



# Woolly Apple Aphid Generalist Predator Feeding Behavior Assessed through Video Observation in an Apple Orchard

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**Abstract** Generalist predators are considered effective biological control agents in many agroecosystems. However, characterizing the behavior of different generalist predator species in realistic field settings is difficult due to challenges associated with directly observing predation events in the field. Here we video recorded woolly apple aphid (*Eriosoma lanigerum*) (Hemiptera: Aphididae) colonies to directly observe the feeding behavior of their generalist predators during the day and night. To observe European earwigs (*Forficula auricularia*) (Dermaptera: Forficulidae), which are thought to be key woolly apple aphid predators but were not present at our study location, we released earwigs into the study area. Across 1413 h of video recorded over 4 weeks, earwigs made the most attacks on woolly apple aphid colonies, but coccinellid larvae spent more total time attacking because their individual attacks were longer. Antagonistic interactions between predators were rare, and earwigs never antagonized other predators. However, ants commonly antagonized earwigs, and incidence of ant-earwig antagonistic interactions was negatively correlated with earwig-aphid attack rates. Overall, these results suggest that coccinellid

larvae and earwigs differ in their feeding behavior in the field, and provide new evidence that ants may hinder aphid biological control by antagonizing earwigs.

**Keywords** Biological control · *Eriosoma lanigerum* · *Forficula auricularia* · formicidae · intraguild predation

## Introduction

Pest consumption in agroecosystems generally increases when different predator taxa complement each other by feeding at different times or in different locations (Straub et al. 2008). However, if niche overlap occurs, intraguild predation can disrupt biological control of pests (Rosenheim 1998; Straub et al. 2008). Predator behavior, including interactions among predators, can therefore have implications for whether generalists are effective or ineffective biological control agents in different contexts.

Although generalist predators are commonly considered important for pest management (Symondson et al. 2002; Naranjo et al. 2015), field evidence showing their effects on biological control is often correlational, and few studies involve direct observation of prey. Furthermore, predator augmentation experiments often do not address how the whole predator community contributes to biological control or how different predator species interact (Symondson et al. 2002). Video recording prey in the field overcomes these limitations by providing direct evidence of predator behavior in a realistic environment (Meyhöfer 2001; Merfield et al. 2004; Frank

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et al. 2007; Grieshop et al. 2012; Smith and Gardiner 2013; Walton and Grieshop 2016; Kistner et al. 2017; Woltz and Lee 2017).

In this study, we observed predation of the woolly apple aphid, *Eriosoma lanigerum*, a worldwide pest of apple, by video recording aphid colonies in an apple orchard. The main natural enemies of woolly apple aphid are thought to include the specialist parasitoid *Aphelinus mali*, the omnivore European earwig (*Forficula auricularia*), and three generalist predator taxa: coccinellids, chrysopids, and syrphids (Brown and Schmitt 1994; Nicholas et al. 2005; Gontijo et al. 2012; Bergh and Stallings 2016; Quarrell et al. 2017; Orpet et al. 2019a). Past field studies on predation of woolly apple aphid do not compare predatory behavior of these different natural enemies, assess intraguild interactions, or involve night-time observations (Gontijo et al. 2012; Bergh and Stallings 2016; Orpet et al. 2019a). In addition, conclusions from laboratory studies of earwig (Noppert et al. 1987; Asante 1995), coccinellid (Asante 1995), and syrphid (Short and Bergh 2004) feeding behavior on woolly apple aphids may differ under more realistic field conditions. To address these knowledge gaps, we video-recorded woolly apple aphid colonies in an apple orchard during the day and the night and assessed: (1) attack rates and durations of different predator taxa, (2) temporal and spatial patterns of woolly apple aphid predator activity, and (3) intraguild predation and other interactions between predators. Overall, our study provides new evidence of behavioral differences among key predators that contribute to woolly apple aphid biological control.

## Methods

**Study Site** Our study was conducted at a 12-tree plot of Golden Delicious within a 0.5 ha block of apple at the Washington State University Sunrise Orchard near Rock Island, WA (47.31°N, 120.07°W). The block was planted in 2007 with Malling 9 rootstock and 0.9 m spacing between trees. The block received no insecticides during our study, but the surrounding orchard was conventionally managed using commercial practices standard to the region.

**European Earwig Releases** European earwigs are common in central Washington apple orchards (Horton et al. 2002), but for unclear reasons have

highly variable abundance between locations and years (Horton et al. 2002; Moerkens et al. 2009, 2012). Because we were specifically interested in observing their behavior, we collected European earwigs from a commercial orchard and released them onto the ground into the study plot. To collect earwigs for release, we placed earwig shelters, which consisted of 7.5 × 35.5 cm strips of single-face corrugated cardboard rolled into cylinders, into trees of a commercially-managed apple orchard. The shelters were affixed 0.5 to 1 m from the ground to the lowest major limb of trees using rubber bands. On each morning of an earwig release, earwigs were collected from shelters of the commercial apple orchard, counted into plastic Ziploc® bags, and released onto the ground evenly across the study plot. On 9 June, 12 June, and 14 June 2017, we released 20 late-instar or adult earwigs per tree, and 60 per tree on 27 June into the study plot to achieve earwig counts of between ca. 5 to 10 in cardboard shelters. This target was chosen because other studies using similar corrugated cardboard shelters for earwig monitoring found that this range was associated with woolly apple aphid biological control (Mueller et al. 1988; Nicholas et al. 2005; Quarrell et al. 2017). Our manipulation artificially affected the abundance but not the phenology of earwigs, as they are univoltine, have low dispersal ability, and are active in tree canopies from late spring to fall (Moerkens et al. 2011).

