Seasonal Distributions of the Western Cherry Fruit Fly (Diptera: Tephritidae) Among Host and Nonhost Fruit Trees

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ABSTRACT. Seasonal distributions of the western cherry fruit fly, Rhagoletis indifferens Curran (Diptera: Tephritidae), in sweet cherry (Prunus avium (L.) L.) (major host), black hawthorn (occasional developmental host) (Crataegus douglasii Lindley), and other trees were determined in a ponderosa pine ecosystem in Washington state, USA. The hypothesis that most fly dispersal from cherry trees occurs after fruit senescence or drop was tested, with emphasis on movement to black hawthorn trees. Sweet cherry fruit developed earlier than black hawthorn, bitter cherry (common host), choke cherry, and apple fruit. Flies were usually captured first in sweet cherry trees but were caught in bitter cherry and other trees throughout the season. Peak fly capture periods in sweet cherry began around the same time or slightly earlier than in other trees. However, peak fly capture periods in black hawthorn and other nonsweet cherry trees continued after peak periods in sweet cherry ended, or relative fly numbers within sweet cherry declined more quickly than those within other trees. Larvae were reared from sweet and bitter cherry but not black hawthorn fruit. Results provide partial support for the hypothesis in that although R. indifferens commonly disperses from sweet cherry trees with fruit, it could disperse more, or more flies are retained in nonsweet cherry trees after than before sweet cherries drop. This could allow opportunities for the flies to use other fruit for larval development. Although R. indifferens infestation in black hawthorn was not detected, early season fly dispersal to this and other trees and fly presence in bitter cherry could make fly management in sweet cherry difficult.

Key Words: Rhagoletis indifferens, dispersal, Prunus avium, Crataegus douglasii, ponderosa pine ecosystem

Data on the seasonal distributions of tephritid fruit flies on host and nonhost trees could contribute to understanding fly dispersal, which affects plant use and fly management. Within the temperate fruit fly genus Rhagoletis (Diptera: Tephritidae), dispersal from host to nonhost trees appears to be common. Captures of five Rhagoletis species in cherry orchards (Madsen 1970), of Rhagoletis pomonella (Walsh) in nonapple or nonhawthorn trees (Alfred and Jorgensen 1993), and development of R. pomonella, Rhagoletis tabellaria (Fitch), Rhagoletis zephyria Snow, and Rhagoletis completa Cresson in a variety of nonnormal host fruit in Washington state (Yee and Goughnour 2008) show that movement off major breeding hosts occurs in a wide range of species. Fruit senescence and loss in major hosts are likely factors for fly dispersal. This hypothesis could be supported by seasonal captures of flies on nonhost trees; these data could also identify periods of fruit availability, important in that differences in fruiting phenology could help explain fly host race formation (Bush 1966, Feder et al. 2003). Such data could also have implications for fly management in that flies in nonhost trees could provide refugia from pesticides applied to host trees.

In the Pacific Northwest of United States, western cherry fruit fly, Rhagoletis indifferens Curran, is a pest of sweet cherry (Prunus avium (L.) L.), an introduced tree that along with introduced sour cherry and Prunus emarginata (Douglas ex Hooker) David Dietrich, the fly’s common native host. Despite the fly’s use of cherries, trap captures and observations of R. indifferens in various noncherry trees near cherry orchards (Frick et al. 1954, Yee 2008b) suggest that the fly frequently disperses from cherry to noncherry trees. Also, flies are not only found in noncherry trees but also occasionally infest their fruit (Yee et al. 2010, Yee and Klaus 2013). Black hawthorn (Crataegus douglasii Lindley) is of special interest because its fruit are occasionally infested by R. indifferens (Yee and Goughnour 2005), and high fly numbers are observed on it (W.L.Y., personal observations). This suggests that increased use of black hawthorn fruit for larval development could occur in the future.

R. indifferens may disperse to black hawthorn and other nonsweet cherry trees after sweet cherries senesce and become unsuitable for oviposition or drop. Most cherries develop before other fruit species. One prediction is that after cherries senesce or drop, fly numbers in nonsweet cherry trees with fruit increase, regardless of whether flies presently use their fruit for larval development or not, or how often they are used. Chances of noncherry fruit being attacked may increase if dispersers are abundant and mostly female, especially females with high egg loads.

Here, seasonal trap captures of R. indifferens in sweet cherry, black hawthorn, and other trees were compared in Washington state, USA. To support the hypothesis that most fly dispersal from cherry trees occurs after fruit senescence or drop, seasonal distributions of flies trapped in sweet cherry and nonsweet cherry trees were determined. Emphasis was placed on movement to black hawthorn trees. Fly abundance, sex ratios, and egg loads of flies captured on different trees were determined. Results are discussed with regard to why fly captures on nonhost trees represent dispersal and why dispersal could be important for fly fitness, plant use, and management.

