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Herbivory of Citrus Fruit by European Earwigs (Forficula auricularia) in California

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Herbivory of Citrus Fruit by European Earwigs (*Forficula auricularia*) in California

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DISSERTATION

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In memory of my friend and labmate Nick Booster. He cheered me on even before I started at UC Davis, showed me the ropes in grad school, and would geek out about all things biology with me.

Abstract

European earwigs (*Forficula auricularia*) are widespread omnivores that can be considered both a pest, natural enemy, or both in different agricultural systems. Growers and pest control advisors of California citrus suspect that earwigs damage young citrus fruit. However, while there has been extensive research on earwigs as predators in citrus, very little is known about herbivory by earwigs on citrus fruit. This dissertation is the first to comprehensively describe herbivory of earwigs on citrus fruit in California and develop management options for earwigs. Overall, this work reports on results from a series of different field experiments that manipulated densities of earwigs conducted at Lindcove Research and Extension Center (LREC) in Lindcove, Tulare County, CA.

The first chapter of this dissertation focuses on elucidating characteristics of damage generated by earwigs on navel orange (*Citrus sinensis (L.)* Osbeck; Sapindales: Rutaceae) fruit. This study is the first to experimentally evaluate whether earwigs damage young citrus fruit, amount of damage caused, and morphological descriptions of the damage. This study further assesses whether the amount of damage earwigs generate differs across developmental stage, sex of adult earwigs, or time. We tracked damaged fruit to determine whether they are retained to harvest and the damage morphology of the damaged fruit at harvest. We suspected that earwig damage may be mistaken for fork-tailed bush katydids (*Scudderia furcata* Brunner von Wattenwyl; Orthoptera: Tettigoniidae), a widely recognized chewing herbivore in citrus. Thus, damage and abscission in response to damage caused by earwigs was compared to that caused by katydids. We found that earwig nymphs generated more damage to young citrus fruit than adults. Earwigs chewed deep holes on fruit from 0 to 3 weeks after petal fall but not after. Fruit damaged by earwigs and katydids were retained by citrus trees, and scars generated by katydids and earwigs were morphologically similar. Exposure to katydids but not earwigs increased fruit

abscission. This study confirms that earwigs can be damaging to *C. sinensis* fruit, and information from this study can help citrus growers recognize earwig damage.

The second chapter of this dissertation aims to describe fruit feeding across three common citrus species: navel oranges (*C. sinensis*), clementines (*C. clementina* hort. ex Tanaka), and 'Tango' mandarins (*C. reticulata* Blanco). Specifically, this study confined earwigs to citrus branch terminals containing fruit to determine differences in amount of fruit feeding, rates of earwig death, preferential abscission of damaged fruit, and healing of damaged fruit for each citrus species. The major finding from this study was that earwigs fed extensively on *C. sinensis* and *C. clementina* fruit, but feeding was less frequent and less severe on *C. reticulata* fruit. This study suggests that, while earwigs may be direct pests in navel oranges and clementines, earwigs may not be significant pests in *C. reticulata*.

The third chapter of this dissertation tests trunk barriers, which takes advantage of the primarily non-flying behavior of earwigs, to manage earwigs by blocking their movement into tree canopies. Trunk barriers may be used to simultaneously manage earwigs along with non-flying arthropod pests. However, trunk barriers may have negative outcomes such as preventing the movement of natural enemies into tree canopies. Densities of pest and natural enemy arthropods across treatments of sticky barrier, insecticide (bifenthrin) barrier, and no barrier (control) were compared. It was discovered that trunk barriers effectively prevented the movement of key citrus pests, earwig, Fuller rose beetles (*Naupactus godmani*; Coleoptera: Curculionidae), and ants (Hymenoptera: Formicidae) into tree canopies. Spiders were not prevented from accessing the canopies, and the reduction of earwig densities caused by trunk barriers did not lead to increased densities of citrus pests that earwigs prey on, aphids (Hemiptera: Aphididae) and California red scale (*Aonidiella aurantia*; Hemiptera: Diaspididae).

Harvested fruit from trees with sticky barriers had less scarring and were infested with Fuller rose beetle eggs less often compared to trees without barriers. Overall, sticky barriers seem to be an effective way to simultaneously manage earwigs along with other arthropod citrus pests.

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Chapter 1

Characterizing Herbivory by European earwigs (Dermaptera: Forficulidae) on Navel Orange Fruit with Comparison to Forktailed Bush Katydid (Orthoptera: Tettigoniidae) Herbivory

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Abstract

In establishing Integrated Pest Management (IPM) plans for understudied pests, it is crucial to understand the nature of their herbivory and resulting damage. European earwig (*Forficula auricularia* L.; Dermaptera: Forficulidae) densities are increasing in citrus orchards in Central California. Field observations suggest that earwigs feed on young, developing citrus fruit, but this hypothesis had not been examined with formal experimentation. Forktailed bush katydid nymphs (*Scudderia furcata* Brunner von Wattenwyl; Orthoptera: Tettigoniidae) are well-known citrus herbivores that feed on young citrus fruit, and it is possible that earwig damage may be misdiagnosed as katydid damage. Here we report findings from two field experiments in navel oranges (*Citrus sinensis* (L.) Osbeck; Sapindales: Rutaceae) that together tested: (i) whether earwigs damage young citrus fruit; (ii) whether the amount of damage earwigs generate differs across developmental stage or sex of adult earwigs; (iii) the window of time during which fruit are most sensitive to earwig damage; (iv) whether damaged fruit are retained to harvest; and (v) the resulting damage morphology caused by earwigs relative to katydids. Earwigs, particularly nymphs, chewed deep holes in young citrus fruit from 0-3 weeks after petal fall. Fruit damaged by earwigs were retained and exhibited scars at harvest. The morphology and distribution of scars on mature fruit only subtly differed between earwigs and katydids. This study establishes that earwigs can be direct pests in mature navel orange trees by generating scars on fruit and likely contribute to fruit quality downgrades.