**Video Monitoring Woolly Apple Aphid Colonies** Within the 12-tree study plot, we recorded a total of 20 woolly apple aphid colonies from 13 Jun to 11 July 2017 using Vivotek Supreme IP8362 outdoor security cameras (VIVOTEK Inc., San Jose, CA) at 30 frames per second and 1920 × 1080 resolution. The cameras were affixed using adjustable U-bolts to metal rods screwed into wooden bases which could easily be moved around the orchard. Up to four cameras were used simultaneously, and each camera recorded one colony at time (Table 1). Lenses of cameras were approximately 20 cm away from recorded colonies. The cameras used infrared light at night and visible light during the day.

For the first 3 weeks of the study, each camera was moved to a new woolly apple aphid colony every week. In addition, colonies were checked every 1 to 2 days, and whenever a colony disappeared the camera recording it was moved to a new colony (Table 1). Colonies were monitored by video from 19:00 to 7:00 each night

from 13 Jun to 4 Jul 2017. We switched to continuous video monitoring of all hours of the day from 4 July to 11 July 2017.

Video was reviewed at up to eight times normal speed using exacqVision Media Player software (Exacq Technologies, Inc.). The viewing area was standardized to approximately  $13 \times 13$  cm, and the area of the branch or trunk hosting the colony was considered the observation area. We did not collect video data on *A. mali* because their small size (<2 mm) made them difficult to see on recordings. The time interval when any predator was present in the observation area was defined as an “appearance” and further defined as a “visit” if a colony was present (each camera continued recording after its colony was destroyed). The time interval when a predator contacted a colony until it moved more than 1 cm away was defined as an “attack”. This definition was used because predators sometimes sat near the margins of a colony apparently engaged in feeding but not in contact with the main colony mass. The woolly fibers produced by woolly apple aphids obscured our ability to assess consumption rates. A recorded colony was considered destroyed starting after the last predator attack before the recorded area was inspected in-person to confirm that no aphids were present. We attempted to record two woolly apple aphid colonies on trunks and two on branches (one camera per colony) at all time periods. After 8 July, only one trunk colony could be found in the study plot, so we recorded it along with three branch colonies. In addition, we could only find a single trunk colony and no branch colonies to record starting 9 July. We stopped video recording on 11 July because no colonies could be found in the study plot at that time.

Any contact between predators resulting in one or both changing direction or speed was defined as an ‘antagonistic interaction’. All ant-predator antagonistic interactions were noted and included in our dataset, but because ants were extremely numerous, their appearances were quantified by counting the number seen in each observation area for the first 10 s of each hour.

**Aphid, Earwig, and Temperature Monitoring** We monitored woolly apple aphid abundance every 2 to 8 days in the plot by counting the total number of colonies on trunks and branches up to a height of 1.5 m on the west side of each study tree. This corresponded to about 25% of the total tree area. Rosy apple aphids (*Dysaphis plantaginea*) and green apple aphids (*Aphis pomi* and

*Aphis spiraecola*) were monitored by counting the number of infested leaves within the same area. We assumed that woolly apple aphid population dynamics would be similar on the east and west side of trees, and for convenience of sampling we arbitrarily chose the west side of trees for monitoring. Furthermore, Asante et al. (1993) found similar seasonal trends in woolly apple aphid abundance at canopy heights above and below 2 m, suggesting that the height range of sampling in our study was suitable for assessing woolly apple aphid population dynamics. Earwigs were counted from 13 June to 1 August every 2 to 8 days by shaking them out of each of five corrugated cardboard shelters (as described above) placed in the study plot in every other tree excluding the southernmost and two northernmost. Daily maximum and minimum air temperatures were measured with a 107-LC temperature probe (Campbell Scientific, Logan, UT) in a Washington State University AgWeatherNet weather station located 350 m from the research block. Woolly apple aphid, earwig, and temperature monitoring data were plotted for visual interpretation to provide descriptive context on the conditions of our study.

**Statistical Analysis** To compare earwig behavior on trunks versus branches, we used Wilcoxon rank-sum tests on their number of visits, number of attacks, total visit time, and total attack time per hour of footage between 19:00 to 7:00 (comprising the range of time within which all but 1 of the 1235 earwig visits occurred). We considered each colony as a replicate, and we excluded colonies from this analysis that did not have at least one complete interval in this range recorded ( $N = 8$  trunk and 8 branch colonies; branch colonies 2, 10, 11, and 12 were excluded). We also similarly analyzed average 10 s hourly ant counts between trunks and branches using the same subset of data. We did not compare behavior of other predator taxa between trunk versus branch locations because coccinellid larvae only made visits to a total of five branch and two trunk colonies, and other taxa made visits to fewer colonies.

We used correlation analyses to assess potential relationships between ant aggression with ant abundance and earwig behavior. Treating individual colonies as replicates, we first plotted the number of ant-earwig antagonistic interactions per hour of earwig visit time by each of four other variables: the average count of ants for the first 10 s of each hour (from 19:00 to 7:00 inclusive), earwig-aphid average attack duration,

**Table 1** Locations, fates, recording periods, hours of video (until destruction or camera repositioning), and ants per minute observed (between 19:00–7:00, i.e., when earwigs were active) for each woolly apple aphid colony, and predator taxa visits, attacks, and total attack durations per colony