Materials and Methods

Field Sites. Study sites were the towns of Cle Elum (47.1956° N, 120.9381° W), Roslyn (47.2236° N, 120.9919° W), and Ronald (47.2350° N, 121.0267° W). Roslyn and Ronald are combined and referred to as “Roslyn–Ronald” (except in 2010 collections, below). Sites were located in the foothills of the Cascade Mountain range in Kittitas County (Figs. 1 and 2) in the ponderosa pine ecosystem (Lyons and Merilees 1995). Although only ~5 km apart, elevations of Cle Elum and Roslyn–Ronald are ~550 m and ~762 m, respectively. Mean monthly temperature and annual rainfall in Cle Elum are 8.4°C and 565 mm, respectively; those of Roslyn–Ronald are 4.4°C and 565 mm, respectively; those of Roslyn–Ronald are 4.4°C and 565 mm, respectively.
Study trees within Cle Elum and within Roslyn–Ronald were ~1 and ~5 km of each other, respectively (Figs. 1 and 2). There was no commercial fruit-growing industry in the area, but there were many noncommercial fruit trees in backyards, roadsides, and in the wilderness.

**General Methods.** In 2010–2012, 8-cm diameter, sticky red sphere traps (Great Lakes IPM, Vestaburg, MI) baited with a vial containing 10 g of ammonium carbonate (Keystone Universal Corp., Melvindale, MI) were hung from trees, one trap per tree. Traps were covered with TangleTrap (The Tanglefoot Co., Grand Rapids, MI) and hung 1–2.5 m above ground and on the south side of 1) introduced sweet cherry (unidentified varieties), 2) native black hawthorn, 3) native bitter cherry, 4) native choke cherry (*Prunus virginiana* L.) (very rare larval host [Yee and Goughnour 2005, Yee 2008a]), 5) introduced ornamental hawthorn (*Crataegus monogyna* Jacquin), and 6) introduced apple (*Malus domestica* Borkhausen) (latter two: nonlarval hosts [Yee 2008a]). Traps were hung in 3–11 trees at each site (two choke cherry trees in Roslyn–Ronald, 2011). Traps were hung in ornamental

![Fig. 1. Cle Elum map showing trees used for trapping *R. indifferens* in (A) 2011 and (B) 2012. SC, sweet cherry; BH, black hawthorn; BC, bitter cherry; CC, choke cherry; OH, ornamental hawthorn; A, apple. Numbers in front of abbreviations are numbers of trees used (no number, one tree).](image-url)
hawthorn only in 2011. Trees were chosen based on their accessibility. All trees were 2–10 m tall and had fruit.

Traps were checked approximately weekly from late June or early July to October in 2011 and 2012. Ammonium carbonate was replenished when needed so that vials were at least one fourth full. Flies were removed from traps approximately weekly, preserved in 70% ethanol, and sexed, and the females were dissected to determine mature egg loads (Yee et al. 2011). Fruit maturity and condition were visually assessed approximately weekly: G, green; Y, yellow; O, orange; Br, brown; R, red; P, purple; Bl, black; *, fruit senescent; d, fruit dried; n, no fruit. While fruit loads could be classified as heavy or light, it was impossible, given the amounts, to accurately count fruit to include for statistical analyses.

Cle Elum. Cle Elum was used for trapping in 2011 and 2012. In total, ~23 sweet cherry, 31 bitter cherry, 17 black hawthorn, 17 choke cherry, 12 ornamental hawthorn, and 8 apple trees were recorded within trap areas in the 2 years. On 17 June 2011, traps were hung in six sweet cherry, six bitter cherry, three black hawthorn, three choke cherry, and six ornamental hawthorn trees (Fig. 1A) and checked approximately every 7 d on 17 dates up to 14 October. On 28 June 2012, traps were hung in 8 sweet cherry, 4 bitter cherry, 7 black hawthorn, and 5 choke cherry trees (Fig. 1B) and checked approximately every 7 d on 16 dates up to 18 October. Traps were hung in six apple trees on 19 July. Fourteen of the same trees (various species) were trapped in both years.

Roslyn–Ronald. Roslyn–Ronald was used for trapping in 2010 and 2011. At least 100 sweet cherry, 40 bitter cherry, 100 black hawthorn, and 30 choke cherry trees were present within combined trap areas in Ronald and Roslyn. Many trees were in thick brush, ravines, inside fenced yards, and were not easily accessible. On 10 August 2010, traps were hung in six black hawthorn trees and on 17 August in four sweet cherry and three bitter cherry trees in Ronald (outside of Fig. 2) and were checked weekly until 8 September. On 17 June 2011, traps were hung in 8 sweet cherry, 4 bitter cherry, 11 black hawthorn, 2 choke cherry, and 10 apple trees (Fig. 2) and checked approximately every 7 d on 17 dates up to 14 October.