KEYWORDS: earwigs, citrus, herbivory, abscission, life stage

Introduction

One of the first steps in developing an integrated pest management plan is to properly identify what is causing plant damage (Bottrell 1979, Flint et al. 2003, Ehi-Eromosele et al. 2013). Without properly identifying which pest is responsible for observed damage, attempts to manage the pest may be misdirected and thus often fail resulting in increased crop damage and costs from ineffective management attempts. Understanding characteristics of herbivory is especially important for pests increasing in abundance.

European earwigs (*Forficula auricularia* L.; Dermaptera: Forficulidae) are omnivores in crop systems, and have been increasing in numbers in orchards due to declines in use of broad-spectrum insecticides (Kallsen 2006, Logan et al. 2011, Romeu-Dalmau et al. 2012a). As omnivores, earwigs can be either damaging herbivores or beneficial predators, and their primary status seems to be crop-dependent. In stone fruit, earwigs can chew holes into fruit and are therefore recognized pests, whereas in apple (*Malus domestica* Borkh; Rosales: Rosaceae) and pear (*Pyrus communis* L. subsp. *communis*; Rosales: Rosaceae) orchards earwigs only cause minor damage and are primarily known instead as natural enemies for their ability to consume a wide range of pest species (Orpet et al. 2019).

The ecological role of earwigs in citrus is unclear (Orpet et al. 2019). Earwigs can defoliate young trees but also consume California red scale (*Aonidiella aurantia* Maskell; Hemiptera: Diaspididae) (Romeu-Dalmau et al. 2012a) and aphids (Piñol et al. 2009a, Piñol et al. 2010, 2012, Romeu-Dalmau 2012b,c). Most research on earwigs in citrus has focused on their predatory role, while very little research has defined the scope of their herbivory (Romeu-Dalmau 2012, Orpet et al. 2019). This is particularly true for damage of citrus fruit by earwigs. While California citrus researchers and farm advisors have suggested that earwigs may chew holes in young citrus fruit on mature trees, because of the lack of experimental research, we do not yet know to what extent earwigs damage citrus fruit and whether earwigs should be actively managed (Grafton-Cardwell et al. 2003; Grafton-Cardwell et al. 2020; Kallsen 2006). Also, young fruit damaged by earwigs had previously not been tracked to harvest to assess whether the damage remains and to examine the morphology of the damage on mature fruit. Therefore, the main goal of this study was to test experimentally the extent of direct damage earwigs cause to navel orange fruit (*Citrus sinensis* (L.) Osbeck; Sapindales: Rutaceae) in mature tree canopies.

Citrus is a valuable crop in California. California produces 58% of the nation's citrus, amounting to 72% of the national citrus value. Navel oranges are the dominant citrus species grown; 45% of the citrus acreage in California is *C. sinensis* navel oranges (CDFA and CASS 2018). Since California citrus is mostly sold fresh rather than processed (CDFA 2018), cosmetic damage to the fruit can decrease profits. Extensive chewing by any pest on young navel orange fruit frequently turns into scars when the fruit matures if the fruit does not abscise (Cass et al. 2019a, Grafton-Cardwell et al. 2020). Depending on the severity of scarring, scarred fruit may be downgraded at the packinghouse or juiced, with substantial economic losses for farmers (Grafton-Cardwell et al. 2003). Thus, early-season chewing pests on navel orange rinds are typically monitored carefully and controlled following detailed management plans (Grafton-Cardwell et al. 2020). The research needed to develop clear management recommendations for earwigs in mature California citrus has not yet been conducted.

Earwigs have four instars, and likely change their feeding habits as they develop (Crumb et al. 1941, O'Connel 2014). The first two instars are protected and fed by the mother inside the nest in a soil cavity, but when earwigs reach the second instar they begin independent foraging (Crumb et al. 1941). Earwig nymphs are thought to consume more vegetation and adults are thought to consume more animal material (Crumb et al. 1941, O'Connel 2014). We found some evidence for this in preliminary experiments conducted in 2018 in 'Parent Washington' *C. sinensis* and 'Tango' mandarins (*Citrus reticulata* Blanco) (Kahl et. al. pers. observations). Furthermore, earwigs may reduce or cease feeding on fruit as fruit develop (Kallsen 2006), leaving a narrow window of time after petal fall when fruit are sensitive to earwig feeding. Petal fall, defined as the time when approximately 75% of petals have dropped from flowers in the region, is used as a convenient marker for the beginning of fruit development. During our preliminary experiments, we found that earwigs damaged fruit at two weeks after petal fall in *C. sinensis* but did not cause damage at six weeks post-petal fall in *C. sinensis* or nine weeks post-petal fall in clementines (*Citrus clementina* hort. ex Tanaka) (Kahl et. al. pers. observations). Male and female earwigs may also differ in their feeding behavior, as the energetic demands of oogenesis may cause females to consume more than males (Wheeler 1996, Malagnoux et al. 2015).

To fully understand the effects of herbivory, it is important to consider not only the phenology and behavior of the insect, but also the response of the plant. Often upwards of 90% of undamaged immature citrus fruit abscise soon after fruit set (Goren 1993). The heaviest abscission of citrus fruit naturally occurs between petal fall and June (Gómez-Cadenas et al. 2000, Kostenyuk and Burns 2004). High abscission rates alone would not reduce damage by herbivores on fruit. However, fruit with herbivore damage may abscise at a higher rate (Kostenyuk and Burns 2004, Planes et al. 2014, Cass et al. 2019a, 2021). If the tree can selectively abscise damaged fruit at a higher rate than undamaged, then the number of damaged fruit present at harvest would decrease. If abscission occurs soon after petal fall, then it likely has little impact on the productivity of the citrus tree. In fact, for many citrus cultivars applying chemicals to increase early fruit abscission is a common practice to ensure remaining fruit are of marketable size (Chapman 1984, Owen-Turner et al. 1997, Greenberg et al. 2010). On the other hand, in some cases, for instance when fork-tailed bush katydids (*Scudderia furcata*; Orthoptera: Tettigoniidae) damage *Citrus clementina* clementine fruit, nearly mature fruit split and drop from the tree. This late abscission likely decreases yield, as the tree has already invested resources in growing the abscised fruit (Cass et al. 2021). However, the relationship between abscission and extent of earwig herbivory in citrus remains to be elucidated. In this study, we will assess whether there is selective abscission of more heavily damaged fruit. If all fruit damaged by earwigs abscise early, then, despite earwig herbivory on fruit, earwig damage would not be economically significant.

