693/T$, where T is the half-life of a radionuclide. For Co-60, T = 5.27 years (Heath 1967) or 63.3 months. Thus, $\lambda = 0.693/63.3 = 0.01095$ per month. Once a radiation dose rate is obtained for a given date, this fraction may be added or subtracted to obtain radiation values at monthly intervals in the past or future. Harmon (1976), using thermoluminescent dosimetry, calibrated several positions within the high flux section of the sample container of the Oregon State University (OSU) Co-60 irradiator. On January 28, 1976, he found a dose rate of 1815.8 rads per min. for position D (about 2 cm high on the perifery of the high flux chamber). From this I calculated a dose rate of 1813.2 rads per min. for February 1, 1976. The values in Table D-1 were generated for dates from January 1, 1975 to December 1, 1977.

To calculate the dose received by an irradiated sample, the dose received while the source is being raised and lowered must be considered, as well as the dose rate while the source is in its fully raised position. Harmon (1976) calculated that a sample received 306.1 rads during source movement on January 28, 1976. Table D-2 lists doses received during source movement for the first day of the months for 1975-77.

Table D-1. Dose-rate in rads per min. for the OSU Co-60 gamma irradiator, 1975-1977.

Date	1975	1976	1977
January 1	2089.0	1833.1	1606.4
February 1	2066.3	1813.2	1588.8
March 1	2044.0	1793.3	1571.4
April 1	2021.8	1773.7	1554.2
May 1	1999.9	1754.3	1537.2
June 1	1978.3	1735.1	1520.4
July 1	1956.8	1716.1	1503.7
August 1	1935.6	1697.3	1487.2
September 1	1914.7	1678.7	1471.0
October 1	1893.9	1660.3	1454.8
November 1	1873.4	1642.1	1438.9
December 1	1853.1	1624.1	1423.1

Table D-2. Doses received (rads) during source movement, 1975-1977.

Date	1975	1976	1977
January 1	353.0	309.8	271.5
February 1	349.1	306.4	268.5
March 1	345.4	303.0	265.6
April 1	341.6	299.7	262.7
May 1	337.9	296.5	259.8
June 1	334.3	293.2	257.0
July 1	330.6	290.0	254.1
August 1	327.1	286.8	251.4
September 1	323.5	283.7	248.6
October 1	320.0	280.6	245.9
November 1	316.6	277.5	243.2
December 1	313.1	274.5	240.5

The OSU Co-60 irradiator was specially designed to give high gamma dose rates and is fitted with a safety interlock system (A, B, C, and D in Figure D-1) to minimize radiation exposure to the operator. The source cannot be raised to a position surrounding the high flux chamber unless the door is open. The lid (plug) cannot be lifted until the door is closed (resting between the source and the high flux chamber. It is thus impossible for the operator to remove both shields (door and plug) at the same time; one or the other will always be between the operator and the source. The safely feature is essential on an irradiator with a high dose-rate capability.

The high flux section of the sample container is a hollow cylinder, 12.7 cm high and 12.7 cm in diam. Position D (of Harmon) is on the perifery of the cylinder, 1.6 cm above the floor of the sample container.