Larval Infestation of Fruit. In 2010, sweet cherry and bitter cherry fruit in Cle Elum and Roslyn–Ronald and black hawthorn fruit in Roslyn–Ronald were collected to determine larval infestation rates. About 10% of trees sampled for fruit were used for trapping in 2011 and 2012. In Cle Elum, 9 sweet cherry and 13 bitter cherry trees were sampled on three dates from 26 July to 8 September; in Roslyn–Ronald, 13 sweet cherry, 17 bitter cherry, and 19 black hawthorn trees were sampled from 2 August to 15 September. Most bitter cherry from Roslyn–Ronald sampled northwest of the area were depicted in Figure 2. Numbers of fruit sampled per tree ranged from 5 to 1,193 depending on fruit loads. All fruit were counted and weighed. Larvae and adult flies were reared per standard protocol (Yee 2008a). Fruit were not collected in 2011 and 2012.

Statistics. Fly capture data were square-root transformed, but in almost all comparisons, transformation was insufficient to make data from one or more tree types normal, based on the Shapiro–Wilk test using the NORMAL command in SAS (SAS Institute 2010). In some cases, data among tree types did not have equal variances based on Brown and Forsythe’s test using the HOVTEST command in SAS. Analysis of variance (ANOVA) was used only when data passed the two tests. The Friedman test (nonparametric repeated-measures ANOVA [Anonymous 2013]) was used to determine weekly effects on fly captures within tree types, followed by the least significant difference (LSD) multiple comparisons procedure (Conover 1980). ANOVA or a Kruskal–Wallis test (T statistic [Conover 1980]; χ2 statistic [SAS Institute Inc. 2010]) was used to determine mean week of capture,
numbers of flies, and fly egg loads among tree types, followed by LSD tests (Conover 1980). Replicates were numbers of trees. Percentage of flies caught that were female was analyzed using a χ² test for more than two proportions followed by multiple comparisons for proportions (Zar 1999). Larval infestation data were analyzed using the Wilcoxon two-sample (Z statistic) or Kruskal–Wallis test.

Results
Timing of Peak Fly Captures. Sweet cherry fruit developed earlier than black hawthorn, bitter cherry, choke cherry, and apple fruit (e.g., sweet cherry fruit were green up to 1 July, whereas black hawthorn fruit were green up to 22 July) (Figs. 3–5). Flies were usually captured in sweet cherry trees first and approximately 1–4 wk earlier on average than in other trees (Table 1). However, flies were caught in nonsweet cherry trees throughout the season until September or October (Figs. 3–5). Flies were most abundant in sweet cherry (Table 2) but due mostly to early season captures (Figs. 3–5). In the following, “peak period” is defined as a time or stretch of time when fly captures did not differ statistically from the highest point in the seasonal capture curve. Peak fly captures in sweet cherry began around the same time or slightly earlier than in other trees (Figs. 3–5). In Cle

Fig. 3. Cle Elum, 2011: seasonal captures of *R. indifferens* in (A) sweet cherry, (B) black hawthorn, (C) bitter cherry, (D) choke cherry, and (E) ornamental hawthorn. Letters above symbols and error bars indicate the color of the majority of fruit. All traps were deployed on 17 June. G, green; Y, yellow; O, orange; Br, brown; R, red; P, purple; Bl, black; *, fruit senescent; d, fruit dried; n, no fruit.
Elum and Roslyn in 2011, peak fly capture periods in black hawthorn and other nonsweet cherry trees continued after peak periods in sweet cherry ended (Figs. 6 and 8). In Cle Elum in 2012, peak periods in black hawthorn and bitter cherry ended at the same time as in sweet cherry, but relative fly numbers within sweet cherry declined more quickly than those within other trees (Fig. 7). Numbers of flies captured in sweet cherry trees were greater than in other trees before sweet cherries senesced and began to dry \( (P < 0.05, \text{analyses not shown}) \), but numbers of flies on sweet cherry and other trees within weeks usually did not differ later in the season (Tables 3 and 4). Taken together, this suggests movement of flies to the other trees. Not all sweet cherry trees near hawthorns had traps, so it is unknown if all hawthorns closer to sweet cherry had high fly numbers. However, in 2011 the three black hawthorns with the most flies (40–306 flies per trap over the season) were only 20–50 m from the more heavily infested sweet cherry trees (103–3,067 flies).

**Sex Ratios.** Overall sex ratios of captured flies (2011 and 2012) in black hawthorn and apple trees were more female biased than in sweet and bitter cherry trees (Table 5). There was more female bias in black hawthorn trees than in sweet cherry or bitter cherry trees or both in three...
comparisons. There was also more female bias in apple than cherry trees in two comparisons.

**Egg Loads.** Within tree types, no seasonal differences in egg loads were detected ($P > 0.05$). Egg loads of flies in sweet cherry and other trees did not differ. In Cle Elum in 2011, flies had means of 16.95–20.33 mature eggs per fly (ranks analyzed; $T = 0.304; P > 0.05$); Cle Elum, 2012, 15.01–19.94 ($T = 3.539; P > 0.05$); Roslyn–Ronald, 2011, 13.67–21.20 ($T = 2.048; P > 0.05$).