Along with addressing whether and when earwigs damage citrus fruit, it is critical to learn how to identify damage caused by earwigs. Because earwigs are nocturnal (Orpet et al. 2019), farmers rarely observe earwig activity and may only see the damage resulting from their feeding. This makes recognition of earwig feeding damage particularly important. It is also crucial to distinguish earwig damage from that caused by other early-season herbivores with chewing mouthparts, so that appropriate management choices can be made by citrus growers. Fork-tailed bush katydids are early-season chewing herbivores that cause a range of damage to young citrus fruit. The damage was classified into categories of: small cut(s) (distinct individual bitemark(s), sometimes in a chevron shape), surface chewed (extensive and overlapping bite marks), or deep hole(s) (crater(s) in the fruit from extensive feeding in one location) (Cass et al. 2019a, 2021). In contrast to earwigs, katydids are readily observed during the day and, widely recognized as key citrus pests in California; pest control advisors regularly scout for them (Cass 2019b,c, Grafton-Cardwell et al. 2020). We suspected that damage of citrus fruit by earwigs may be similar to and frequently be mistaken for katydid damage. This could lead to misdirected and ineffective pesticide applications. It is thought that earwigs often feed near the junction of the fruit with the calyx, perhaps more so than katydids (Carroll et al. 1985, Kallsen 2006, Grafton-Cardwell et al. 2020), but this has not yet been tested. Furthermore, early-season herbivory by citrus thrips (*Scirtothrips citri* Moulton; Thysanoptera: Thripidae) can lead to fruit deformity in several citrus species (Mueller et al. 2019). While citrus IPM guidelines suggest that katydid feeding may cause distortion of expanding fruit (Grafton-Cardwell et al. 2020), there have been no studies examining whether feeding by chewing herbivores, such as earwigs or katydids, causes asymmetrical fruit growth.

In this study, we conducted two experiments to characterize earwig herbivory in navel oranges (herein '*C. sinensis*'). We asked: (i) whether earwigs damage young citrus fruit; (ii) whether the amount of damage earwigs generate differs across earwig developmental stage or the sex of adult earwigs; (iii) what is the window of time during which fruit are sensitive to earwig damage; (iv) whether damaged fruit are selectively abscised, or instead, retained to harvest; (v) can the distribution of scarring on mature fruits can be used to distinguish earwig damage from katydid damage.

Materials and Methods

Experiments were conducted in a navel orange (*Citrus sinensis*) cv. "Washington" block (#83) at the Lindcove Research and Extension Center (LREC) in Exeter, CA (36.360895, -119.062348) in Tulare County. Petal fall was declared by Tulare County Agricultural Commissioner on Monday April 29, 2019.

Experiment 1.

Experiment 1 was performed to assess earwig damage across earwig life stage and sex and to compare damage caused by earwigs and katydids.

Insect collection and maintenance. Earwigs (mostly 2nd to 4th instars) were collected March 27 - April 19, 2019 from wraps placed on young citrus trees at LREC. Earwig nymphs and adults were separated to prevent cannibalism of nymphs by adult males. Groups of 50-100 earwigs were kept in plastic containers with mesh lids. Earwigs were fed lettuce and ground up dry dogfood (Purina ALPO Come & Get It! Cookout Classics, Vevey, Switzerland). Containers were lined with potting soil and misted weekly to provide moisture. Folded paper towel sheets were also placed in containers to provide hiding spaces for earwigs.

Katydids (mostly first and second instar) were collected April 10-18, 2019 from a commercial block of 'Gold Nugget' mandarins (*Citrus reticulata*) and an adjacent block of 'Ventura' and 'San Joaquin' blueberries (*Vaccinium corymbosum* L.; Ericales: Ericaceae) in Fresno County, California. Katydids were maintained indoors at room temperature in four mesh cages (two BugDorm-2400F Insect Tents L75 x W75 x H115 cm, and two BugDorm-2021F Insect Tents L61 x W61 x H61 cm, MegaView Science, Taiwan). Two water vials with cotton wicks and a bouquet of ~30 cm cuttings with fruit from untreated trees of mixed citrus species ('Parent Navel' *C. sinensis*, 'Tango' *C. reticulata*, 'Clausellina' *C. unshiu* Marcovitch, and 'Clemenules,' 'Corsica 1,' 'Fina,' and 'Fina Sodea' *C. clementina*) were placed in each cage. The cuttings were kept in beakers with water and a floral foam brick (OASIS Micro Brick 3230, Oasis Floral Products, USA). Cotton wicks and foliage cuttings were replaced approximately weekly.

Damage initiation. On April 30 - May 1, 2019 (Days 1-2 post-petal fall) we selected five ~20 cm long branch terminals with 3-18 young fruits on each of 32 trees in an experimental block. We counted and recorded the number of fruits for each replicate branch terminal. Then, we enclosed either (i) no insects (control), (ii) an earwig nymph (mixed instars), (iii) an earwig adult female, (iv) an earwig adult male, or (v) a katydid nymph (mostly first and second instars) onto each branch terminal using 19-liter (5 gallon) mesh paint strainer bags secured with wire. Before caging, earwig body lengths (not including antennae) were measured to the nearest millimeter with a ruler. Average body lengths have been reported for each earwig instar (Crumb et al. 1941), allowing us to use insect body length to approximate nymphal instar.

Damage assessment. Six days after insects were caged, the bags and enclosed insects were removed, and the numbers of fruit abscised (lying at the bottom of the bag) and still present on terminals were counted. We tagged each attached fruit with a numbered piece of tape on a loosely-fitting twist-tie (4" black plastic; Brand: EuTengHao) so that we could track each individual fruit. Then, for each attached fruit we estimated the proportion of fruit surface area covered with each of three increasingly serious categories of chewing damage: (1) small cut(s), (2) surface chewed, and (3) deep hole(s). The proportion of each fruit's total surface area damaged (damage size) was calculated by summing proportions across all categories of damage. To increase the numbers of damaged fruit that would be retained to harvest, all fruit that had no damage were counted and then removed from branch terminals; other studies in citrus have shown that lightening the fruit load can enhance the retention of remaining fruit (Ouma 2012).