Colony	Recording	Fate	Start time	Total time (h)	Ants per min (19:00–7:00)										Number of attacks										Total attack duration (min)														
					7:00–19:00					19:00–7:00					E					C					S					Ch					O				
					E	C	S	Ch	O	E	C	S	Ch	O	E	C	S	Ch	O	E	C	S	Ch	O	E	C	S	Ch	O										
Trunk 1	Camera moved	13-Jun 19:00	0	84	7.6	85	0	0	0	2	6	0	0	0	0	0	0	0	0	0	1	16	0	0	0	0	1												
Trunk 2	Camera moved	13-Jun 19:00	0	84	7.8	54	0	0	0	2	9	0	0	0	0	0	0	0	0	0	0	81	0	0	0	0	0												
Branch 1	Destroyed	13-Jun 19:00	0	79	0.2	15	0	0	0	8	12	0	0	0	0	0	0	0	0	0	5	72	0	0	0	0	58												
Branch 2	Destroyed	13-Jun 19:00	0	7	0.0	4	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	26	0	0	0	0	0												
Branch 3	Camera moved	15-Jun 19:00	0	60	0.6	14	0	0	0	2	15	0	0	0	0	0	0	0	0	0	1	220	0	0	0	0	6												
Trunk 3	Camera moved	20-Jun 19:00	0	84	41.8	184	0	0	0	5	10	0	0	0	0	0	0	0	0	0	0	13	0	0	0	0	0												
Branch 4	Camera moved	20-Jun 19:00	0	84	0.2	39	0	0	0	1	5	0	0	0	0	0	0	0	0	0	0	21	0	0	0	0	0												
Trunk 4	Camera moved	20-Jun 19:00	0	84	5.6	48	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0												
Branch 5	Camera moved	20-Jun 19:00	0	84	1.8	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0												
Branch 6 <sup>1</sup>	Destroyed	27-Jun 19:00	48	141	4.7	89	38	5	2	3	24	28	0	3	3	56	283	0	93	11																			
Trunk 5 <sup>1</sup>	Destroyed	27-Jun 19:00	36	125	5.4	122	2	0	1	18	26	2	0	1	8	89	170	0	83	31																			
Branch 7	Destroyed	27-Jun 19:00	0	44	2.3	110	0	0	0	0	12	0	0	0	0	1	28	0	0	0																			
Trunk 6	Camera moved	27-Jun 19:00	0	60	16.1	334	0	0	0	0	33	0	0	0	0	0	47	0	0	0																			
Branch 8	Destroyed	2-Jul 19:00	0	33	1.7	20	28	0	0	3	8	18	0	0	3	16	67	0	0	1																			
Trunk 7 <sup>1</sup>	Destroyed	3-Jul 19:00	11	36	3.9	65	0	5	1	8	6	0	2	0	1	33	0	318	0	0																			
Branch 9	Destroyed	5-Jul 8:00	36	35	1.3	0	34	7	0	0	0	29	5	0	0	1173	30	0	0	0																			
Trunk 8	Destroyed	6-Jul 7:00	60	50	7.7	25	31	0	1	1	19	25	0	0	2	115	921	0	0	0																			
Branch 10	Destroyed	8-Jul 7:00	12	7	1.5	0	5	0	0	0	0	7	0	0	0	147	0	0	0	0																			
Branch 11	Destroyed	8-Jul 7:20	12	8	4.7	22	0	0	0	0	12	0	0	0	0	57	0	0	0	0																			
Branch 12	Destroyed	9-Jul 7:00	9	0	n/a	0	13	0	0	0	0	6	0	0	0	140	0	0	0	0																			
<b>SUM:</b>				<b>224</b>	<b>1189</b>	<b>1235</b>	<b>151</b>	<b>17</b>	<b>5</b>	<b>54</b>	<b>199</b>	<b>115</b>	<b>7</b>	<b>4</b>	<b>25</b>	<b>890</b>	<b>2901</b>	<b>348</b>	<b>176</b>	<b>109</b>																			

E earwigs, C coccinellid larvae, S syrphid larvae, Ch chrysopid larvae, O other (coccinellid adults, chrysopid adults, harvestmen, goldfinch)

<sup>1</sup> Video-recording started as 19:00–7:00 only, and later was switched to continuous

earwig-aphid attacks per earwig visit, and earwig-aphid attack time per earwig visit time. We analyzed data from the same subset of colonies as above, but also excluded one colony which had no earwig visits (branch colony 9) and one which had only five earwig visits and no earwig-aphid attacks (branch colony 5) (thus,  $N = 14$ ). We analyzed each relationship using Spearman's rank correlations because relationships were non-linear.

**Results**

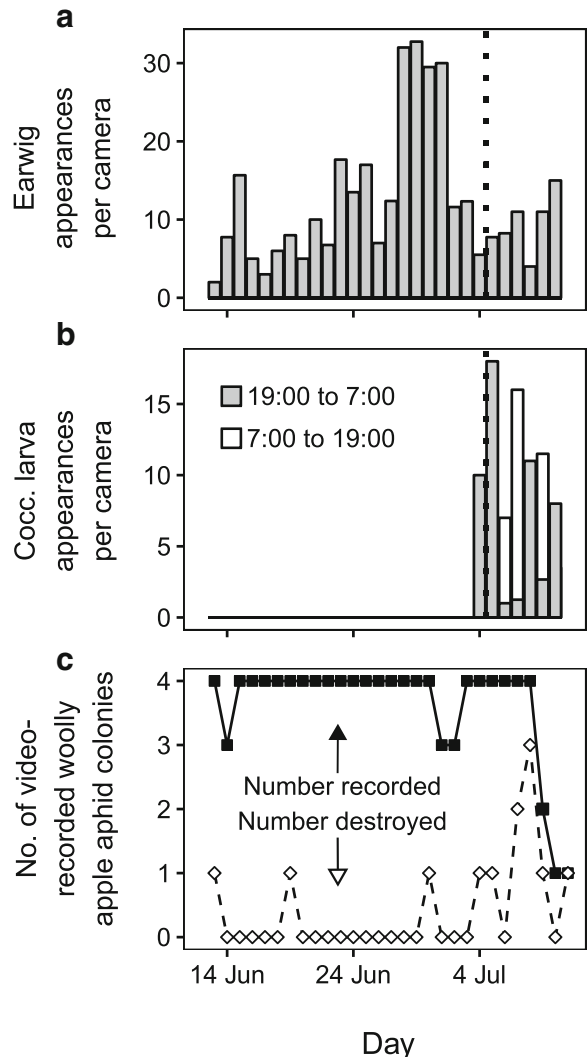
*Video Monitoring Woolly Apple Aphid Colonies* Predators were observed to destroy 12 of the 20 woolly apple aphid colonies recorded during our study (Table 1). During the period of night-only recording, no colonies disappeared in between recordings during the day. The species of coccinellid larvae, syrphids, chrysopids, and harvestmen could not be identified from video, but all coccinellid adults (11 total appearances across two colonies and three different days from 2 July to 6 July) were identified as *Hippodamia convergens* based on their coloration. Among all predators observed attacking colonies, earwigs and coccinellid larvae spent the most total time attacking (Table 2). Although earwigs made more visits and attacks than coccinellid larvae (Table 2), coccinellid larvae had greater total attack time because their individual attack durations were longer (Table 2). For both taxa, most attacks were short and other attacks were very long, hence mean attack durations were higher than