**Larval Infestation of Fruit.** Numbers of *R. indifferens* pupae per sweet cherry were higher than per bitter cherry in both Cle Elum and Roslyn–Ronald, although pupae per gram of fruit did not differ (Table 6). No larvae were reared from black hawthorn fruit (Table 6).

**Discussion**

For the following reasons, most captures of *R. indifferens* in non-cherry trees indicated dispersal, which is “any movement of individuals or propagules with potential consequences for gene flow across space” (Ronce 2007). First, it is unlikely that many flies captured in black hawthorn and choke cherry developed in their fruit, and it is almost certain that none in ornamental hawthorn and apple did (Frick et al. 1954, Yee 2008a). Thus, flies had to have dispersed to them from elsewhere. Second, trees used for trapping were close together (Figs. 1 and 2). *R. indifferens* flew an average of 63.6 m and up to 287 m from release points in one study (Jones and Wallace 1955), so dispersal among these trees would not have been difficult. Finally, red spheres are not highly

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**Fig. 5.** Roslyn–Ronald 2011: seasonal captures of *R. indifferens* in (A) sweet cherry, (B) black hawthorn, (C) bitter cherry, (D) choke cherry, and (E) apple. Letters above symbols and error bars indicate the color of the majority of fruit. All traps were deployed on 17 June. G, green; Y, yellow; O, orange; Br, brown; R, red; P, purple; Bl, black; *, fruit senescent; d, fruit dried; n, no fruit.
Table 1 Mean week posttrap deployment of all *R. indifferens* captures per sphere ± SE or ranks (R) in sweet cherry and nonsweet cherry trees in Cle Elum (2011, 2012) and Roslyn–Ronald (2011), Washington state, USA

| Tree               | Cle Elum, 2011 | Cle Elum, 2012 | Roslyn–Ronald, 2011 |
|--------------------|---------------|---------------|---------------------|
|                    | N\(^a\) | Mean Week | N\(^a\) | Mean Week | N\(^a\) | Mean Week (R) |
| Sweet Cherry       | 6 | 6.56 ± 0.23C | 8 | 3.47 ± 0.25B | 8 | 8.88 (7.8B) |
| Black Hawthorn     | 3 | 8.45 ± 0.22B | 7 | 5.11 ± 0.27A | 11 | 10.53 (19.0A) |
| Bitter Cherry      | 6 | 10.59 ± 0.41A | 10 | 4.87 ± 0.15A | 4 | 10.97 (25.0A) |
| Choke Cherry       | 3 | 3.41 ± 0.96B | 5 | 8.01 ± 0.40A | 2 | 10.88 (24.5A) |
| Ornamental         | 6 | 6.63 ± 0.38C | — | — | — | — |
| Apple              | — | — | — | — | 10 | 10.04 (20.0A) |
| Test Statistic     | F = 18.12\(^c\) | F = 10.06\(^c\) | T = 11.49\(^c\) |
| \(P\)              | < 0.0001 | < 0.0001 | < 0.025 |

\(^a\)No. of trees.

\(^b\)Traps in apple trees were deployed 3 weeks after traps were deployed in other trees. —, no flies caught.

\(^c\)Kruskal–Wallis test (Conover 1980). Mean numbers or ranks within columns followed by same letter are not significantly different (Fisher’s LSD test, \(P > 0.05\)).

Table 2 Mean numbers of *R. indifferens* captured per sphere per day and ranks (R) over 91–119 d in sweet cherry and nonsweet cherry trees in Cle Elum (2011, 2012) and Roslyn–Ronald (2011), Washington state, USA

| Tree               | Cle Elum, 2011 | Cle Elum, 2012 | Roslyn–Ronald, 2011 |
|--------------------|---------------|---------------|---------------------|
|                    | N\(^a\) | Mean/tree | Mean/day (R) | N\(^a\) | Mean/tree | Mean/day (R) | N\(^a\) | Mean/tree | Mean/day (R) |
| Sweet Cherry       | 6 | 263.0 | 2.21 (19.2A) | 8 | 193.2 | 1.29 (31.4A) | 8 | 805.6 | 6.77 (30.1A) |
| Black Hawthorn     | 3 | 5.17 | 0.14 (10.7B) | 7 | 40.9 | 0.36 (16.4B) | 11 | 53.8 | 0.45 (13.6B) |
| Bitter Cherry      | 6 | 60.8 | 0.51 (13.4AB) | 10 | 43.5 | 0.39 (14.2B) | 4 | 73.5 | 0.62 (16.2B) |
| Choke Cherry       | 3 | 39.0 | 0.08 (9.8B) | 5 | 32.0 | 0.29 (13.9B) | 2 | 155.5 | 1.31 (21.5AB) |
| Ornamental Hawthorn| 6 | 4.2 | 0.05 (7.1B) | — | — | — | 11 | 10.53 (19.0A) |
| Apple              | — | — | — | 6 | 37.2 | 0.41 (14.8B) | 10 | 69.7 | 0.58 (13.2B) |
| Test Statistic     | F = 10.97\(^c\) | F = 10.59\(^c\) | T = 21.99\(^c\) |
| \(P\)              | 0.0005 | 0.0005 | 0.025 |

\(^a\)No. of trees. —, no flies caught. Cle Elum and Roslyn–Ronald, 2011: 119 d; Cle Elum, 2012, other than apple: 112 d, apple: 91 d.