Literature cited in Appendix D

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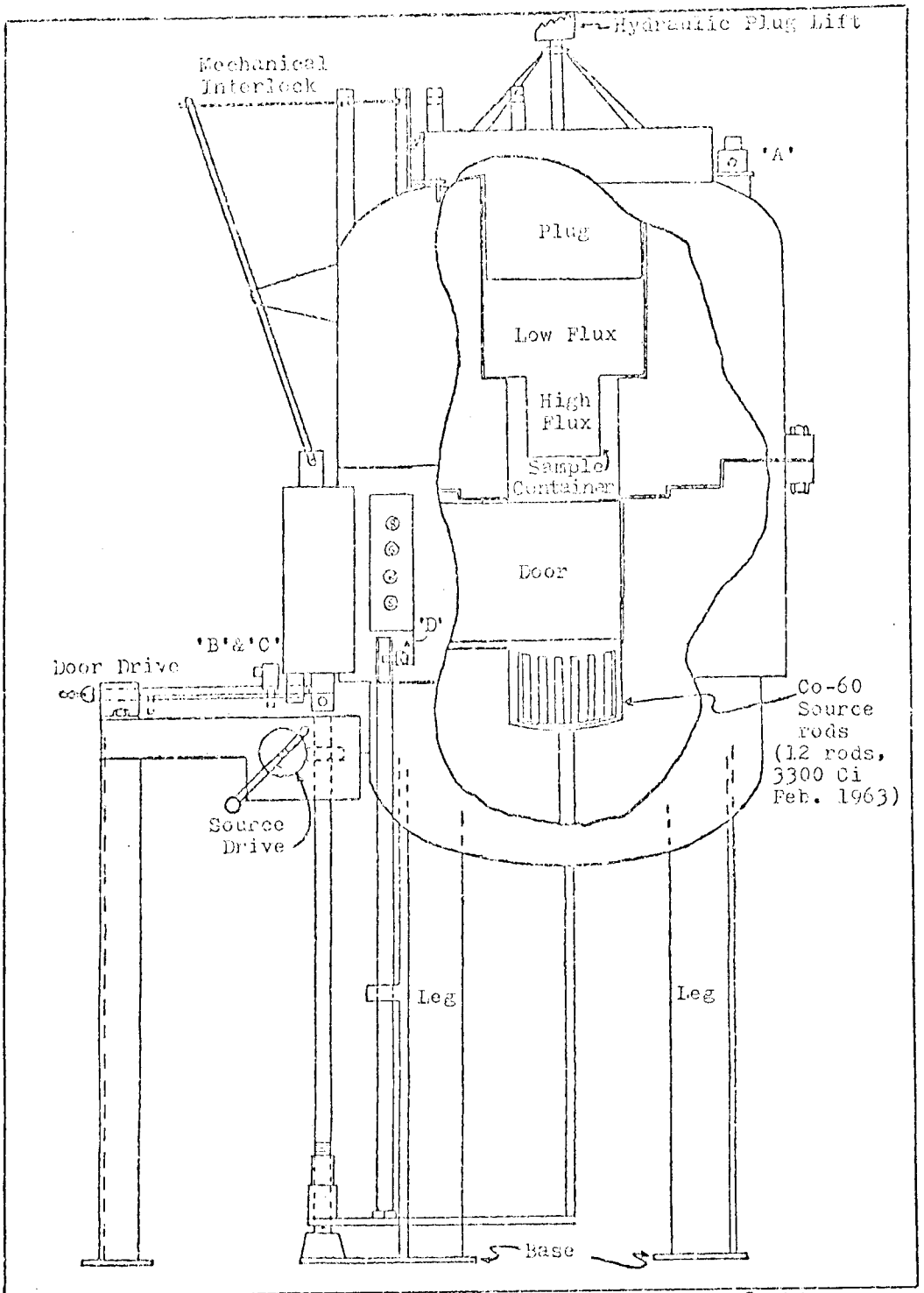

Figure D-1. The OSU Co-60 irradiator. The letters A-D indicate the key positions of the interlock system. Flies were irradiated in the high flux section of the sample container. Illustration from the Instruction Manual, (Cobalt-60) Gamma Radiation Facility, Oregon State University. Unpublished, no date. 20 pp.

APPENDIX E: Competitiveness Indices

Indices of competitiveness have been used to provide point estimates of total competitiveness (Fried 1971). Such indices are desirable to make comparisons easier when the per cent hatch of control groups varies among experiments. Indices are designed to vary between 0 and 1, with a value of 1 indicating complete competitiveness. (Values above 1 indicate hypercompetitiveness.)

The index of Ahmed et al. (1976) is excellent for experiments with 1:1 sterile to normal male ratios, but results from experiments with other ratios are not directly comparable. Fried (1971) and Haisch (1970) developed identical indices with which results with various sterile to normal male ratios can be directly compared. The formula for this index (Haisch's notation) is:

$$e = \frac{q-f}{n\ (f-p)}\ ,$$

where q = the hatching rate (%) of eggs from a normal population (control); f = the hatching rate (%) of eggs from a population of normal pairs and irradiated males (treatment groups); p = hatching rate (%) of eggs from a population of normal females and irradiated males; and n = the sterile to normal male ratio.

This formula is basically the expected egg hatch (E) divided by the observed egg hatch (O), where E = q(u + pv), and O = f; u = percentage of unsterilized males, and v = percentage of sterilized males in the treatment cage. The value e differs from E/O in that the value f is subtracted from q in the numerator. Without this modification the value cannot go to 0 when the irradiated flies have no effect, but the minimum value that could be reached would be equal to u.

Literature cited in Appendix E

Ahmed, M. Y. Y., E. W. Tilton, and J. H. Brower. 1976. Competitiveness of irradiated adults of the Indian meal moth. J. Econ. Entomol. 69: 349-52.