Fruit monitoring and harvest. We observed development of fruit damage and recorded whether each tagged fruit had abscised on four dates: June 13 (45 days post-petal fall), August 8 (113 days post-petal fall), and October 16 (169 days post-petal fall), 2019, and February 3, 2020 (harvest; 280 days post-petal fall). This allowed us to determine whether damaged fruit were retained to harvest. At harvest, we measured the polar and equatorial diameters of fruit using wide-arm calipers. The maximum length and width of every scar were measured using digital calipers. The total proportion of each harvested fruit's surface area that was scarred was calculated by summing the areas of all scars, estimated as rectangles, and dividing by the total surface area of the fruit estimated as a spheroid. To assess potential differences in the locations of scars produced by earwigs versus katydids, the distance from the center of the scar to the calyx was measured using a soft tape measure and divided by the distance from the calyx to the style to produce a metric of scar location on the fruit. To determine whether feeding by earwigs and katydids caused fruit deformity, the distances from calyx to style on the side of each fruit with the most scarring damage and the least scarring damage, usually on the opposite side (180º away), were measured using a soft tape measure. The ratio of these two semiperimeters provided a measure of fruit asymmetry (deformation). If a fruit had no scarring, then a side of the fruit was measured haphazardly for semiperimeter1 and semiperimeter2 was measure on the opposite side.

Experiment 2.

Experiment 2 was conducted to determine the window of sensitivity of *C. sinensis* fruit to damage by earwigs. Earwigs were reared as described above for Experiment 1. For each week from the third to the fifth week after petal fall (May 15-29, 2019), we chose six branch terminals with two to eight young fruit from each of five trees. Experimental methods were the same as those described above for Experiment 1, except we enclosed three replicates of either (i) no earwigs (control) or (ii) four earwig adults (mixed sex) onto branch terminals. Only earwig adults were used in this experiment, because from past experiments we knew that most, if not all, developing earwigs would have already molted to adults by the fifth week post-petal fall (Kahl et al., pers. observation). Fruit from this experiment were not monitored to harvest.

Statistical Analyses.

Since fruit damage is evaluated at the packinghouse based on a combination of the size and depth of each scar (Grafton-Cardwell et al. 2003), we analyzed insect treatment impacts on both damage size (proportion of surface area damaged) and damage category. Then, we analyzed factors influencing abscission. Finally, we analyzed resultant scar severity (proportion of fruit surface area scarred) and morphology of damage of harvested fruit. All statistical analyses were conducted using R version 4.0.2 (R Core Team 2020). *Tidyverse* was used to explore, process, and manipulate data (Wickham et al. 2019).

Initial Damage Category. A Bayesian regression model (*brm*; package brms; Bürkner, 2017, 2018) was used to analyze differences in initial damage category on fruit across treatments for Experiment 1. The worst damage category on each fruit was used as the response variable, and cage and tree were treated as random effects. The brms package was used due to its flexibility in fitting multilevel, category-specific, and unequal variance ordinal models (Bürkner and Vuorre 2019). We used weakly informative priors. Expected parameter values for proportion of each damage type were extracted from the model's predictive distribution and statistics (mean differences and 95% mean quantile intervals) for custom contrasts were computed. The custom contrasts were: (i) earwig (average of nymph, adult male, and adult female) vs. control treatments; (ii) katydid vs. control treatments; (iii) earwig nymph vs. earwig adults (average of male and female) treatments, and (iv) earwig male vs. earwig female treatments. In the Bayesian models, mean quantile intervals that crossed 0 indicated weak and highly variable differences between contrasts (Korner-Nievergelt et al. 2015, Bürkner and Vuorre 2019, McElreath 2020).

For more details on the Bayesian regression analyses used see Supplementary material (Supplementary methods A1.1).

For Experiment 2, Bayesian ordinal regression models (*brm*) were also used to test treatment differences in damage severity on a fruit-level for each week post-petal fall (week 3, week 4, and week 5). This model was similar to those described above except, treatment, week post-petal fall, and treatment x week interaction were fixed effects. Differences between the control and earwig treatment for each week post-petal fall were computed by drawing expected parameter values from the model's predictive distribution and evaluated (Supplementary methods A1.1).

Damage size. Differences in fruit damage size across treatments in Experiment 1, were analyzed using a generalized linear mixed-effect model (GLMM) with beta distributions, logit link, and zero-inflation (*glmmTMB*; package glmmTMB; Brooks et al., 2017). In this analysis, the zero-inflated models address two questions: 1) do treatments differ in whether or not feeding occurred (comp= "zi"; zero-inflated component) and 2) if feeding did occur, were there differences in extent of feeding across treatments (comp= "cond"; conditional component). Cage and tree were treated as random effects. Model effects were assessed using analysis of deviance Type II Wald Chi-square tests (*Anova*; package car; Fox & Weisberg, 2019) and the marginal means of the custom contrasts mentioned above (average earwigs vs. control, katydid vs. control, average earwigs vs. katydid, earwig nymphs vs. average earwig adults, and earwig adult male vs. earwig adult female) were made using *emmeans* t-tests (package emmeans; Lenth, 2020) for both the continuous and zero-inflated model components.

To examine the influence of insect size and treatment on initial damage size on a fruit-level, a generalized linear mixed-effect model (GLMM) with a beta distribution, logit link, and zero-inflation (*glmmTMB*; package glmmTMB; Brooks et al., 2017) was used, but only earwig treatments were considered, since with this model we were interested in examining at what stage in development earwigs generate damage. We similarly used analysis of deviance (*Anova*) tests to assess model effects and *emmeans* t-tests to compare slopes of insect size versus total proportion of initial fruit surface area damaged across earwig treatments.