\(^b\)Kruskal–Wallis test (Conover 1980). Mean numbers or ranks within columns followed by same letter are not significantly different (Fisher’s LSD test, \(P > 0.05\)).

Attractive to *R. indifferens* (Yee 2013), so flies captured on them were likely already in trees or had flown to trees irrespective of traps (Yee and Goughnour 2005, Yee 2008b). The hypothesis that most fly dispersal from cherry trees occurs after fruit senescence or drop was not completely supported, as peak periods of fly abundance in sweet cherry, black hawthorn, and other trees started around the same time, and fly numbers among tree types within weeks did not differ consistently. This indicates that flies dispersed from sweet cherry even when cherries were optimal for oviposition. Fruit loads in native bitter cherry trees are unreliable, so this could be a strategy that flies evolved to spread eggs among trees, one that has carried over into *R. indifferens* (Yee 2013), so flies captured on them were likely already in trees or had flown to trees irrespective of traps (Yee and Goughnour 2005, Yee 2008b).

Other factors in addition to high fly mortality could explain how greater dispersal to nonsweet cherry trees occurred after cherry drop without increases in fly captures. The different sweet cherry varieties had asynchronous fruit drop, so flies moved off trees at different times, not all at once. Flies could have flown to many trees not used in the study, so a small population was spread over a large area. Finally, many nonsweet cherry trees were too far from sweet cherry trees for flies to find quickly. *R. pomonella* leaves trees when model trees are closer.
than farther (Green et al. 1994) and apparently have difficulty locating trees > 1.6 m away (Roitberg and Prokopy 1982).

The ends of peak fly periods in sweet cherry and other trees in Cle Elum in 2012 were similar and may have been statistical artifacts because the capture trends were similar to those in 2011. The less sudden decline in fly numbers in black hawthorn (Fig. 7) still indicates that flies stayed in some hawthorn trees after cherries dropped. Tree shape and size variability may have caused slight differences between 2011 and 2012. In 2012, four of the seven black hawthorn trees with traps had low amounts of foliage and fruit loads. Flies may have bypassed these because of their silhouette (Moericke et al. 1975) and fruit loads, causing the overall peak period to end sooner.

More female than male *R. indifferens* appeared to disperse from sweet and bitter cherry trees. Red spheres attract more males than females (Yee 2013), but as red spheres were used in all trees, sex ratio differences must be caused by tree type. Female-biased data support the ideas that dispersal is related to oviposition and that females seeking cherry trees rest or feed on other trees before leaving to continue their search. Females of the Mediterranean fruit fly, *Ceratitis capitata*

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**Fig. 6.** Cle Elum, 2011: rankings of *R. indifferens* caught by week in (A) sweet cherry, (B) black hawthorn, (C) bitter cherry, (D) choke cherry, and (E) ornamental hawthorn. Within tree type, bars with same letters are not statistically different (*P* > 0.05). Friedman test statistics: sweet cherry: $T_2=24.801$; critical $F=1.80$; black hawthorn: $T_2=9.636$; critical $F=2.00$; bitter cherry: $T_2=4.873$; critical $F=1.80$; choke cherry: $T_2=3.221$; critical $F=2.00$; ornamental hawthorn: $T_2=4.833$; critical $F=1.80$ (Conover 1980). Shaded boxes are periods when the ranks did not differ from the highest rank.
(Hendrichs et al. 1991), and females of the tephritid Paroxyna plantaginis Haliday showed a stronger immigration rate than males (Albrectsen and Nachman 2001).

Female dispersal could be induced by an oviposition-deterring or dissuasive pheromone (Mumtaz and AliNiazee 1983, Roitberg et al. 1984) and male dispersal by territorial behaviors (AliNiazee 1974).

