

Reproductive Maturity of Cherry Fruit Fly (Diptera: Tephritidae) in Managed and Natural Habitats

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ABSTRACT We studied the timing of reproductive maturity of cherry fruit fly, *Rhagoletis cingulata* (Loew), a key pest of sweet and tart cherries in the eastern United States. To determine when cherry fruit fly females become reproductively mature in managed and natural habitats, we deployed traps in sweet and tart cherry orchards and nearby stands of the ancestral host tree, black cherry. Flies were removed from the traps and females were dissected to determine the presence of fully developed eggs. We found that capture of reproductively mature female flies occurred earlier in orchards that are not sprayed with insecticides than in sprayed orchards or in black cherry tree sites. In addition, the gap between the flights of immature and mature females in unmanaged sweet or tart cherry orchards was shorter than in managed orchards or black cherry tree sites. We also determined fruit color, size, and skin hardness to characterize the progression of fruit maturity. We found that fruit became mature earlier in sweet and tart cherry orchards than in black cherry tree sites. This study indicates that the timing of female reproductive maturity is plastic and varies among cherry fruit fly populations present in distinct habitats. Variation in the timing of reproductive maturity is related to the fruit maturity period of distinct host plant species and to orchard management.

KEY WORDS ovary, egg, tart cherry, sweet cherry

Cherry fruit fly, *Rhagoletis cingulata* (Loew), is part of the *cingulata* sibling species group of Tephritid fruit flies, together with the western cherry fruit fly *R. indifferens* Curran, *R. osmanthi* Bush, *R. chionanthi* Bush, and *R. turpiniae* Hernández-Ortiz (Bush 1966, Hernández-Ortiz 1993, McPheron and Han 1997, Smith and Bush 1997). Cherry fruit fly primarily infests the fruit of black cherry, *Prunus serotina* Ehrh., and rarely fire cherry, *P. pennsylvanica* L., and chokecherry, *P. virginiana* L. (Family Rosaceae) (Glasgow 1933). The geographic range of cherry fruit fly includes eastern North America, from southern Ontario to northern Florida, and west to Iowa. The distribution of cherry fruit fly is assumed to closely follow that of its most important native host (Bush 1966). Black cherry is commonly found in eastern American temperate forests and at the edges of cultivated fields (Eyre 1980). Cherry fruit fly also infests the fruit of non-native *Prunus* trees introduced to its range, such as sweet cherry, *P. avium* L., and tart cherry, *P. cerasus* L. Similar to most other flies in the genus *Rhagoletis*, cherry fruit fly is univoltine throughout its range. Females lay eggs singly in the fruit of host plants. Eggs hatch and larvae develop within the pulp. When larvae reach the end of the third instar, they exit the fruit and burrow into the soil. There, larvae form

puparia and pupae enter diapause. Finally, morphological development resumes in the spring of the following year, and flies emerge coinciding with the fruiting period of host plants (Boller and Prokopy 1976). Populations of cherry fruit fly with distinct flight periods occur in managed and neglected cherry orchards and in stands of black cherry trees (Teixeira et al. 2007). Variation in the duration of diapause underlies this phenological plasticity in *Rhagoletis* (Teixeira and Polavarapu 2005).

Rhagoletis fruit flies are anautogenous, and females need a continuous intake of protein to maintain egg production throughout their adult stage (Webster and Stoffolano 1978, Webster et al. 1979). Food resources used by *Rhagoletis* flies include aphid honeydew, nectar from floral and extrafloral nectaries, fruit juices from wounds and oviposition sites, and insect frass and bird droppings (Hendrichs and Prokopy 1990, 1994; Yee 2002). Flies also spend a large portion of their active time feeding on substances diffused on the leaf surface, such as microorganisms, pollen, and plant exudates (Hendrichs et al. 1993). *Rhagoletis* flies are strongly attracted to ammonia (Hodson 1943), presumably because it signals the presence of protein. Studies with the walnut fly, *R. juglandis* Cresson, have shown that the preoviposition period is variable and that ovarian development is dependent not just on nutrition but also on host fruit cues such as color, shape, and size and presence of conspecific larvae in the fruit (Alonso-Pimentel et al. 1998, Papaj 2005). Other studies with the walnut husk fly, *R. completa*

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Cresson, have shown that the duration of the preoviposition period is temperature dependent (Kasana and AliNiazee 1994). With the western cherry fruit fly, *R. indifferens* Curran, Senger et al. (2008) showed that the presence of conspecific flies and access to fruit resources significantly increased mature egg counts in caged flies.