Factors influencing fruit abscission. Insect treatments influenced the proportion of damaged fruit, and therefore the proportion of fruit that we removed from the branch, because all undamaged fruit were removed as part of the experimental design. We expected that an increased proportion of fruit surface area damaged would increase fruit abscission, whereas an increased proportion of fruit removed from the branch would decrease abscission. Therefore, to analyze the fruit abscission response in Experiment 1, we built statistical models that tested the influence of the proportion of a fruit's surface area damaged, the proportion of fruit we removed from the branch, and treatment as predictor variables influencing whether or not a fruit abscised. We used generalized linear mixed-effects models with binomial distributions (*glmer*; package lme4; Bates et al., 2015). Cage was a random effect. We then calculated test statistics and p-value for every parameter in every model and AIC scores for each model to compare models. We also performed backward model selection using "anova" (package stats; R Core Team, 2020) to confirm our choice of the most informative and parsimonious model. Separate analyses were performed for early and late abscission (before and after 62 days post-petal fall, respectively); 62 days was chosen because it was the time from petal fall to the last day in June, which includes natural abscission from a pulse of abscission of young fruit that is sometimes termed the "June drop". We also looked at the effect of the proportion of fruit surface damaged on early and late fruit abscission for earwig-damaged fruit only with generalized linear mixed-effects models with a binomial distribution and cage as a random effect.

Scarring. A generalized linear mixed-effect model (GLMM) with a Beta distribution, logit link, and zero-inflation (*glmmTMB*; package glmmTMB; Brooks et al., 2017) was used to assess scarring on fruit at harvest for Experiment 1, similar to the initial damage size analysis above. This tested: 1) does the number of fruit that healed, represented by fruit with zero damage, vary across treatment (zero-inflated component) and 2) for scarred fruit, does fruit scar size (proportion of fruit scarred) differ across treatment (conditional component). Analysis of deviance was used, as above, to assess the effect of treatment. Scarring across the same custom contrasts mentioned above (average earwigs vs. control, katydid vs. control, average earwigs vs. katydid, earwig nymphs vs. average earwig adults, and earwig adult male vs. earwig adult female) was compared using marginal means as above.

Fruit Morphology. We tested whether scars caused by earwigs and katydids differed in their spatial distribution across the fruit. Scar locations on the fruit, measured by proportional distance from the calyx (with 0 meaning touching the calyx and 1 meaning touching the style) were analyzed using generalized linear mixed-effects models with beta distributions and a logit link (*glmmTMB*; package glmmTMB; Brooks et al., 2017). Analysis of deviance Type II Wald Chi-square tests were used to assess model effects (*Anova*; package car, Fox & Weisberg, 2019).

We also tested whether initial damage size influenced fruit deformity. The ratio of damaged versus undamaged semiperimeters was analyzed using a linear model with random effects (*lmer*; package lme4; Bates et al., 2015). The predictor variable was initial damage size. Tree was a random effect, but cage was dropped due to model singularity, as few fruit were retained to harvest. We used analysis of deviance Type II Wald Chi-square tests (*Anova*) to test model effects.

Results

Experiment 1.

Early Damage.

At initial fruit evaluation (directly after the six-day treatment exposure), earwig-exposed fruit had all three damage types (small cut(s), surface chewed, and deep hole(s)) (Fig. 1.1, Fig. 1.2). Damage in the controls was likely due to foliage rubbing fruit before the experiment was set up and not insect chewing. Compared with the control treatment, the earwig treatments had 0.32-0.52 (95% mean quantile interval (QI)) smaller proportions of fruit with no damage, 0.14-0.32 larger proportions with small cuts, 0.06-0.13 larger proportions with surface chewed, and 0.05-0.15 larger proportions with deep holes. Similarly, the katydid treatment had 0.66-0.85 smaller proportions of fruit with no damage, 0.33-0.49 larger proportions with surface chewed, and 0.15-0.37 larger proportions with deep holes compared to the control treatment. There was less evidence for a difference in the proportions of fruit with small cuts between katydid and control fruit (QI: -0.02-0.21). Compared to the katydid treatment, the earwig-exposed branches had 0.24-0.42 larger proportions of fruit with no damage, 0.03-0.24 larger proportions with small cuts, 0.22-0.41 smaller proportions of fruit with surface chewed, and 0.05-0.29 larger proportions with deep holes. There were also differences in proportion of deep hole damage caused by earwig nymphs and adults (Fig. 1.2). Fruit exposed to earwig nymphs had a 0.01-0.22 larger proportion of deep holes than those exposed to earwig adults, but there were no differences in surface chewed, small cuts, and fruit with no damage between these treatments. There were also no differences in damage caused by earwig males and females for any of the damage categories (QIs overlapped 0).

Also, at initial fruit evaluation, the proportion of fruit surface area damaged roughly corresponded with damage category (small cuts: mean=0.02, range=0.01-0.3; surface chewed: mean=0.14, range=0.01-0.75; deep hole(s): mean=0.27, range=0.02-0.99). There were significant differences in numbers of damaged fruit across treatment (zero-inflated component; X^2=127.8, df=4, P<0.001; Fig. 1.2) and the proportion of fruit surface damaged on damaged fruit (conditional component; X^2=79.6, df=4, P<0.001; Fig. 1.3). For fruit with damage, fruit exposed to katydids had a significantly higher proportion of fruit surface area damaged than those in the control ("emmeans" t-test using the Sidak method; β=0.31, df=753, t=5.89, P<0.001) and earwig treatments (β=1.30, df=753, t=8.46, P<0.001).

In our study, the earwig nymphs tested ranged from 8 - 11.5 mm, and thus were likely mostly third and fourth instars (Crumb et al. 1941). Fruit surface area damaged was significantly influenced by the interaction of insect body size and earwig treatment for the conditional component (X^2=6.66, df=2, P=0.04). Earwig nymphs caused a higher proportion of fruit surface area damage when they were smaller (β= -2.00, t = -2.33, df = 78, P = 0.02; Fig. 1.4). None of the effects were significant for the zero-inflated model components (P>0.05). The influence of insect body length on fruit surface area damaged was not significant for male or female adult earwigs (P>0.05).

Influence of fruit damage and fruit removal on abscission.

Out of 766 fruit evaluated, 39 fruit were detached from the branch while we handled them to attach labels after the six days of insect exposure (these were likely fruit that would have abscised). Of the remaining fruit, 355 were not damaged and were removed after the 6-day insect exposure. This left 372 damaged fruit, of which 84.4% abscised before harvest. The majority (86.6%) of fruit abscission happened early, before 62 days post-petal fall.