*R. indifferens* in nonsweet cherry trees carry high egg loads throughout the season, in contrast with eastern cherry fruit fly, *R. cingulata* (Loew), where variations in timing of reproductive maturity are linked to the fruit maturity period of the host plants (Teixeira et al. 2009). The inconsistencies between findings may have been caused by *R. indifferens* of different ages dispersing, fly emergence times overlapping, or traps not being deployed early enough to capture young flies with immature eggs. High egg loads apparently do not decrease dispersal from cherry trees by *R. indifferens*, although fitness tradeoffs between carrying high egg loads and dispersal ability have been postulated

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**Fig. 7.** Cle Elum, 2012: rankings of *R. indifferens* captures by week in (A) sweet cherry, (B) black hawthorn, (C) bitter cherry, (D) choke cherry, and (E) apple. Within tree type, bars with same letters are not statistically different (*p* > 0.05). Friedman test statistics: sweet cherry: $T^2=11.078$; critical $F=1.70$; black hawthorn: $T^2=27.299$; critical $F=1.70$; bitter cherry: $T^2=27.605$; critical $F=1.70$; choke cherry: $T^2=14.672$; critical $F=1.84$; apple: $T^2=19.888$; critical $F=1.92$ (Conover 1980). Shaded boxes are periods when the ranks did not differ from the highest rank.
Females that land on black hawthorn and other trees therefore have the potential to lay many eggs into their fruit. Presence of bitter cherry in the study areas throughout the season complicates the interpretation that *R. indifferens* on black hawthorn originated from sweet cherry. Although bitter cherry trees close to black hawthorns may have been a source of some flies, they were unlikely a source in hawthorns farther away that also had high fly numbers. Also, numbers of flies captured in bitter cherry and black hawthorn did not differ, so unless the two were equally attractive, most flies in hawthorn did not originate from bitter cherry. Numbers of flies captured in bitter cherry, choke cherry, ornamental hawthorn, and apple trees also did not differ, probably due to close proximity of the last three trees to sweet cherry. Presence of bitter cherry also complicates explanations of the origin of flies in sweet cherry. Some flies from bitter cherry could emerge early enough (Fig. 3C) to move onto sweet cherry, contributing to continual infestations and affecting fly control.

Black hawthorn is a developmental host for *R. indifferens*, but no larval infestation was detected in its fruit in this study. Based on

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**Fig. 8.** Roslyn–Ronald, 2011: rankings of *R. indifferens* captures by week in (A) sweet cherry, (B) black hawthorn, (C) bitter cherry, (D) choke cherry, and (E) apple. Within tree type, bars with same letters are not statistically different (*P* > 0.05). Friedman test statistics: sweet cherry: $T^2=26.313$; critical $F = 1.70$; black hawthorn: $T^2=36.381$; critical $F = 1.70$; bitter cherry: $T^2=10.895$; critical $F = 1.80$; choke cherry: $T^2=6.574$; critical $F = 2.30$; apple: $T^2=7.510$; critical $F = 1.70$ (Conover 1980). Shaded boxes are periods when the ranks did not differ from the highest rank.
combined results from previous (Yee and Goughnour 2005) and current studies, R. indifferens appears to have difficulty using black hawthorn for larval development even though it is an abundant fruit in central Washington. It is not clear whether few or no flies laid eggs in hawthorns or whether no larvae survived in them. However, as numbers of flies that visit hawthorn trees increase, chances of some of them being genetically predisposed to attack hawthorn fruit and producing off-spring capable of surviving in the fruit should also increase. In southwestern Washington, three R. indifferens pupae were reared from 5,194 black hawthorn fruit (Yee and Goughnour 2005). Genetic differences may explain inconsistencies between this and the current result, perhaps similar to why R. pomonella attacks domesticated cherries in Utah (Alfred and Jorgensen 1993) and apparently not in Washington (Yee and Goughnour 2008). Alternatively, greater sample sizes of black hawthorns in Cle Elum and Roslyn could have resulted in larval detections.

In the ponderosa pine ecosystem, dispersal of R. indifferens among various trees could make fly management in sweet cherry difficult. In theory, near-reproductively mature flies that leave sweet cherry trees and reside in any nonsweet cherry tree for just a few days when sweet cherries are ripening could mature (~7 d old; Frick et al. 1954) and return to attack sweet cherries. This and development in bitter cherry could reduce chances of controlling flies. For fly management, all fruit trees may need to be considered as possible refugia for flies during the return to attack sweet cherries. This and development in bitter cherry (Allred and Jorgensen 1993) and apparently not in Washington (Yee and Goughnour 2008). Alternatively, greater sample sizes of black hawthorns in Cle Elum and Roslyn could have resulted in larval detections.

Table 3. Mean numbers of R. indifferens captured per sphere (ranks) in sweet cherry and nonsweet cherry trees during select 6-week periods when sweet cherries began dropping in high numbers in Cle Elum and Roslyn–Ronald, Washington state, USA