**Table 2** Number of attacks, and mean, median, maximum, and sum attack durations pooled for all attacks across all cameras and days

Predator	No. of attacks	Time per attack (min)			
		Mean	Median	Maximum	Sum
Earwig	199	4.5	1.3	55.2	890
Coccinellid larva	115	25.2	3.7	449.2	2901
Coccinellid adult	10	3.1	0.5	21.0	31
Syrphid larva	7	49.6	5.6	237.7	348
Chrysopid adult	6	10.8	9.0	24.9	65
Chrysopid larva	4	43.9	42.2	91.0	176
Harvestman	4	2.7	0.7	9.2	11
Goldfinch	4	0.6	0.1	2.2	2

median attack durations (Table 2). All other predators made  $\leq 10$  total attacks (Table 2). Although ants often contacted colonies, they rarely appeared to move aphids and it was not possible to identify tending behaviors.

Earwigs (Fig. 1a) were observed throughout the study, which was expected because we released them into the study area. Coccinellid larvae (Fig. 1b) were not seen until 4 July, and the other main predators were not



**Fig. 1** Phenology of earwigs (a) and coccinellid larvae (b) shown as the number of appearances per camera on different days, and the number of woolly apple aphid colonies observed or destroyed on video per day (c). Appearances (panels A and B) were binned into days based on the midpoint time of the appearance. The dotted vertical lines in panels A and B show when cameras were switched from recording only from 19:00 to 7:00 to recording all hours, and shaded versus white bars indicate which half of the day appearances were observed. No coccinellids were observed before 4 July

observed until 3 July (chrysopid larvae) or 4 July (syrphid larvae). All earwig appearances occurred between 19:00 to 7:00 except for one individual seen at 13:30, and 97% of appearances occurred between 21:00 to 4:30. This diel periodicity corresponded to sunset ( $20:59 \pm 2$  min throughout our study) and sunrise ( $5:10 \pm 6$  min). Coccinellid larvae were seen during the day and night (Fig. 1b). Considering footage where all 24 h of a day was available, ants were most abundant during night hours (22:00 to 5:00; 55% of appearances per hourly 10 s sampling interval). During the day, most ant appearances were in the morning (6:00 to 9:00; 23%) and evening (18:00 to 21:00; 16%) and there was little ant activity mid-day into the afternoon (10:00 to 17:00; 6%). Other taxa had too few visits to allow for effective description of their diel periodicity.

Comparing earwig behavior between trunks and branches, earwigs made significantly more visits per hour of video on trunks, but the duration of time spent visiting, number of attacks, and duration of time spent attacking per hour was similar between locations (Table 3). Ants were more abundant on trunks than branches (Table 3).

Ants observed were predominantly small (<ca. 5 mm) and brown (although color could only be seen on day-time footage) but their species could not be identified using video footage. Sticky tapes (Scotch® Brand, 3 M Company, St. Paul, MN) were placed on tree trunks for a different project in the same orchard plot (Orpet et al. 2019b), and ants trapped on these tapes were consistent with descriptions of *Formica* and *Myrmica* genera ants common in Washington State apple orchards (Beers et al. 1993).

We observed 94 ant-earwig antagonistic interactions, each resulting in earwigs moving away. Across colonies, the number of ant-earwig antagonistic interactions per hour of earwig visit time had a marginally significant positive correlation to ant abundance (Fig. 2a), no

significant correlation to earwig-aphid average attack duration (Fig. 2b), a negative correlation to earwig-aphid attacks per earwig visit (Fig. 2c), and a negative correlation to earwig-aphid attack time per earwig visit time (Fig. 2d). Coccinellid larvae were antagonized by ants only eight times. In five of the interactions, coccinellid larvae changed direction and speed after contacting an ant. In the other three interactions, coccinellid larvae stayed in place, raised their abdomens, and the ant moved away. Ants also antagonized two coccinellid adults on trunks and one chrysopid adult on a branch. These predators always flew away after contacting the ant.

Antagonistic interactions not involving ants were relatively rare. Earwigs were never observed antagonizing other predator species. Across five intra-species antagonistic interactions, earwigs quickly moved away from each other after contact. Twice, a coccinellid larva contacted a syrphid larva and moved away. Once, a coccinellid larva caused a syrphid larva to drop from the tree after they contacted. We also observed one coccinellid larva eat a smaller one, and one larva which dropped to the ground after contacting another coccinellid larva.