The selected model for early abscission contained insect exposure treatment (X^2=10.77, df=4, *P*=0.03) and the proportion of fruit removed from the branch (X^2=5.2, df=1, *P*=0.02) as significant predictors (Table S1.1: Model 3). Increasing the proportion of fruit removed decreased early fruit abscission (β= -1.27, z= -2.27, *P*=0.02). Fruit exposed to katydids also abscised marginally more frequently compared fruit exposed to the control (β=1.07, z=1.95, *P*=0.052; Fig. 1.5A; Table S1.1), while fruit exposed to earwig treatments did not significantly differ in abscission rate compared to the control (*P*>0.05). When alone in the model, the proportion of fruit surface area damaged had a significant effect on early abscission (X^2=5.97, df=1, *P*=0.01); increased damage to the fruit increased early fruit abscission (β=2.39, z=2.44, *P*=0.01; Table S1.1: Model 6 and Fig. 1.5B). However, once treatment and proportion of fruit removed were included in the model, there was no additional impact of proportion of fruit surface area damaged. There were relatively few fruit that abscised late and, none of the models examining impacts on late abscission contained significant effects. However, when considered with other effects, proportion of fruit surface area damaged was marginally significant in many of the models (Table S1.2). When earwig-damaged fruit were considered alone, proportion of fruit surface area damaged did not significantly affect early or late abscission of fruit (*P*>0.05). Most branch terminals had some fruit removed, but ~30%, had no fruit removal because all fruit on the branch were damaged. Even when there was no fruit removed from the branch terminal, heavily damaged fruit from the earwig treatment were retained. On the branch terminals without fruit removal, ~88% of fruit abscised leaving 19 fruit that did not abscise. Of the retained fruit, 10 were seriously damaged (six initially had surface chewed and four had deep holes). Of these, most (three fruit each with surface chewed and deep hole damaged) were from the earwig treatments (with the rest from the katydid treatment) and none were from the control.

Influence of abscission on numbers of damaged fruit retained to harvest.

High fruit abscission in all treatments produced small sample sizes for all treatments at harvest. Fifty-eight damaged fruit were retained by the citrus trees until harvest. All insect treatments retained some fruit with serious damage at harvest (Fig. 1.6). All fruit with more than 75% of the surface damaged were from the katydid treatment and all of these fruit abscised. Because the abscission rate was selectively higher for these heavily-damaged katydid-exposed fruit, fewer fruit with serious damage from the katydid treatment were retained to harvest compared to the earwig nymph treatment, which had extensive but more moderate damage with 35% or less of the surface damaged (Fig. 1.5B & Fig. 1.6).

Scarring on harvested fruit.

The proportion of fruit surface area scarred at harvest ranged from 0 to 0.20 with a mean of 0.02 across all treatments. Eight fruit had healed and had no scarring detected at harvest. Five of these eight initially had small cut(s) and two of the eight had surface chewed damage. Fruit exposed to earwigs that received damage categorized as surface chewed or deep holes generally developed prominent scars that ranged from rectangular to jagged (Fig. 1.7B-E), whereas katydid scars were often irregularly shaped and branching (Fig. 1.7F&G), but scars generated by earwigs and katydids were generally morphologically similar. There were no significant differences in the number of fruit with no scarring (zero-inflated component; $P>0.05$), but, there were significant differences for the conditional component ($X^2=19.7$, df=4, $P<0.001$; Fig. 1.8). There was a non-significant trend of increased fruit scarring on fruit exposed to earwigs compared to controls ($\beta=0.51$, df=45, $P>0.05$). Fruit exposed to katydids had higher proportions of scarring than those in the control (β=1.86, df=45, t=2.84, *P*=0.03) or earwig treatments (β=1.35, df=45, t=3.84, *P*=0.002).

Scarring damage caused fruit to grow asymmetrically, resulting in mildly deformed fruit at harvest: the relationship between initial surface area damaged and ratio of the semi-perimeters (from calyx to style) on the most heavily scarred side of the fruit relative to the lightest scarred side was significant (X^2=4.01, df=1, *P*=0.05), but there was large of variation and the relationship was weak (β= -0.002, t=-2.0 Fig. S1).

The distributions of scar locations (distance from the calyx) were marginally different for earwigs versus katydids (X^2=2.98, df=1, *P*=0.08; Fig. 1.9). There was a trend for earwig scars to be found closer to the calyx and katydid scars closer to the style, leading to a lower proportional position for earwigs (mean=0.5; SE=0.02) compared to katydids (mean=0.58; SE=0.03). However, feeding directly at the calyx was rare for both earwigs and katydids (Fig. 1.9).

Experiment 2: Damage across time.

Experiment 2 was designed to determine the time period during which developing citrus fruit are vulnerable to earwig damage, so we only assessed initial damage caused by earwigs across week post-petal fall. In the third week post-petal fall, there were small differences in all fruit damage types between earwig-exposed fruit and the control (Fig. 1.10); in the earwig treatment there was a 0.01-0.43 (95% mean quantile interval (QI)) smaller proportion of fruit with no damage, a 0.01-0.35 larger proportion with small cuts, a 0-0.12 larger proportion with surface chewed, and a 0-0.01 larger proportion with deep holes compared to the control treatment. However, the percentage of severe fruit damage was much lower for the third week post-petal fall (~6% of fruit with surface chewed and ~1% with deep holes) than for the first week post-petal fall (Experiment 1) when ~20% of fruit had surface chewed or deep holes. By the fourth week post-petal fall, there were no clear differences between the earwig and control treatments (QIs overlapped 0), and there was a lot of background damage (55.6% of control fruit were damaged, perhaps by snails which were abundant in the trees in the plot at that time). In the fifth week post-petal fall, we selected branch terminals with less background damage, but there were again no clear differences between the earwig and control treatments (Fig. 1.10).

Discussion

Early Damage.

