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Detection of an apple-infesting population of *Rhagoletis pomonella* (Walsh 1867) (Diptera: Tephritidae) in the state of Colorado, USA

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Abstract. The apple maggot fly, *Rhagoletis pomonella* (Walsh 1867) (Diptera: Tephritidae), is an economically important pest of apples (*Malus domestica* Borkh.) (Rosaceae) throughout much of the United States. The fly is endemic to the eastern U.S., where its primary host plants are several species of native hawthorns (*Crataegus* spp.) (Rosaceae). About 150 years ago the fly shifted to apples in the Northeast. More recently, the fly has been introduced to the western U.S. outside of its native range. In the state of Colorado, *R. pomonella* attacks the fruits of a number of different native and introduced hawthorn species, but is generally absent from apples. While orchards in apple growing regions are closely monitored, backyard and non-commercial apples often go largely unexamined. Here, we report results from a survey of non-commercial apples at 16 locations in eight counties across Colorado. We document the discovery of one *R. pomonella* infestation of apple at low density in Boulder, Colorado in close proximity to highly attacked, introduced downy hawthorn (*C. mollis* Scheele) in a residential neighborhood. Our finding represents the first confirmed infestation of apple in the state in 25 years. We discuss the implication of our findings for apple maggot management.


INTRODUCTION

The apple maggot fly, *Rhagoletis pomonella* (Walsh 1867), is a model for understanding both incipient ecological speciation via host plant shifting and the ramifications of insect host shifts for economically important fruit crops (Bush 1966, Berlocher & Feder 2002). The fly is endemic to the eastern U.S. Sometime in the mid 1800s in the Northeast, *R. pomonella* shifted from its native host (*Crataegus mollis* Scheele) (Rosaceae) to introduced, domesticated apple (*Malus domestica* Borkh.) (Rosaceae). More recently, *R. pomonella* was introduced to the Pacific Northwestern U.S., likely via larval-infested apples from the eastern U.S. Subsequently, the fly has become a quarantine pest and is now impinging on the apple growing regions of central Washington (AliNiazee & Wescott 1986, Brunner 1987). In addition to apples, *R. pomonella* also attacks native black hawthorn (*C. douglasii* Lind.) and introduced ornamental hawthorn (*C. monogyna* Jacq.) in the Pacific Northwest (Yee 2008, Linn et al. 2012, Sim et al. 2012, Hood et al. 2013).

*Rhagoletis pomonella* appears to have been introduced into other regions of the U.S. in addition to the Pacific Northwest. In particular, the fly infests a native black hawthorn (*C. rivularis* Nutt.) and several species of native (*C. macracantha* Lodd. ex Loudon and *C. erythropoda* Ashe) and introduced red hawthorns (*C. mollis*) throughout parts of the Mountain West (defined as the interior western states of Idaho, Montana, Wyoming, New Mexico, Colorado and Utah), including northern Utah, southeastern Idaho, southwestern Wyoming, western Colorado in the Rocky Mountains, and along
the eastern front range of Rocky Mountains in Colorado (Hood et al. 2013). During the 1980s, extensive statewide trapping programs in Utah and Colorado resulted in the capture of adult *R. pomonella* of unknown host origin in or near apple orchards (Jorgensen et al. 1986; Kroening et al. 1989a, 1989b). However, no apples were found infested in Utah or Colorado with two exceptions: (1) in 1987, 16 larvae were found infesting a single, non-commercial apple tree in the center of a 3.2-ha highly infested black hawthorn stand in northern Utah (Jones & Davis 1989), and (2) in 1988, an unreported number of larvae were found infesting ‘Golden Delicious’ fruit in Denver, Colorado (Kroening et al. 1989b). In neither case, however, were fly larvae reared to adulthood to verify that they were *R. pomonella*. Thus, there is no definitive confirmation of apple being infested by *R. pomonella* in the Mountain West. A recent statewide survey of non-commercial apples in Utah conducted by Hood et al. (2013) similarly found no evidence for *R. pomonella* infesting apples. Here, we report results from a survey of non-commercial apples to confirm whether the same is currently true in the neighboring state of Colorado.