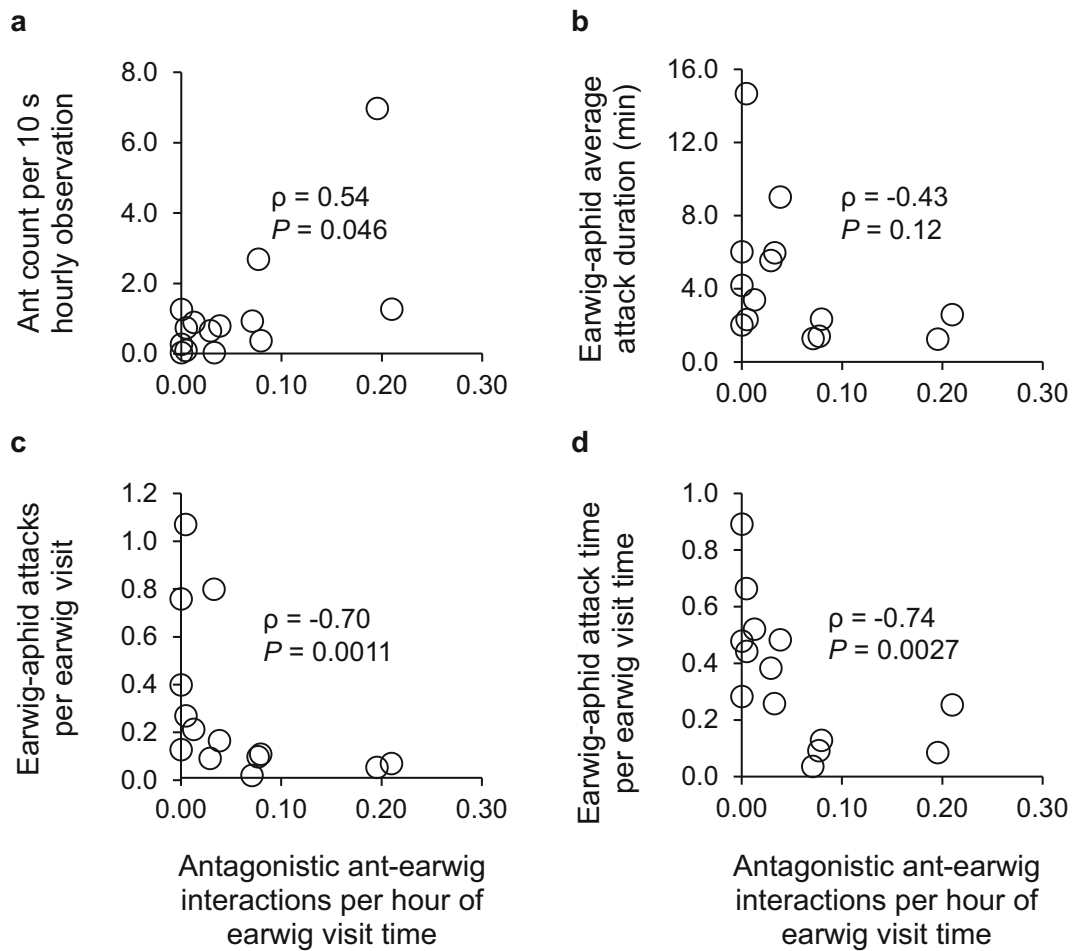
*Aphid, Earwig, and Temperature Monitoring* Woolly apple aphid colonies were present during our study until a population crash occurring from 4 July to 11 July (Fig. 3a). Although there was a decrease in earwig counts from shelters during this time (Fig. 3b), this was likely an artifact of our sampling method, as earwigs abandon shelters when temperature exceeds 38 °C (Lamb 1975). Earwigs were observed on video during this period (Fig. 1a). The woolly apple aphid population crash coincided with the appearance of coccinellid (Fig. 1b), chrysopid, and syrphid larvae (Table 1), and high temperatures (Fig. 3d). In addition, more video-recorded colonies were destroyed by predators during the population crash than before it: from 4 July to 11 July, nine

**Table 3** Median numbers and durations of earwig visits per h and earwig-aphid attacks per hour, and median ant counts per hourly 10 s counting interval on trunk versus branch woolly apple aphid

Location	Median earwig visits per hour		Median earwig attacks per hour		Median ant counts per hourly 10 s counting interval
	No.	Minutes	No.	Minutes	
Trunk	0.99a	1.63a	0.14a	0.74a	1.10a
Branch	0.35b	0.95a	0.16a	0.44a	0.24b

Different letters in the same column indicate significant differences (Wilcoxon rank-sum tests, all  $P < 0.04$ ), same letters indicate non-significant differences (Wilcoxon rank sum-sum tests, all  $P > 0.4$ )

colony recordings from 19:00 to 7:00 (i.e., when earwigs were active);  $N = 8$  trunk and 8 branch colonies



**Fig. 2** Scatterplots and Spearman's correlations between the number of antagonistic ant-earwig interactions per hour of earwig visit time with: ant counts per 10 s hourly observation (between 19:00 to 7:00, i.e., when earwigs were active) (**a**), average earwig-aphid

attack duration (**b**), earwig-aphid attacks per earwig visit (**c**), and earwig-aphid attack time per earwig visit time (**d**). Each circle represents data from one unique woolly apple aphid colony