In the eastern United States, cherry fruit fly is a major pest of economically important fruit crops such as sweet cherry and tart cherry (Liburd et al. 2001, Pelz-Stelinski et al. 2005, Teixeira et al. 2007). In Michigan, infestations of cultivated cherries have been reported since the early 1900s (Farleman 1933, Bush 1966). In addition to flies dispersing yearly from black cherry into commercial cherry orchards, some orchards harbor resident populations that exploit fruit left after mechanical harvesting (Teixeira et al. 2007). Growers rely almost exclusively on insecticide coverage of the fruit in the period before harvest to meet the zero tolerance quality standards for fruit infestation (USDA-AMS 1976). Because larvae are difficult to control once in the fruit pulp, growers spray insecticides targeting mature flies before they lay eggs in the fruit (Wise et al. 2003). Current management guidelines advise the application of an insecticide spray within 10 d of the capture of the first cherry fruit fly in the area of the orchard. This recommendation assumes that the first fly captured is not yet reproductively mature and that the duration of the preoviposition period is ≈ 10 d. We hypothesize that the later fruiting phenology of black cherry compared with that of sweet and tart cherry (Teixeira et al. 2007) will lead to distinct timings of female maturity in different habitats. Information on habitat-specific ovarian maturation periods in cherry fruit fly will help to better estimate the risk of infestation.

The objective of this study was to determine when female cherry fruit flies become reproductively mature in managed and natural habitats. For this purpose, we deployed traps for collecting cherry fruit fly and dissected female flies to determine their reproductive maturity status. In addition, we measured fruit maturity characteristics such as color, diameter, and skin hardness in different host plants.

Materials and Methods

Reproductive Maturity of Flies Captured on Traps.

We followed female ovarian maturity status by collecting cherry fruit flies from mid-June to late August using yellow sticky traps baited with ammonium carbonate dispensers. In 2007, three yellow cardboard Pherocon AM traps (Trece, Adair, OK) were deployed in five tart cherry orchards, and three yellow plastic Rebell traps (Great Lakes Integrated Pest Management, Vestaburg, MI) were deployed on two black cherry tree stands. In tart cherry orchards, traps were hung from 3-m PVC poles and placed at the upper height of tree canopies. In black cherry, traps were hung from 6 m metal or bamboo poles leaning to the side of large black cherry trees. Rebell traps are made of plastic and can better withstand wind damage when

placed high in the tree canopy than Pherocon AM traps. Every 3 wk, Pherocon AM traps were replaced, and the ammonium carbonate dispensers placed near both Pherocon AM and Rebell traps were refilled. All captured flies were collected from the traps twice-weekly, brought to the laboratory, sexed, and counted, and females were dissected to evaluate reproductive maturity. We categorized females as mature when there was at least one fully developed egg in the ovaries (Neilson et al. 1984, Reynolds and Prokopy 1997).

Tart cherry 1 site was located on the grounds of the Trevor Nichols Research Center (TNRC) in Fennville, MI. This orchard is only managed against fungal diseases and was classified as neglected according to the terminology of Teixeira et al. (2007). In addition, we monitored four commercial tart cherry orchards in Bainbridge (sites tart cherry 2 and 3) and Hartford, MI (sites tart cherry 4 and 5). The Bainbridge sites were located 55 km south of Fennville, and the Hartford sites were 16 km northeast of Bainbridge. The orchards in Bainbridge and Hartford were sprayed with insecticides for cherry fruit fly on 27 June, 6 July, and 11 July (tart cherry 2), 18 June and 12 July (tart cherry 3), 20 June (tart cherry 4), and 20 June and 11 July (tart cherry 5). Harvest at these sites took place between 25 June and 11 July. The black cherry 1 site consisted of a black cherry tree stand located ≈ 300 m from the tart cherry 1 site, also on the grounds of TNRC in Fennville. The black cherry 2 site consisted of black cherry trees at the edge of the tart cherry 3 orchard, in Bainbridge. Air temperature measurements were taken hourly at each site using a HOBO UA-002-64 temperature data logger (Onset, Pocasset, MA) deployed on a tree.