In Colorado, the apple industry is worth $5 million annually (U.S. Apple Association 2011). Apples are the state’s largest fruit export (Colorado Dept. Agriculture 2012). There is a zero tolerance policy for *R. pomonella* infesting commercial apples. Interstate market rules dictate that apple growers whose orchards are within one-half mile of where an apple maggot adult has been caught must adhere to a strict bi-monthly pesticide treatment program throughout the season. Thus, while the fly has not been reported from commercial apples in the Rocky Mountains, *R. pomonella* is still a financial burden and if it becomes established in orchards, could cost apple growers millions of dollars in control measures annually (Zhao et al. 2007).

Apple maggot fly monitoring programs are typically conducted near commercial apple orchards using baited sticky traps hung in apples and hawthorns. Thus, the host origins of trapped flies are unknown, and many, if not all, individuals caught in apple may originate from surrounding hawthorns rather than apples. If flies trapped in apple all originate from hawthorn in Colorado and these flies do not attack apples, then they may pose little or no threat to commercial orchards. In this case, the presence of larvae in apple fruit would be the most important consideration for pest management. Establishing such a criterion for pest management could potentially save growers substantial expenses by avoiding unneeded spraying for essentially harmless local hawthorn flies. As the last putative case of *R. pomonella* infesting apples was reported in Colorado 25 years ago, we conducted a survey for *R. pomonella* larvae in non-commercial apples distributed throughout the state to determine whether there is any evidence for current apple-infestation.

**Materials and Methods**

From 17–21 September 2012, as part of a broader survey for *Crataegus*-infesting *R. pomonella* in the Rocky Mountain region, we dissected non-commercial feral and homeowner apples at 16 different locations throughout Colorado in areas where we detected flies in black or red hawthorns (Table 1). At each site, we dissected as many as 150 apples using a paring knife and inspected the fruit for larval instars or feeding tracks characteristic of *Rhagoletis*. At half the locations, a single apple tree was present, while in the remaining cases, multiple trees were screened for larvae (Table 1). If a larva or putative feeding tracks were observed (sites 5 and 14), apples were randomly collected
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Table 1. Locations 1–16 in Colorado where apples were surveyed for *Rhagoletis pomonella* infestation in 2012. Site 17 represents the only known *R. pomonella* infestation of apples from an abandoned apple orchard in Denver County, Denver, Colorado in 1988 (Kroening et al. 1989b).