We found that earwigs damaged young navel orange fruit during the week of petal fall, leading to more fruit with surface chewed and deep holes during the week of petal fall. While katydid damage has been assessed experimentally in a handful of studies (Cass et al., 2019a, 2021; Headrick, 2000), to our knowledge, this study is the first to demonstrate with experimentation that European earwigs damage young citrus fruit. Some studies have claimed that earwigs are harmless in citrus (Malagnoux et al. 2015), and other studies on earwigs in citrus have highlighted their role as predators of aphids (Piñol et al. 2009a, b, Piñol et al. 2010, Romeu-Dalmau et al. 2012a,b,c). One study surveyed citrus fruit for damage generated by earwigs on 'Rush' navel oranges (*C. sinensis*) but did not find any (Romeu-Dalmau et al. 2012a). However, earwig densities were very low (on average less than one earwig per beating sheet on most of the sampling dates). Earwig densities can be highly variable from field-to-field and year-to-year (Moerkens et al. 2008). The present study provides experimental support for previous anecdotal observations made by extension personnel and farmers that earwigs extensively chew the rind and can chew deep holes into young citrus fruit. While earwigs may provide some benefits as predators, to avoid fruit damage, earwig densities and evidence of chewing damage in citrus groves should be monitored; in certain scenarios it may be necessary to apply control measures to manage earwigs.

Katydids are recognized as notorious early-season citrus pests, and damage caused by katydids has been carefully studied (Cass 2019a,b,c, Cass et al. 2021). Thus, it is not surprising that initial damage severity and intensity caused by katydids surpassed damage observed in both control and earwig treatments. Still, earwigs frequently damaged young citrus fruit, meaning chewing damage on young fruit detected in citrus orchards cannot merely be assumed to be from katydids. Katydid and earwig densities should be carefully monitored in the field and the morphology of scarring damage at harvest should be assessed to determine the likely culprit of fruit feeding. If there are high earwig densities, no or very few katydids observed, and extensive chewing damage similar to that depicted in this study is detected, it is likely that earwigs and not katydids are causing fruit damage.

Earwig nymphs cause more serious damage to citrus fruit than earwig adults, and smaller earwig nymphs damage a greater proportion of the fruit surface area than larger nymphs. This is in agreement with previous research on earwigs, as well as our personal observations, that have shown that as earwigs mature they shift feeding preference from plant to animal material (Crumb et al. 1941, Romeu-Dalmau et al. 2012a, O'Connel 2014). However, this is the first time that the shift in feeding preference has been extended to earwigs feeding on citrus fruit. Along with causing less damage to fruit than earwig nymphs, earwig adults may offer more predation of pest insects. Some studies that directly tested or observed predation by earwigs focused on earwig adults (He et al. 2008, Romeu-Dalmau et al. 2012a,b), and in one study earwig adults showed higher predation rates than fourth-instar nymphs (Malagnoux et al. 2015). In our study, the earwig nymphs tested were likely third and fourth instars (Crumb et al. 1941). The finding that smaller nymphs consumed more fruit suggests that when earwigs leave the nest to begin foraging on their own and climb into the tree canopy, they consume more vegetative matter than later instars (Crumb et al. 1941, Orpet et al. 2019). This may be because of different nutritional needs, hunger, or naivete in feeding (Simpson & White, 1990). Understanding how earwig development impacts the risk of fruit damage will help growers decide if control measures to manage earwigs are necessary. Third and fourth instar nymphs in the tree canopy are likely more problematic than earwig adults.

Contrary to our expectations of increased fruit damage by females compared to males, there were no significant differences between the sexes. In fact, there was a non-significant trend of increased fruit damage by earwig males. Whereas females have significant energy demands for oogenesis and care for nymphs, male earwigs have to compete to gain access to females, and males with larger forceps have been shown to be more successful competitors (Radesäter and Halldórsdóttir 1993, Tomkins and Simmons 1995). These large forceps and fighting for access to females could be energetically expensive. Although earwig sex does not affect fruit feeding, there is some evidence suggesting that it may influence predation, with adult females consuming aphids at a higher rate than males (Malagnoux et al. 2015).

Damage across time.

There appears to be a very narrow window from petal-fall to three weeks post-petal fall during which earwigs cause serious damage (surface chewed and deep holes) to citrus fruit. In Experiment 2 during the fourth week post-petal fall, fruit had high background damage, likely due to snails, but there was no difference between the earwig and control treatments. This implies that management for earwigs is time-sensitive and should occur before or at petal-fall to effectively reduce earwig damage. Since only adults were used in Experiment 2, the observed change in damage was not due to earwig development. Many early-season citrus pests of fruit such as katydids and citrus thrips (*Scirtothrips citri*; Thysanoptera: Thripidae) also have limited windows of time during which they cause damage to citrus fruit (Grafton-Cardwell et al. 2020), but their windows do not appear to be as narrow as the window of vulnerability to earwig damage. Earwigs and other early-season pests may reduce feeding as the fruit ages due to chemical or physical changes in the citrus rind that deter herbivory (Kekelidze et al. 1989, Rodríguez et al. 2011). However, most work on rind chemistry of citrus has been done near fruit harvest. Future research is needed to identify specific changes in the rind that deter early-season herbivores.

Influence of fruit removal on numbers of damaged fruit.

Removal of undamaged fruit reduced early fruit abscission. Mechanical or chemical fruit thinning is commonly used in citrus to increase retention of larger fruit, but there have not been many studies of fruit thinning in citrus (Ouma 2012). We used removal of undamaged fruit to increase the number of damaged fruit that were retained to harvest, allowing us to analyze the morphology of scars. Overall, the majority of fruit still abscised, and most of the abscission was early, as has been seen in other studies (Cass et al. 2019a, Cass et al. 2021).

Selective abscission of damaged fruit.

Treatment also influenced early fruit abscission, with fruit exposed to katydids, but not earwigs, more likely to abscise than fruit exposed to control treatments. This is likely because of differences in fruit feeding intensity. While both katydids and earwigs generated deep holes on fruit, there was a higher proportion of deep holes chewed by katydids and katydid chewed holes were often larger, prompting fruit abscission. This provides some evidence that the tree may have selectively abscised fruit in response to the highly extensive damage generated by katydids, but there was no selective abscission of the more moderate but still economically serious damage generated by earwigs.