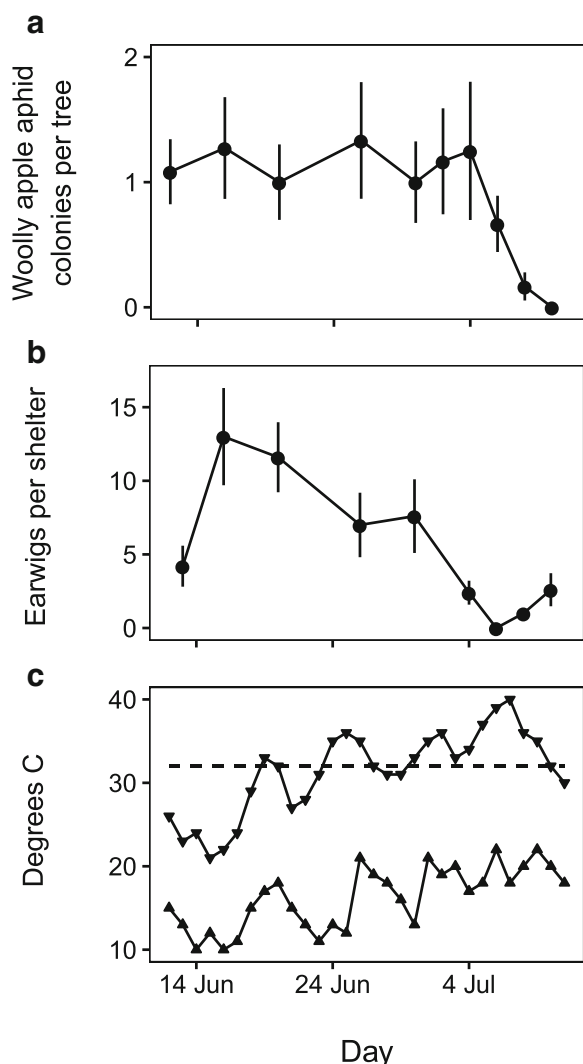
video-recorded woolly apple aphid colonies (1.13 per day) were destroyed by predators, whereas from 13 June to 3 July, only three (0.14 per day) were destroyed (Fig. 1c). Other aphid species were rare during our observation period. Pooled across all 12 trees and 10 sampling times in the study plot, no green apple aphid colonies were found, and two rosy apple aphid colonies were seen on one tree on 16 June.

## Discussion

During our study, coccinellid larvae and earwigs spent the most time attacking woolly apple aphids.

Chrysopids and syrphids are likely important woolly apple aphid predators (Brown and Schmitt 1994; Gontijo et al. 2012; Bergh and Stallings 2016), but were not abundant at the particular timeframe and location our study. Therefore, our main findings relate to the behavior of earwigs and coccinellid larvae, the behavior of earwigs on trunks compared with branches, and interactions between earwigs and other species.

Although we found that earwigs made the most total attacks on woolly apple aphid colonies and coccinellid larvae were only present during the last week of observations, coccinellid larvae spent the most time attacking woolly apple aphid colonies. Assuming a similar consumption rate between the two predator taxa, coccinellid larvae may have been the most important woolly apple



**Fig. 3** Mean ( $\pm 1$  SEM) woolly apple aphid colonies across the 12 trees (a), mean ( $\pm 1$  SEM) earwigs across the five shelters (b), and daily temperatures (max: downward triangle; min: upward triangle) (c) at the study plot. The horizontal dashed line in panel C shows the 32 °C upper developmental threshold of woolly apple aphid (Asante et al. 1991)

aphid predator during our study. However, we were unable to assess the number of aphids consumed per attack or per attack time. In a laboratory setting, European earwigs consumed more woolly apple aphids per day than larvae of the coccinellid *Harmonia conformis* (Asante 1995). However, the functional response of European earwig to any single prey type is likely lessened in the field, where there are many alternative foods. Coccinellids can consume multiple prey species and plant structures, but have a narrower dietary range than earwigs (Weber and Lundgren 2009). Therefore,

earwigs might have spent more of their time consuming non-aphid foods during our study compared with coccinellid larvae, helping to explain why earwig-aphid attack durations and total attack times were shorter.

Piñol et al. (2009) suggested that European earwigs have an important role in aphid pest suppression because they can be present before syrphids, chrysopids, and coccinellids build up populations. This is possible because European earwigs are omnivorous, have low dispersal ability, and are active from spring to fall in apple orchards (Moerkens et al. 2009, 2010, 2011). Coccinellids, syrphids, and chrysopids often show variation in abundance within and between seasons (Brown and Schmitt 1994; Bergh and Short 2008; Gontijo et al. 2012; Bergh and Stallings 2016), perhaps due to greater density-dependence on prey populations and greater dispersal ability of winged adults. Our observations were consistent with the conclusions of Piñol et al. (2009), as earwigs spent considerable time feeding on woolly apple aphid colonies before coccinellids, syrphids, and chrysopids appeared in the fourth week of our study. It is possible that coccinellids, syrphids, and chrysopids were present but not observed during the first 3 weeks of our study (when video was only collected between 19:00 to 7:00). However, their larvae were active during the day and night, and we did not see any at night during those weeks, suggesting that they were not yet present.

Earwigs show a strong preference for foraging in plant canopies rather than the ground by their fourth instar (the final instar) (Frank et al. 2007; Moerkens et al. 2011), but we found only a minor difference in earwig foraging behavior within tree canopies at the scale measured in our study. Earwigs made significantly more visits per hour of recorded video on trunks compared with branches, but they showed a similar amount of visit time, number of attacks, and attack time per hour between locations. This was because earwigs visited observation areas without stopping to make attacks more often on trunks compared with branches. The higher surface area of trunks compared with branches may have decreased the discovery rate of woolly apple aphid colonies or increased our chance of observing an earwig. Another possible explanation is that ants, which were more abundant on trunks, altered earwig behavior (discussed below).

Earwigs were never observed to attack syrphid larvae or other predator species. In agreement with our



observations, earwigs rarely attack syrphid larvae when confined together with aphids in the laboratory (Dib et al. 2011, 2016). In contrast, intraguild predation is common in coccinellid larvae (Weber and Lundgren 2009), and they occasionally attacked syrphid larvae or each other in our study. Earwigs can consume woolly apple aphid mummies parasitized by *A. mali* (McLeod and Chant 1952), but we were unable to assess earwig consumption of parasitized versus non-parasitized aphids with our video footage. However, other field evidence suggests that a combination of earwigs with *A. mali* (Quarrell et al. 2017), other predators with *A. mali* (Gontijo et al. 2015; Bergh and Stallings 2016), or of earwigs with syrphids (Dib et al. 2016), does not interfere with aphid pest suppression, but rather can increase it. Overall, our results and others suggest that there is limited intraguild predation by European earwigs.