<table>
<thead>
<tr>
<th>Site number</th>
<th>Location</th>
<th>County</th>
<th>Number of trees</th>
<th>Coordinates (latitude N/longitude W)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Pagosa Springs</td>
<td>Archuleta</td>
<td>1</td>
<td>37.27/107.01</td>
</tr>
<tr>
<td>2</td>
<td>Chimney Rock</td>
<td>Archuleta</td>
<td>1</td>
<td>37/19/107.31</td>
</tr>
<tr>
<td>3</td>
<td>Durango</td>
<td>La Plata</td>
<td>2</td>
<td>37.35/108.38</td>
</tr>
<tr>
<td>4</td>
<td>Piedra River outside Durango</td>
<td>La Plata</td>
<td>1</td>
<td>37.29/107.88</td>
</tr>
<tr>
<td>5</td>
<td>West of Durango near Mancos</td>
<td>La Plata</td>
<td>1</td>
<td>37.35/108.28</td>
</tr>
<tr>
<td>6</td>
<td>West Mesa Verde Nat’l Park near Cortez</td>
<td>Montezuma</td>
<td>2</td>
<td>37.35/108.55</td>
</tr>
<tr>
<td>7</td>
<td>Cortez</td>
<td>Montezuma</td>
<td>3</td>
<td>37.38/108.55</td>
</tr>
<tr>
<td>8</td>
<td>Between Cortez and Dolores</td>
<td>Montezuma</td>
<td>2</td>
<td>37.42/108.55</td>
</tr>
<tr>
<td>9</td>
<td>Dolores</td>
<td>Montezuma</td>
<td>5</td>
<td>37.47/108.51</td>
</tr>
<tr>
<td>10</td>
<td>Montrose</td>
<td>Montrose</td>
<td>1</td>
<td>38.42/107.85</td>
</tr>
<tr>
<td>11</td>
<td>Collbran</td>
<td>Mesa</td>
<td>2</td>
<td>39.24/107.95</td>
</tr>
<tr>
<td>12</td>
<td>Northeast of Collbran</td>
<td>Mesa</td>
<td>1</td>
<td>39.24/107.95</td>
</tr>
<tr>
<td>13</td>
<td>New Castle</td>
<td>Garfield</td>
<td>1</td>
<td>39.58/107.54</td>
</tr>
<tr>
<td>14</td>
<td>Boulder</td>
<td>Boulder</td>
<td>5</td>
<td>40.00/105.28</td>
</tr>
<tr>
<td>15</td>
<td>Eldorado Springs</td>
<td>Boulder</td>
<td>1</td>
<td>39.96/105.23</td>
</tr>
<tr>
<td>16</td>
<td>Colorado Springs</td>
<td>El Paso</td>
<td>2</td>
<td>38.86/104.86</td>
</tr>
<tr>
<td>17</td>
<td>Denver</td>
<td>Denver</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Results

Of the 31 trees from 16 locations surveyed across Colorado, possible evidence for *R. pomonella* larval infestation in the form of feeding tracks was found in apples at two sites: (1) from a single tree west of Durango, near Mancos (site 5) and (2) from a single tree (from five surveyed) located in a residential neighborhood in Boulder (site 16) (see Table 1 and Fig. 1). No pupae were recovered from the collection of 16 apples near Mancos. However, we obtained five pupae from which five adult flies (3 males and 2 females) were reared from a total of 167 apples collected at the Boulder site (3% infestation rate). Morphological analysis confirmed that all five adult flies were *R. pomonella*, as they possessed three characters: (1) a distinct F-shaped pattern in the apical half of their wings, (2) the lack of a subapical band and (3) heavy black shading on the posterior surface of their forefemur (Bush 1966, Foote et al. 1993). In addition, we also used the difference in genitalia traits documented by Yee et al. (2011) to confirm that the species was *R. pomonella* and not the morphologically similar snowberry-attacking fly, *R. zephyria* (Snow 1894).
Figure 1. (A) Locations in Colorado where apples were surveyed for *Rhagoletis pomonella* infestation in 2012. Site numbers correspond to sampling locations listed in Table 1. Shaded area designated as Denver County. (B) Location in Denver County where the only previous documentation of *R. pomonella* infestation in apple in Colorado was reported by Kroening et al. (1989b) in 1988. (C) Location of four uninfested apples trees (unfilled circles) and the single infested apple tree (filled circle) in relation to infested, introduced downy hawthorns (filled triangles) in a residential neighborhood in Boulder, Colorado.

**DISCUSSION**

The five flies collected from Boulder represent the only known *R. pomonella* infestation of apples in the Rocky Mountain region in the last 25 years and the first
definitely established infestation of apple reported in Colorado. However, apples appear to still be rarely infested in Colorado and when attacked, are done so at low levels, as we reared adults from only one tree, from one site, in relatively low abundance throughout the state.