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APPENDIX F: Per cent emergence by sex

Days at 3° C	Per cent males	Days at 3° C	Per cent males	Days at 3° C	Per cent males
90	60.0	150	25.0	220	40.9
	57.1		53.8		52.4
	40.0		41.9		48.0
	33.3		38.5		48.4
			58.3		42.2
99	57.1				
	50.0	165	33.3	235	50.0
	77.8		48.4		43.4
	52.6		41.7		
			50.0	240	46.2
110	54.2		43.8		50.0
					40.0
125	55.6	179	60.3		46.4
	56.3		45.1		
	36.4		22.2	250	47.8
	50.0		48.0		45.5
	70.6				53.4
	40.0	190	61.4		50.9
	75.0		51.9		
	63.6			260	34.0
		192	38.6		40.0
127	51.9		46.0		
				263	50.0
137	38.9	201	43.8		36.4
	58.3		37.6		46.9
			42.9		44.4
140	25.0		60.0		
	75.0		50.0	290	37.9
			69.2		44.6
150	41.2				39.3
	35.3	210	36.4		

Linear regression line: $Y = -0.0526\ X + 57.27$

Correlation coeffficient: $r = -0.29$ (significant, $P < .05$).

APPENDIX G. Emergence of adult flies

Emergence of flies after varying time in 3° C. One-hundred pupae per dish unless indicated otherwise.

Dish No.	Days in +3°C	Ave. No. days until emergence	S.D.	No. of flies that emerged	Median	Mode	Range
75-1	99	41.44	± 5.20	41	42	42	32-59
a	"	41.00	± 4.45	40	41.5	42	-52
-2	"	39.19	± 5.01	31	39	43	30-47
-3	"	38.58	± 4.49	36	38	38	30-48
-4	"	38.35	± 4.20	37	38	36	28-46
Total	"	39.46	± 4.91	145/400	40	40	28-59
75-5	127	34.69	± 4.30	26	35	33,35	25-48
a	"	34.16	± 3.45	25	35	33,35	-41
75-6	150	33.00	± 4.69	20	31.5	28,31	26-42
-7	"	29.05	± 3.59	38	28	28	24-36
-8	"	31.08	± 3.74	26	31	31	24-41
-9	"	28.56	± 3.42	34	28	28	24-35
Total	"	30.03	± 4.12	118/400	30	28	24-42
75-10	179	30.74	± 3.36	68	30	27,34	25-41
-11	"	29.25	± 3.54	51	28	27	25-41
-12	"	29.78	± 5.36	18	28.5	30	25-50
a	"	28.59	± 2.22	17	28	30	-33
-13	"	31.40	± 4.10	25	32	34	25-40
Total	"	30.27	± 3.89	162/400	30	27	25-50
75-14	192	28.69	± 3.68	59/158	28	25,27	24-44
75-15	201	25.43	± 1.76	7	25	25	23-28
-16	"	25.50	± 3.40	40	25	25	23-45
a	"	25.00	± 1.36	39	25	25	-28
-17	"	27.08	± 4.78	13	25	25	24-42
a	"	25.83	± 2.15	12	25	25	-32
-18	"	24.81	± 1.24	26	25	25	23-28
Total	"	25.52	± 3.17	86/400	25	25	23-45
75-19	240	27.36	± 3.08	39	27	26	23-38
-20	"	27.31	± 2.78	42	27	26	23-36
-21	"	27.55	± 2.73	20	27	26,27	24-34
-22	"	27.46	± 2.75	28	27	25	24-37
Total	"	27.40	± 2.86	129/400	27	26	23-38

(Appendix G, continued)

Dish No.	Days in +3°C	Ave. No. days until emergence	S.D.	No. of flies that emerged	Median	Mode	Range
75-23	263	25.56 ± 1.56		34	26	26	23-30
-24	"	26.09 ± 1.35		44	26	25	24-30
-25	"	26.00 ± 1.06		32	26	26	24-28
-26	"	25.56 ± 1.38		45	25	25	24-29
Total	"	25.80 ± 1.37		155/400	26	26	23-30
75-27[b]	288	27.45 ± 3.34		20/200	26	24,29	24-36
75-28	295	25.96 ± 2.16		26/148	25	24,25	24-33
-29	"	26.25 ± 1.64		4/130	25.5	25	25-29
Total	"	26.00 ± 2.10		30/278	25	25	24-33
75-30	305	27.33 ± 2.05		12	27	26,27	25-33
-31	308	25.62 ± 2.20		13/169	25	24	23-30
-32	312	25.86 ± 2.75		7/48	24	29	23-29
-33	316	26.18 ± 2.73		17/165	25	25	23-33
Total		26.27 ± 2.53		49/482	26	24	23-33
75-34	343	27.63 ± 3.60		8/152	27.5	--	23-35
76- 1	50[c]	51.50 ± 6.50		34	51	54	40-74
76- 2	75[d]	45.80 ± 2.95		2	45	45	42-45
- 3	"			3			45-50
76- 4	90	44.20 ± 6.06		5	44	--	36-51
- 5	"	41.14 ± 5.01		7	40	--	35-48
- 6	"	39.80 ± 4.57		10	38.5	38	33-47
- 7	"	42.08 ± 5.98		12	39.5	39	33-52
Total	"	41.53 ± 5.36		34/100	40	38	33-52
76- 8	110	37.42 ± 4.73		24	38.5	39	27-47
76- 9	125	33.81 ± 4.53		16	33	--	27-44
-10	"	34.27 ± 3.44		11	35	--	27-50
-11	"	35.29 ± 3.02		17	34	34	32-44
-12	"	35.69 ± 4.44		16	35	34,35	25-43
-13	"	35.89 ± 4.31		9	35	35	30-44
-14	"	36.27 ± 3.72		11	36	34	30-43
-15	"	36.50 ± 4.43		4	35	35	33-43
-16	"	36.80 ± 3.42		5	38	38	31-40
Total	"	35.46 ± 3.42		90/800	35	34	25-50