Eisner (1960) observed that European earwigs used their forceps to “seize” ants when confined with them in the laboratory, but earwigs we observed in the field always responded to contact with ants by moving away. Incidence of these interactions was negatively correlated with earwig-aphid attack rates, suggesting ants may interfere with woolly apple aphid biological control. The ants observed in our study plot belonged to the genera *Formica* and *Myrmica*. Miñarro et al. (2010) found representatives of these genera tending to rosy apple aphid and green apple aphid colonies in apple orchards. However, among the six aphid-tending ant species they observed, none tended woolly apple aphid colonies, and we were unable to assess tending behaviors in our study. Miñarro et al. (2010) also found woolly apple aphid abundance was higher on apple tree shoots where ants were excluded, although this could have occurred if the ant barriers co-excluded predators. Rosy apple aphid and green apple aphids were rarely observed during our study, so it is not clear why ants were highly abundant. Given our observations, future studies are warranted to clarify the direct and indirect interactions between ant communities and woolly apple aphid colonies and how they may influence woolly apple aphid abundance.

Woolly apple aphid colonies were present in our study plot until a rapid decline during July, which is common for woolly apple aphid populations (Beers et al. 2010). In our study this crash coincided with

the appearance of coccinellid larvae and a high rate of colony destruction by predators observed on video. These observations provide circumstantial evidence that predation may contribute to woolly apple aphid population crashes. However, parasitism by *A. mali* and high temperatures are likely also important (Asante et al. 1991; Beers et al. 2010). Temperatures above the 32 °C upper developmental threshold of woolly apple aphid (Asante et al. 1991) occurred during July in our study plot. Therefore, we believe parasitism and high temperatures, in combination with generalist predators with differing feeding behavior, have important roles in woolly apple aphid population dynamics.

Overall, our study complements experimental and correlational evidence obtained by others on the importance of natural enemy diversity in woolly apple aphid biological control (Nicholas et al. 2005; Gontijo et al. 2015; Bergh and Stallings 2016; Quarrell et al. 2017). European earwigs can be active and consuming woolly apple aphids before coccinellid, syrphid, and chrysopid larvae build high populations. In addition, European earwigs were not observed to antagonize other predator species. However, aside from differing phenology and lack of intraguild predation, we found no strong evidence of spatial or temporal complementarity between European earwigs and coccinellid larvae. We artificially introduced earwigs into the study plot to increase their abundance, so different results might be obtained in orchards with a naturally-occurring community of earwigs and other organisms. In addition, because our study was limited to a single site and a limited timeframe, it is possible that differing observations would occur under different orchard contexts, where factors such as the weather, woolly apple aphid densities, natural enemy communities, ant communities, and tree canopy structures may differ. Nonetheless, in agreement with other studies (Dib 2011, 2016, Quarrell et al. 2017), our observations provide evidence that presence of European earwig in a natural enemy community would improve aphid biological control in apple orchards.