*Rhagoletis pomonella* larvae were reportedly found in apples in Denver where apple was apparently the only available host (Kroening et al. 1989b). In contrast, the infested apple site in Boulder was immediately across the street (20 m), as well as down the block (100 m), from several highly infested downy hawthorn trees (*C. mollis*) planted as ornamentals from the eastern U.S. A collection of 80 hawthorn fruit from one of the hawthorn trees in the yard across the street from the infested apple yielded 183 maggots (mean number of emerging larvae per fruit = 2.25). Thus, we hypothesize that the infested apple site in Boulder was the result of a spillover of flies from the nearby downy hawthorn trees and are therefore uncertain whether or not the apple infestation is an established population that will persist.

Understanding why *R. pomonella* only rarely attack apples in the Mountain West has important management and evolutionary implications. With the exception of central Washington, in all other areas in the range of *R. pomonella*, including the introduced population in the Pacific Northwest, both hawthorn and apples are readily attacked (Bush 1966, Yee 2008, Hood et al. 2013). Why flies do not readily use apple as a host in Colorado and Utah therefore requires explanation. One hypothesis is that apples in the region tend to be late fruiting fall varieties that ripen too late and are not favorable for fly survival (Jorgensen et al. 1986, Messina & Jones 1990). However, in our survey of Colorado and in our previous sampling of apples in Utah (Hood et al. 2013), we frequently encountered earlier fruiting apple varieties which appeared quite suitable for larval development. Thus, there are reasons to question the generality of the late fall hypothesis for accounting for the rarity of apple infestation.

A second possibility is that populations in the Mountain West represent a separate introduction from the Pacific Northwest. In the Pacific Northwest, evidence suggests that the initial introduction was via the transport of larval-infested apple fruit from the East (AliNiazee & Penrose 1981, Dowell 1988, Linn et al. 2012, Sim et al. 2012, Hood et al. 2013). In contrast, it is possible that the flies in Colorado/Utah were originally introduced via infested hawthorns, perhaps from a more southern source in the native range of *R. pomonella* in the East, where apples are rare. Indeed, south of central Illinois, Indiana, Ohio, and Pennsylvania, apples are not often attacked by the fly except in the Appalachian Mountains (Bush 1966). If true, then the hawthorn introduction hypothesis could account for why apples are not readily infested in the Rocky Mountains; hawthorn-infesting populations in the region have not made a host shift to apple. In central Washington, apples are also less often infested by *R. pomonella* than hawthorns, although fly populations have been too low to show statistical differences (Yee 2008).

Given that a host shift to apple and a self-sustaining apple race of *R. pomonella* evolved in the eastern United States, the potential exists for an eventual shift to apple in the Mountain West. However, apples were first introduced to North America over 400 years ago by European settlers, and the first reported attack of apples in the Northeast was in the mid-1800s (Walsh 1867). Thus, it appears that over 250 years elapsed before hawthorn flies shifted to and established permanent populations on apples in the native portion of *R. pomonella*'s range in the eastern U.S. This suggests that when extensive standing variation is not present there may be a delay in hawthorn-attacking
R. pomonella evolving the life history timing and host recognition traits needed to establish in apple. Further analyses of diapause timing and host fruit choice behavior of Mountain West hawthorn and the Boulder apple flies are needed to confirm this hypothesis.

From an applied perspective, whether Mountain West R. pomonella populations possess the potential to establish permanent populations on apple is an important issue to commercial fruit growers. The presence of R. pomonella larvae infesting apples in Boulder should be of some concern as a potential vanguard of apple race formation in the region. While we believe the presence of infested apple represents a limited spillover of flies from nearby hawthorn trees, the hypothesis requires further testing. Regardless, our results suggest that hawthorn-origin flies in Colorado can explore apple as an alternate host when local densities of flies are high. Moreover, the Boulder site is within the commercial apple production region of Colorado, which is centered in the northwestern slopes of Rocky Mountains and stretches from Fort Collins south through Boulder and Denver into Colorado Springs. The discovery of infested apples in Boulder affirms the need to continue the current management practice of spraying when R. pomonella are trapped near commercial apple orchards.

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LITERATURE CITED


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