| Date     | Sweet Cherry | Black Hawthorn | Bitter Cherry | Choke Cherry | O. Hawthorn | Kruskal–Wallis |
|----------|--------------|----------------|---------------|-------------|-------------|----------------|
|          | N = 6        | N = 3          | N = 6         | N = 3       | N = 6       |                |
| 29 July  | 68.3 (19.5)  | 1.3 (9.3)      | 8.0 (11.1)    | 1.3 (9.0)   | 2.3 (10.2)  | 8.30 0.0812    |
| 5 Aug    | 60.8 (19.2A) | 5.3 (14.0AB)   | 7.8 (11.5AB)  | 2.7 (12.8AB)| 0.7 (5.8B)  | 11.31 0.0233   |
| 12 Aug   | 34.5 (18.0)  | 5.7 (16.7)     | 2.5 (11.9)    | 0.7 (8.7)   | 0.5 (7.5)   | 9.06 0.0596    |
| 19 Aug   | 13.7 (19.1A) | 3.7 (13.3AB)   | 6.0 (12.8AB)  | 1.0 (8.2AB)| 0.8 (7.4B)  | 9.81 0.0437    |
| 26 Aug   | 3.8 (15.6)   | 4.7 (15.0)     | 8.8 (15.2)    | 0.7 (11.3)  | 0.0 (6.0)   | 8.47 0.0759    |
| 2 Sep    | 0.8 (11.1AB) | 2.7 (18.3AB)   | 8.0 (17.1A)   | 0.3 (10.3AB)| 0.0 (7.5B)  | 10.11 0.0386   |

Cle Elum, 2012

| Date     | Sweet Cherry | Black Hawthorn | Bitter Cherry | Choke Cherry | Apple | Kruskal–Wallis |
|----------|--------------|----------------|---------------|-------------|-------|----------------|
|          | N = 8        | N = 7          | N = 10        | N = 5       | N = 6 |                |
| 26 July  | 33.6 (30.1A) | 5.4 (10.9B)    | 12.9 (18.1B)  | 5.8 (10.78)| 16.0 (19.2AB)| 16.28 0.0027   |
| 2 Aug    | 11.4 (18.5)  | 8.9 (20.1)     | 8.6 (17.6)    | 6.0 (15.1)  | 10.5 (21.1) | 1.12 0.8904    |
| 9 Aug    | 4.9 (19.4)   | 5.6 (18.0)     | 3.5 (15.0)    | 6.4 (21.60)| 6.0 (21.2)  | 2.08 0.7206    |
| 17 Aug   | 1.0 (16.5)   | 3.0 (24.2)     | 1.7 (19.7)    | 0.4 (10.4)  | 1.7 (19.2)  | 5.84 0.2116    |
| 23 Aug   | 1.0 (18.7A)  | 1.9 (23.7)     | 0.9 (17.1)    | 0.6 (13.4)  | 1.2 (18.8)  | 3.67 0.4524    |
| 30 Aug   | 0.9 (14.1B)  | 2.9 (30.5A)    | 0.9 (14.4B)   | 1.8 (25.5A)| 0.7 (11.5B) | 19.61 0.0006   |

Roslyn–Ronald, 2011

| Date     | Sweet Cherry | Black Hawthorn | Bitter Cherry | Choke Cherry | Apple | Kruskal–Wallis |
|----------|--------------|----------------|---------------|-------------|-------|----------------|
|          | N = 8        | N = 11         | N = 4         | N = 2       | N = 10 |                |
| 12 Aug   | 101.9 (29.4A)| 6.0 (16.5B)    | 3.0 (14.1AB)  | 2.0 (12.2AB)| 8.4 (13.2B)| 13.71 0.0083   |
| 19 Aug   | 134.9 (27.8A)| 16.6 (17.4AB)  | 7.0 (14.8AB)  | 8.0 (18.5AB)| 12.5 (12.1B)| 11.19 0.0245   |
| 26 Aug   | 141.8 (26.5A)| 31.8 (15.5B)   | 8.8 (11.1B)   | 21.5 (17.2AB)| 12.4 (9.5B) | 14.50 0.0509   |
| 2 Sep    | 127.6 (27.9A)| 29.6 (17.7AB)  | 9.5 (13.2AB)  | 73.0 (22.8AB)| 9.1 (11.3B) | 13.14 0.0106   |
| 9 Sep    | 97.4 (25.9A)| 37.2 (19.2AB)  | 17.5 (17.0AB) | 24.0 (18.5AB)| 10.0 (10.6B) | 10.16 0.0378   |
| 16 Sep   | 35.8 (19.8)  | 9.7 (17.3)     | 11.0 (18.8)   | 15.5 (24.0) | 3.3 (15.9)  | 1.42 0.8400    |

Kruskal–Wallis test (SAS Institute 2010). Values within a row followed by same letter are not significantly different (P > 0.05).