In 2008, cherry fruit fly reproductive maturity was determined in two each of sweet (sweet cherry 1 and 2 sites) and tart cherry orchards (tart cherry 1 and 2 sites) on the grounds of the Northwest Michigan Horticultural Research Station (NWMHRS) near Traverse City, MI, ≈ 200 km North of Fennville, and in two black cherry stands near Honor (black cherry 1) and Maple City (black cherry 2), 33 and 9 km southwest of NWMHRS, respectively. Methods were as described for 2007, except that three Pherocon AM traps were deployed at each site and that six traps were placed at tart cherry 1 and black cherry 1 sites. Traps were deployed on 12 June and removed during the second week of September. Flies were collected twice per week in sweet and tart cherry orchard sites and weekly in black cherry sites. Cherry orchards at NWMHRS were only treated for fungal diseases and were classified as neglected according to the terminology of Teixeira et al. (2007). Black cherry trees were completely unmanaged, and trees were ≈ 75 and 3 m from the edge of managed tart and sweet cherry orchards in black cherry 1 and 2 sites, respectively.

Fruit Phenology. In 2008, 10 fruits were collected on each sampling date from each tree with a trap, with three or six replicate trees per site. Fruit was classified for color on a 1–4 scale ranging from predominantly green, yellow, rose, or red for sweet and tart cherry

Table 1. Median date of capture, difference between the median capture date of immature and mature flies, date of capture of the first female fly, estimated 1 and 99% female fly capture date, duration of the flight period, and total no. of immature and mature female cherry fruit flies captured at tart cherry orchards and stands of black cherry trees in southwest Michigan, 2007

Site	Capture of immature and mature female cherry fruit fly						Flies ^b (n)
	Median ^a (date)	Diff. (d)	First fly (date)	1% (date)	99% (date)	Duration (d)	
Tart cherry 1							
Immature	21 Jun. a	0	14 Jun.	14 Jun.	19 Jul.	35	167a
Mature	21 Jun. A		18 Jun.	18 Jun.	6 Aug.	49	21
Tart cherry 2							
Immature	9 Jul. bc	28 ^c	29 Jun.	29 Jun.	6 Aug.	38	126d
Mature	6 Aug. CD		5 Jul.	9 Jul.	16 Aug.	38	214
Tart cherry 3							
Immature	16 Jul. d	21 ^c	29 Jun.	29 Jun.	2 Aug.	34	157c
Mature	6 Aug. C		18 Jun.	9 Jul.	13 Aug.	35	143
Tart cherry 4							
Immature	5 Jul. b	28 ^c	25 Jun.	25 Jun.	6 Aug.	42	214c
Mature	2 Aug. B		29 Jun.	9 Jul.	13 Aug.	35	237
Tart cherry 5							
Immature	16 Jul. cd	17 ^c	21 Jun.	21 Jun.	6 Aug.	46	23e
Mature	2 Aug. BC		9 Jul.	12 Jul.	16 Aug.	35	130
Black cherry 1							
Immature	5 Jul. b	32 ^c	14 Jun.	18 Jun.	9 Aug.	52	668b
Mature	6 Aug. D		21 Jun.	25 Jun.	16 Aug.	52	235
Black cherry 2							
Immature	5 Jul. b	28 ^c	14 Jun.	21 Jun.	6 Aug.	46	403d
Mature	2 Aug. BC		2 Jul.	9 Jul.	16 Aug.	38	625

^a Capture dates of immature and mature female flies followed by the same lowercase or uppercase letter, respectively, are not significantly different (Wilcoxon, Bonferroni $\alpha = 0.05/21$).

^b The proportions of immature and mature female flies followed by the same letter are not significantly different (Pearson χ^2 , experimentwise $\alpha = 0.05$).

^c Differences between the capture dates of immature and mature female flies are significant (Wilcoxon, Bonferroni $\alpha = 0.05/7$).

fruits, and green, red, purple, or black for black cherry fruits. Fruit diameter was measured using Vernier calipers, and fruit skin firmness was determined using a FT 01 standard fruit penetrometer with a 1-mm-diameter tip (QA Supplies, Norfolk, VA).

Data Analyses. The median and 1 and 99% capture dates of immature and mature female cherry fruit flies were estimated using PROC UNIVARIATE of SAS (SAS Institute 2001). Differences among sites in the distribution of captures of immature and mature flies were analyzed using the Kruskal-Wallis nonparametric test as implemented in PROC NPARIWAY. Multiple comparisons among distributions were conducted using Wilcoxon tests followed by the Bonferroni correction. Within a site, the difference in the distribution of captures of immature and mature flies was analyzed using Wilcoxon tests followed by Bonferroni correction. Differences in the proportions of reproductively immature and mature flies were analyzed using contingency tables and Pearson χ^2 tests performed with PROC FREQ. Multiple comparisons for proportions among sites were conducted using the macro %COMPPROP of SAS using a Tukey-type multiple comparison test (Zar 1999).