(Appendix G, continued)

Dish No.	Days in +3°C	Ave. No. days until emergence	S.D.	No. of flies that emerged	Median	Mode	Range
76-17	137	33.17 ± 4.03		18	33	30,34,35	28-46
a	"	32.41 ± 2.53		17	33	30,34,35	-37
-18	"	34.45 ± 5.54		24	34	34	24-51
a	"	33.74 ± 4.37		23	34	34	-41
Total	"	33.90 ± 4.94		42/200	34	34	24-51
76-19	140	33.87 ±	12.02	8	29.5	--	25-62
a	"	29.86 ± 4.22		7	29	--	25-38
-20	"	33.58 ± 5.09		12	33.5	33	25-42
Total	"	33.70 ± 8.26		20/200	32.5	--	25-62
Total	137-140	33.84 ± 6.14		62/400	34	34	24-62
76-21	150	28.88 ± 4.18		17	28	24,25	24-35
-22	"	30.65 ± 2.98		17	32	32	25-35
-23	"	32.17 ± 3.19		12	31.5	31	27-39
Total	"	30.39 ± 3.68		46/300	31	32	24-39
76-24	165	28.58 ± 4.17		12	29.5	31	22-35
-25	"	29.60 ± 2.95		10	29.5	27,29	25-35
-26	"	30.55 ± 5.07		31	30	25	23-40
-27	"	30.69 ± 5.25		16	31	33	23-43
a	"	29.87 ± 4.24		15	30	33	-36
-28	"	30.86 ± 4.90		14	30.5	30,31	23-39
Total	"	30.23 ± 4.70		83/500	30	30	22-43
76-29	170	27.15 ± 3.26		13	26	30	23-32
76-30	190	25.14 ± 2.14		44	24.5	24	23-32
-31	"	25.12 ± 2.26		77/200	24	23	22-38
Total	"	25.23 ± 2.49		121/300	24	23	22-38
76-32	192	27.84 ± 3.12		88/200	27	25	24-34
-33	"	28.37 ± 3.52		63/200	27	26	24-36
Total	"	28.06 ± 3.29		151/400	27	25	24-36
76-34	201	25.71 ± 1.94		89/200	25	25	23-33
-35	"	25.68 ± 1.88		117/200	25	25	23-32
Total	"	25.69 ± 1.90		206/400	25	25	23-33
76-36	210	25.60 ± 1.65		99/200	25	25	23-34

(Appendix G, continued)

Dish No.	Days in +3°C	Ave. No. days until emergence	S.D.	No. of flies that emerged	Median	Mode	Range
76-37	220	23.80	± 0.80	35	24	24	22-26
-38	"	24.88	± 2.18	42	24	24	23-31
-39	"	25.02	± 3.44	50	24	24	22-42
a	"	24.67	± 2.44	49	24	24	-35
Total[e]	"	24.64	± 2.57	127/300	24	24	22-42
76-40	220	25.51	± 1.67	93/200	25	25	23-33
-41	"	25.25	± 1.63	102/200	25	25	23-30
Total[f]	"	25.37	± 1.65	195/400	25	25	23-33
Total	220	25.08	± 2.09	322/700	25	24	22-42
76-42	260	25.62	± 1.93	50	25	25	23-32
76-43	290	27.31	± 2.26	65	27	27	25-33
-44	"	26.86	± 1.72	56	26	26	24-33
Total	"	27.10	± 2.03	121/200	27	26	24-33

[a]The dish immediately preceding was recalculated without the last-emerging fly (always six or more days after the penultimate fly).

[b]Dishes 75-27 to 75-33 were kept in (dry) dirt.

[c]50 days at 3° C after 60 days at 10-12° C.

[d]No flies emerged from 200 pupae at 15, 30, 45, and 60 days chilling at 3° C.

[e]1976

[f]1977