Table 4. Mean numbers of R. indifferens captured per sphere (ranks) in sweet cherry and nonsweet cherry trees in 2010 in Roslyn, Washington state, USA

| Trap dates | Sweet Cherry | Black Hawthorn | Bitter Cherry | Kruskal–Wallis |
|------------|--------------|----------------|---------------|----------------|
|            | N = 4        | N = 6          | N = 3         |                |
| 10–17 Aug  | —            | 115.5          | —             |                |
| 17–24 Aug  | 21.2 (8.2)   | —              | 52.3 (7.1)    |                |
| 24 Aug–2 Sep| 10.5 (5.3)  | 73.2 (8.3)     | 11.7 (6.7)    | 1.10 0.5785    |
| 2–9 Sep    | 1.5 (3.4)    | 27.8 (9.3)     | 6.0 (7.2)     | 5.67 0.0587    |
| 10 Aug–9 Sep| 33.2 (6.4)  | 153.3 (8.2)    | 28.0 (5.5)    | 1.09 0.5800    |

aNo (two trees) or high (two trees) fruit loads.
bLow to high fruit loads.
cNo (one tree) or moderate (two trees) fruit loads.
dNo fruit.
sweet cherry growing season. The sites here are similar with respect to tree diversity and abundance to those near Wenatchee, Washington state, and Hood River, Oregon, two areas of major commercial sweet cherry production.

In summary, the results provide partial support for the hypothesis in that although R. indifferens commonly disperses from sweet cherry trees with fruit, it could disperse more, or more flies are retained in nonsweet cherry trees after than before sweet cherries drop. This could allow opportunities for the flies to use other fruit for larval development. Although R. indifferens infestation in black hawthorn was not detected, early season fly occurrence in this and other trees and fly presence in bitter cherry could make fly management in sweet cherry difficult in the ponderosa pine ecosystem. In the sagebrush–bunchgrass ecosystem where sweet cherry orchards are more prevalent, lower tree abundance may reduce fly dispersal to or fly presence in nonsweet cherry trees.

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Table 5. Percentages of R. indifferens captured on spheres that were females in different trees over the season in Cle Elum (2011, 2012) and Roslyn–Ronald (2011), Washington state, USA

| Tree                  | Cle Elum, 2011 | Cle Elum, 2012 | Roslyn–Ronald, 2011 | Overall |
|-----------------------|---------------|---------------|---------------------|---------|
|                       | N   | % Female | N   | % Female | N   | % Female | N   | % Female |
| Sweet Cherry          | 1,457 | 36.5C    | 1,156 | 40.6AB  | 6,448 | 30.4C    | 32.7C |
| Black Hawthorn        | 94   | 52.2AB   | 291  | 46.4A   | 1,518 | 38.3B   | 40.2B |
| Bitter Cherry         | 294  | 21.4D    | 424  | 30.7C   | 292  | 30.5BC  | 27.9D |
| Choke Cherry          | 27   | 33.3B    | 160  | 33.1BC  | 311  | 49.5A   | 43.4AB|
| Ornamental Hawthorn   | 37   | 70.3A    |       |         | 222  | 45.0AB  |       |
| Apple                 |      |         | 720  | 50.9A   |       |         | 49.5A |
| % Female              | 56.942|         | 25.284|         | 173.706|         | 166.182|
| P                    | < 0.001|         | < 0.001|         | < 0.001|         | < 0.001 |

—, no flies caught. Percentages females within columns followed by same letter are not significantly different (test of multiple proportions, P > 0.05).

*Due to low sample size from ornamental hawthorns compared with others, not included in overall analysis.

Table 6. Larval infestations by R. indifferens in fruit of sweet cherry, bitter cherry, and black hawthorn trees in 2010 in Cle Elum and/or Roslyn–Ronald, Washington state, USA

| Fruit picked          | Dates         | No. of trees | No. of fruit | % Trees Pos. | No. of pupae | Pupae/fruit* | Pupae/g Fruit* | No. of adults |
|-----------------------|---------------|--------------|--------------|--------------|--------------|--------------|----------------|--------------|
| Sweet Cherry          | 7/26          | 9            | 764          | 100%         | 743          | 1.108 (18.0A) | 0.623 (13.1A) | 256 248       |
| Bitter Cherry         | 9/2, 9/8      | 13           | 5,742        | 76.9%        | 1,018        | 0.127 (7.0B)  | 0.436 (10.4A) | 356 353       |
| Roslyn–Ronald         |               |              |              |              |              |              |                |              |
| Sweet Cherry          | 8/2, 8/10     | 13           | 1,276        | 100%         | 607          | 0.468 (41.6A) | 0.219 (39.3A) | 222 184       |
| Black Hawthorn        | 8/17–9/15     | 19           | 21,248       | 0%           | 0            | 0 (16.0C)     | 0 (16.0C)     |              |
| Bitter Cherry         | 9/2, 9/8      | 17           | 3,432        | 29.4%        | 735          | 0.069 (22.4B) | 0.234 (24.1B) | 220 214       |

*Means (rank). Ranks followed by same letter within columns are not significantly different (P > 0.05). Cle Elum: Pupae/Fruit: Z = 3.88; P < 0.0001; Pupae/g Fruit: Z = 0.94; P = 0.3493 (two-sided); Roslyn–Ronald: Pupae/Fruit: $\chi^2 = 34.41; P = 0.0001$; Pupae/g Fruit: Z = 27.63; P < 0.0001.
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