Results

Reproductive Maturity of Flies Captured on Traps.

In southwest Michigan, the median date of capture of reproductively immature female flies in the unmanaged tart cherry 1 site in Fennville was 21 June (Table 1), earlier than the median capture date of reproductively immature flies in the managed tart cherry 2–5

sites in Bainbridge and Hartford or the black cherry 1–2 sites in Fennville and Bainbridge (Kruskal-Wallis $\chi^2 = 331.5$; $df = 6$; $P < 0.001$). The median date of capture of reproductively immature flies at the managed tart cherry 2–5 sites was the same or later than at the black cherry sites. With reproductively mature females, the median date of capture at the tart cherry 1 site was 21 June, much earlier than the median date of capture of mature females at all other sites (Kruskal-Wallis $\chi^2 = 188.2$; $df = 6$; $P < 0.001$). There was no difference between the median date of capture of reproductively immature and mature female flies at the unmanaged tart cherry 1 site. The difference between the median date of capture of reproductively immature and mature female flies at the tart cherry 2–5 sites varied from 17 to 28 d. At the black cherry sites 1 and 2, the difference between the median date of capture of reproductively immature and mature females was 32 and 28 d, respectively.

In southwest Michigan, the first female fly was captured immediately at the beginning of the monitoring period on 14 June at the tart cherry 1 and black cherry 1 and 2 sites or up to 2 wk later at the other sites. At the tart cherry 3 site, the first female fly was captured on 18 June and was already reproductively mature. At this site, the first reproductively immature fly was captured 11 d later, on 29 June. The duration of the flight period of reproductively immature females, determined from the estimated date of capture of 1 and 99% of flies, ranged from 34 d at tart cherry 3 site to 52 d at black cherry 1 site. With reproductively mature flies, the flight period lasted from 35 d at the tart cherry 3–5 sites to 52 d at the black cherry 1 site. The pro-

Table 2. Median date of capture, difference between the median capture date of immature and mature flies, date of capture of the first female fly, estimated 1 and 99% female fly capture date, duration of the flight period, of immature and mature female cherry fruit flies captured at sweet cherry orchards, tart cherry orchards, and stands of black cherry trees in northwest Michigan, 2008

Site	Capture of immature and mature female cherry fruit fly						Flies ^b (n)
	Median ^a (date)	Diff. (d)	First fly (date)	1% (date)	99% (date)	Duration (d)	
Sweet cherry 1							
Immature	21 Jul. ab	0	19 Jun.	24 Jun.	8 Aug.	45	209bc
Mature	21 Jul. A		7 Jul.	7 Jul.	2 Sep.	57	68
Sweet cherry 2							
Immature	25 Jul. c	0	1 Jul.	1 Jul.	19 Aug.	49	206ab
Mature	25 Jul. A		7 Jul.	7 Jul.	26 Aug.	50	56
Tart cherry 1							
Immature	21 Jul. a	7 ^c	24 Jun.	1 Jul.	26 Aug.	56	507a
Mature	28 Jul. A		1 Jul.	1 Jul.	2 Sep.	63	98
Tart cherry 2							
Immature	25 Jul. c	11 ^c	7 Jul.	7 Jul.	26 Aug.	50	175d
Mature	5 Aug. B		7 Jul.	11 Jul.	8 Sep.	59	123
Black cherry 1							
Immature	24 Jul. bc	42 ^c	9 Jul.	9 Jul.	28 Aug.	50	149e
Mature	4 Sep. D		31 Jul.	7 Aug.	11 Sep.	35	230
Black cherry 2							
Immature	4 Aug. d	24 ^c	16 Jul.	16 Jul.	28 Aug.	43	68cd
Mature	28 Aug. C		31 Jul.	31 Jul.	11 Sep.	42	42

^a Capture dates of immature and mature female flies followed by the same lowercase or uppercase letter, respectively, are not significantly different (Wilcoxon, Bonferroni $\alpha = 0.05/15$).

^b The proportions of immature and mature female flies followed by the same letter are not significantly different (Pearson χ^2 , experimentwise $\alpha = 0.05$).

^c Differences between the capture dates of immature and mature female flies are significant (Wilcoxon, Bonferroni $\alpha = 0.05/6$).

portion of reproductively immature flies in relation to mature flies captured at tart cherry 1 was much larger than in any of the other sites ($\chi^2 = 477.6$; $df = 6$; $P < 0.001$). The proportion of reproductively immature flies in relation to mature flies captured at the other sites did not show distinct trends between tart cherry and black cherry sites.