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## References

- Asante SK (1995) Functional responses of the European earwig and two species of coccinellids to densities of *Eriosoma lanigerum* (Hausmann) (Hemiptera: Aphididae). *J Aust Entomol Soc* 34:105–109
- Asante SK, Danthanarayana W, Heatwole H (1991) Bionomics and population growth statistics of apterous virginoperae of woolly apple aphid, *Eriosoma lanigerum*, at constant temperatures. *Entomol Exp Appl* 60:261–270
- Asante S, Danthanarayana W, Cairns S (1993) Spatial and temporal distribution patterns of *Eriosoma lanigerum* (Homoptera: Aphididae) on apple. *Environ Entomol* 22:1060–1065
- Beers EH, Brunner JF, Willett MJ, Warner GM (1993) Orchard pest management: a resource book for the Pacific northwest. Good Fruit Grower, Yakima
- Beers EH, Cockfield SD, Gontijo LM (2010) Seasonal phenology of woolly apple aphid (Hemiptera: Aphididae) in Central Washington. *Environ Entomol* 39:286–294
- Bergh JC, Short BD (2008) Ecological and life-history notes on syrphid predators of woolly apple aphid in Virginia, with emphasis on *Heringia calcarata*. *BioControl* 53:773–786
- Bergh JC, Stallings JW (2016) Field evaluations of the contribution of predators and the parasitoid, *Aphelinus mali*, to biological control of woolly apple aphid, *Eriosoma lanigerum*, in Virginia, USA. *BioControl* 61:155–165
- Brown MW, Schmitt JJ (1994) Population dynamics of woolly apple aphid (Homoptera: Aphididae) in West Virginia apple orchards. *Environ Entomol* 23:1182–1188
- Dib H, Jamont M, Sauphanor B, Capowiez Y (2011) Predation potency and intraguild interactions between generalist (*Forficula auricularia*) and specialist (*Episyrphus balteatus*) predators of the rosy apple aphid (*Dysaphis plantaginea*). *Biol Control* 59:90–97
- Dib H, Jamont M, Sauphanor B, Capowiez Y (2016) Individual and combined effects of the generalist *Forficula auricularia* and the specialist *Episyrphus balteatus* on *Dysaphis plantaginea* – are two predators better than one? *Entomol Exp Appl* 161:1–10
- Eisner T (1960) Defense mechanism of arthropods. II. The chemical and mechanical weapons of an earwig. *Psyche* 67:62–70
- Frank SD, Wratten SD, Sandhu HS, Shrewsbury PM (2007) Video analysis to determine how habitat strata affects predator diversity and predation of *Epiphyas postvittana* (Lepidoptera: Tortricidae) in a vineyard. *Biol Control* 41: 230–236
- Gontijo LM, Cockfield SD, Beers EH (2012) Natural enemies of woolly apple aphid (Hemiptera: Aphididae) in Washington state. *Environ Entomol* 41:1364–1371
- Gontijo LM, Beers EH, Snyder WE (2015) Complementary suppression of aphids by predators and parasitoids. *Biol Control* 90:83–91
- Griehop MJ, Werling B, Buehrer K, Perrone J, Isaacs R, Landis D (2012) Big brother is watching: studying insect predation in the age of digital surveillance. *Am Entomol* 58:172–182
- Horton DR, Broers DA, Hinojosa T, Lewis TM, Miliczky ER, Lewis RR (2002) Diversity and phenology of predatory arthropods overwintering in cardboard bands placed in pear and apple orchards of Central Washington state. *Ann Entomol Soc Am* 95:469–480
- Kistner E, Lewis M, Carpenter E et al (2017) Digital video surveillance of natural enemy activity on *Diaphorina citri* (Hemiptera: Liviidae) colonies infesting citrus in the southern California urban landscape. *Biol Control* 115:141–151
- Lamb RJ (1975) Effects of dispersion, travel and environmental heterogeneity on populations of the earwig *Forficula auricularia* L. (Dermaptera, Forficulidae). *Can J Zool* 53: 1855–1867
- McLeod JH, Chant DA (1952) Notes on the parasitism and food habits of the European earwig *Forficula auricularia* L. (Dermaptera: Forficulidae). *Can Entomol* 84:174–180
- Merfield CN, Wratten SD, Navntoft S (2004) Video analysis of predation by polyphagous invertebrate predators in the laboratory and field. *Biol Control* 29:5–13
- Meyhöfer R (2001) Intraguild predation by aphidophagous predators on parasitised aphids: the use of multiple video cameras. *Entomol Exp Appl* 100:77–87
- Miñarro M, Fernández-Mata G, Medina P (2010) Role of ants in structuring the aphid community on apple. *Ecol Entomol* 35: 206–215
- Moerkens R, Leirs H, Peusens G, Gobin B (2009) Are populations of European earwigs, *Forficula auricularia*, density dependent? *Entomol Exp Appl* 130:198–206
- Moerkens R, Leirs H, Peusens G, Gobin B (2010) Dispersal of single- and double-brood populations of the European earwig, *Forficula auricularia*: a mark-recapture experiment. *Entomol Exp Appl* 137:19–27
- Moerkens R, Gobin B, Peusens G, Helsen H, Hilton R, Dib H, Suckling DM, Leirs H (2011) Optimizing biocontrol using phenological day degree models: the European earwig in pipfruit orchards. *Agric For Entomol* 13:301–312
- Moerkens R, Leirs H, Peusens G, Beliën T, Gobin B (2012) Natural and human causes of earwig mortality during winter: temperature, parasitoids and soil tillage. *J Appl Entomol* 136: 490–500
- Mueller TF, Blommers LHM, Mols PJM (1988) Earwig (*Forficula auricularia*) predation on the woolly apple aphid, *Eriosoma lanigerum*. *Entomol Exp Appl* 47:145–152
- Naranjo SE, Ellsworth PC, Frisvold GB (2015) Economic value of biological control in integrated pest management of managed plant systems. *Annu Rev Entomol* 60:621–645
- Nicholas AH, Spooner-Hart RN, Vickers RA (2005) Abundance and natural control of the woolly aphid *Eriosoma lanigerum* in an Australian apple orchard IPM program. *BioControl* 50: 271–291
- Noppert F, Smits JD, Mols PJM (1987) A laboratory evaluation of the European earwig (*Forficula auricularia* L.) as a predator of the woolly apple aphid (*Eriosoma lanigerum* Hausm.). *Med Fac Landnouw Rijksuniv Gent* 52:413–422
- Orpet RJ, Goldberger JR, Crowder DW, Jones VP (2019a) Field evidence and grower perceptions on the roles of an omnivore, European earwig, in apple orchards. *Biol Control* 132:189–198
- Orpet RJ, Jones VP, Reganold JP, Crowder DW (2019b) Effects of restricting movement between root and canopy populations of woolly apple aphid. *PLoS One* 14:e0216424

- Piñol J, Espadaler X, Pérez N, Beven K (2009) Testing a new model of aphid abundance with sedentary and non-sedentary predators. *Ecol Model* 220:2469–2480
- Quarrell SR, Corkrey R, Allen GR (2017) Predictive thresholds for forecasting the compatibility of *Forficula auricularia* and *Aphelinus mali* as biological control agents against woolly apple aphid in apple orchards. *BioControl* 62:243–256
- Rosenheim JA (1998) Higher-order predators and the regulation of insect herbivore populations. *Annu Rev Entomol* 43:421–447
- Short BD, Bergh JC (2004) Feeding and egg distribution studies of *Heringia calcarata* (Diptera: Syrphidae), a specialized predator of woolly apple aphid (Homoptera: Eriosomatidae) in Virginia apple orchards. *J Econ Entomol* 97:813–819
- Smith C, Gardiner M (2013) Oviposition habitat influences egg predation of native and exotic coccinellids by generalist predators. *Biol Control* 67:235–245
- Straub CS, Finke DL, Snyder WE (2008) Are the conservation of natural enemy biodiversity and biological control compatible goals? *Biol Control* 45:225–237
- Symondson WOC, Sunderland KD, Greenstone MH (2002) Can generalist predators be effective biocontrol agents? *Annu Rev Entomol* 47:561–594
- Walton NJ, Grieshop MJ (2016) Video observations of the natural enemies of eggs of codling moth, *Cydia pomonella*, in apple orchards in Michigan, USA. *Entomol Exp Appl* 159:375–377
- Weber DC, Lundgren JG (2009) Assessing the trophic ecology of the Coccinellidae: their roles as predators and as prey. *Biol Control* 51:199–214
- Woltz J, Lee J (2017) Pupation behavior and larval and pupal biocontrol of *Drosophila suzukii* in the field. *Biol Control* 110:62–69

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