In northwest Michigan, the earliest median date of capture of reproductively immature flies was 21 July at sweet cherry 1 and tart cherry 1 sites (Table 2), 14 d earlier than 4 August, the latest median immature fly capture date at the black cherry 2 site (Kruskal-Wallis $\chi^2 = 132.1$; $df = 5$; $P < 0.001$). With reproductively mature female flies, the median date of capture in sweet cherry and tart cherry sites occurred from 21 July to 5 August, whereas the median capture date of mature flies in black cherry sites was 28 August and 4 September (Kruskal-Wallis $\chi^2 = 217.9$; $df = 5$; $P < 0.001$). The median capture date of both reproductively immature and mature flies at sweet cherry 1 and 2 sites occurred on 21 and 25 July, respectively. At tart cherry 1 and 2 sites, the difference between the median capture date of reproductively immature and mature flies was 7 and 11 d, respectively, and at black cherry 1 and 2 sites, this difference was 42 and 24 d, respectively.

In northwest Michigan, the first fly was captured in mid-late June at sweet cherry 1 and tart cherry 1 sites, in early July at sweet cherry 2 and tart cherry 2 sites, and in early to mid-July at the black cherry sites. The duration of the flight period of reproductively immature females, determined from the estimated date of capture of 1 and 99% of flies, ranged from 43 d at black cherry 2 to 56 d at tart cherry 1. The duration of the flight period of reproductively mature females ranged

from 35 d at black cherry 1 to 63 d at tart cherry 1. The proportion of reproductively mature flies in relation to immature flies tended to be greater in sites with later date of median capture of mature females ($\chi^2 = 247.3$; $df = 5$; $P < 0.001$).

Fruit Phenology. The progression of fruit maturity was marked by an increase in color rating and diameter and a decrease in skin firmness (Fig. 1). Fruit maturity in sweet and tart cherry was reached throughout July, when the color rating increased from 1 to 2 (green-yellow) to 4 (red), the diameter increased from ≈ 1.5 to >2 cm, and the skin firmness decreased from ≈ 400 to 100 g/cm². In black cherry, fruit only started to ripen in late August to early September. The color rating was ≈ 2 (green-red) and became ≈ 3 (purple), fruit diameter increased from 0.7 to 1.0 cm, and skin firmness decreased from ≈ 500 to 250 g/cm².

Discussion

This study showed that the timing of reproductive maturity in populations of cherry fruit fly depends on host plant species and orchard pest management intensity. Teixeira et al. (2007) have previously shown that the flight period of cherry fruit fly populations is habitat dependent. Here, we show that the timing of female reproductive maturity also varies according to the biotic and abiotic environment. We found in southwest Michigan that median fly reproductive maturity was reached much earlier in a tart cherry orchard that is not sprayed with insecticides than in tart cherry orchards that are sprayed with insecticides or in black cherry tree stands. In northwest Michigan, fly reproductive maturity occurred earlier in sweet and

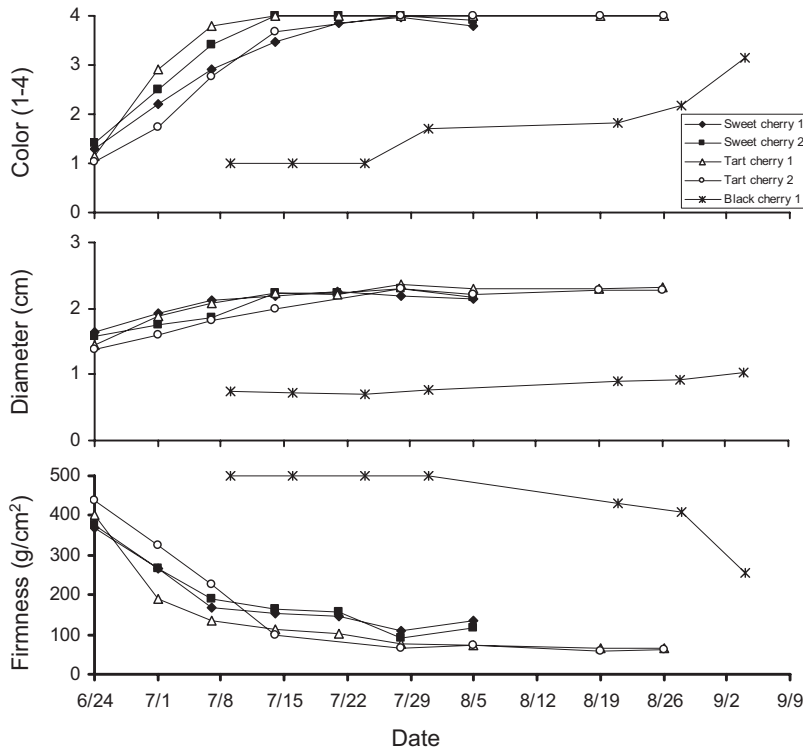


Fig. 1. Average color, diameter, and skin firmness of sweet, tart, and black cherry fruit at sites sweet cherry 1 and 2, tart cherry 1 and 2, and black cherry 1 in northwest Michigan in 2008.

tart cherry orchards that are not sprayed with insecticides than in black cherry tree sites. In addition to varying timing of reproductive maturity, the relationship between reproductively immature and mature female flight is distinct in different habitats. In orchards that are not sprayed with insecticides, we found that an early reproductively immature female flight period was immediately followed by an early flight of reproductively mature flies. In sprayed orchards and black cherry, the gap between the flights of reproductively immature and mature females was wider. These results, together with our measurements of fruit maturity, indicate that the flight of reproductively mature females coincides with the maturity period of host fruit, in the absence of insecticide sprays (see below).

Host fruit reach maturity much earlier in sweet and tart cherry orchards than in black cherry stands. In cherry orchards that are not sprayed with insecticides, flies seem to take advantage of this early onset of the period when fruit is suitable for oviposition by reaching reproductive maturity earlier than in black cherry. In orchards that are sprayed with insecticides before harvest, a large proportion flies is killed before reaching reproductive maturity. However, as we found in some sprayed orchards in southwest Michigan, flies that are not killed also have the ability for early reproductive maturity. In black cherry, there is less pressure for flies to become reproductively mature early because of late fruit maturation. At this time, the

mechanism of the variation in the timing of reproductive maturity is not known, but we exclude temperature differences because tart cherry orchards and black cherry trees in Fennville were located in close proximity, and we recorded differences of <math><1^{\circ}\text{C}</math> in average air temperature between sites. With the western cherry fruit fly, Senger et al. (2008) showed that access to ripe fruit significantly increased mature egg counts, suggesting an effect of ripe fruit on reproductive maturity that may extend to the timing of egg maturation. With several other insects, the timing of reproductive maturity is determined by host availability and quality (Papaj 2000). It is possible that cherry fruit fly time reproductive development using fruit cues such as color and skin hardness, because these cues change markedly throughout the season (Smith 1984, Teixeira et al. 2007). Another possibility is that the maturity period is affected by the different nutritional environment in cherry orchards and black cherry trees, because feeding on nutrient-rich cherry juice can sustain egg-laying (Yee 2003). It is also possible that variation in the timing of ovarian maturation among populations living in different habitats, such as variation in the duration of diapause in other *Rhagoletis*, reflects adaptation to the phenology of different host plants (Smith 1988). With Hawaiian *Drosophilidae*, for example, variation in ovarian development underlies adaptation to different environmental conditions (Kambyzellis and Heed 1971).

The current management practice of applying an insecticide spray within 10 d of the capture of the first cherry fruit fly in the area of the orchard is based on the estimated average duration of the female preoviposition period (Wise et al. 2003). The weakness of this approach was evident at tart cherry site 3, where dissection showed that the first female fly captured was already reproductively mature. Tart cherry site 3 and the other managed tart cherry orchards in Hartford and Bainbridge harbor resident populations of cherry fruit fly (Teixeira et al. 2007). In all these managed sites, we captured reproductively mature flies before and during the harvest period, in early July, even though these orchards were sprayed with insecticides. From a pest management perspective, the capture of reproductively mature flies before harvest is of great concern for growers, because of increased risk of fruit contamination and costly rejection by fruit processors, and is another risk factor associated with having resident populations of cherry fruit fly in managed orchards. This study also suggests that the habitat of origin of the flies, either cherry orchard or black cherry, may be important in determining the timing of female reproductive maturity, because of environmental and/or genetic factors. Phenological models constructed based on capture of flies from resident populations risk overestimating the risk in orchards that do not contain such populations, and where fruit infestation is caused by flies that disperse from black cherry. Study of the factors that influence the timing of reproductive maturity will help to estimate the duration of the preoviposition period of flies dispersing between different habitats, and improve phenological model predictions.

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