While the proportion of fruit surface area damaged did have an effect on abscission when considered alone, this effect was minimal, and was lost when either effects of treatment or proportion of fruit removed from the branch were considered and when earwig-damaged fruit were considered alone. This suggests that selective fruit abscission occurs more in response to factors operating at the branch-level (e.g. extreme overall herbivory) than factors operating at the level of the individual fruit (proportion of the fruit with surface damaged).

Several fruit heavily damaged by earwigs and some heavily damaged by katydids were retained to harvest. This was observed even on branches where we did not remove any fruit to enhance retention. This suggests that abscission of damaged fruit is not complete for both katydids and particularly for earwigs, leaving harvested fruit with extensive damage that would likely result in fruit being downgraded at the packinghouse. While katydids severely damaged many fruit, because the tree selectively abscised fruit on branches exposed to katydids, few fruit heavily damaged by katydids remained to harvest. However, the few remaining katydid-exposed fruit were heavily scarred. On the other hand, because the tree did not selectively abscise fruit exposed to earwig nymphs, there was higher proportions of seriously damaged fruit remaining from the earwig nymph treatment, despite lower early damage, compared to the katydid treatment.

Scarring on harvested fruit.

Capturing statistically meaningful differences at harvest from fruit exposed to damage soon after petal-fall is difficult, because of the very high abscission rates (Cass et al., 2019a). Yet, it appears that there is substantial damage generated by earwigs on fruit that are retained to harvest. However, more research is needed that assesses how earwig densities impact fruit damage on a larger scale, supporting the creation of quantitative economic injury levels for European earwigs.

This study also elucidated the morphology of damage caused by earwigs compared to damage caused by katydids. Damage by both katydids and earwigs caused minor fruit deformity. Scars made by earwigs were often more rectangular, while scars made by katydids were large and often branching. Differences in shape of the scars could be due to differences in feeding behavior on the fruit or differences in the response of the fruit to feeding by earwigs compared to katydids. While the location of earwig and katydid feeding damage does not seem to be very different, this study provided some evidence to support our hypothesis that only earwigs feed directly adjacent to the calyx. Earwigs often hide during the day and may feed on the calyx because it allows them to keep cover in the cluster of fruit while feeding. We also found that only katydids fed directly adjacent to the style. It could be that katydids preferentially feed on flower parts that remain attached to the developing fruit and then feed on adjacent parts of the developing fruit. The difference in location of feeding of earwigs and katydids may also be due to the size and shape of the two insects. Katydids are larger and rounder, while earwigs are smaller and flatter allowing them to easily squeeze into the narrow space beside the calyx. Farmers and pest control consultants could use the position of scars relative to the calyx or style to diagnose chewing herbivore culprits, with scars next to the calyx and style indicative of earwig and katydid feeding, respectively. However, overall, the damage generated by earwigs and katydids was similar. More research needs to be done with higher replication to discern whether feeding positions of these two herbivores can be reliably distinguished to avoid misdiagnosis of damage-generating species.

Conclusions.

In this study, several discoveries were made that improve pest management guidelines and recommendation for earwigs in California citrus. Our primary discovery was that earwigs cause damage to young fruit that were retained to harvest and developed large prominent scars. To our knowledge, this is the first time scars generated by earwigs on mature citrus fruit from a controlled experiment have been photographed and described. Evidence of extensive earwig damage to young navel orange fruit at petal fall suggests that earwigs can be economically important citrus herbivores in mature trees. Smaller earwig nymphs in the canopy directly after petal-fall are likely especially damaging to fruit, but after three weeks post-petal fall earwigs in the canopy are likely not damaging and may serve as beneficial predators. When considering whether to manage earwigs, the life stage of earwigs in the canopy, time of fruit development, and presence of katydids should be considered. *Citrus sinensis* trees responded to removal of fruit by reducing abscission and responded to exposure to katydids by increasing abscission. The abscission of damaged fruit by citrus trees is imperfect, particularly for fruit damaged by earwig nymphs, allowing for several heavily damaged fruit to be retained on trees to harvest. Our findings provide improved knowledge on when to monitor for earwig damage and how to identify their damage. While this study focuses on the role of earwigs as herbivores, the role of earwigs as predators has been well-established, and future studies will seek to understand the net impact of earwigs in citrus tree canopies. Further research is also necessary to determine sampling methods and economic thresholds for earwigs in citrus.

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Figures

Figure 1.1. Examples of initial fruit damage. A) surface chewed on earwig-exposed fruit. B) deep holes and small cuts on earwig-exposed fruit. The arrows point at examples of small cuts. C) surface chewed on katydid-exposed fruit. D) deep hole on katydid-exposed fruit. Damage category definitions: small cut(s): distinct individual bitemark(s) in fruit; surface chewed: extensive and overlapping shallow chewing of the surface of the fruit; deep hole(s) - a crater in the fruit from extensive feeding in one location.

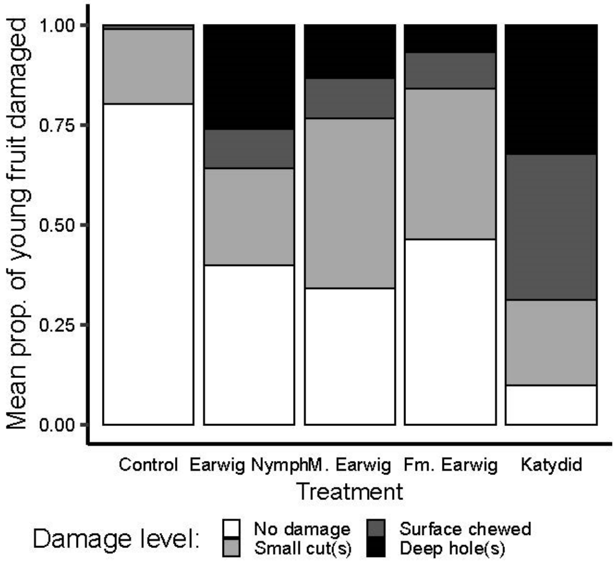

Figure 1.2. Mean proportion of fruit that had each damage level (no damage, small cut(s), surface chewed, and deep hole(s)) across insect treatments (control, earwig nymph, male earwig adult, female earwig adult, and katydid) in Experiment 1 averaged first by cage and then treatment.

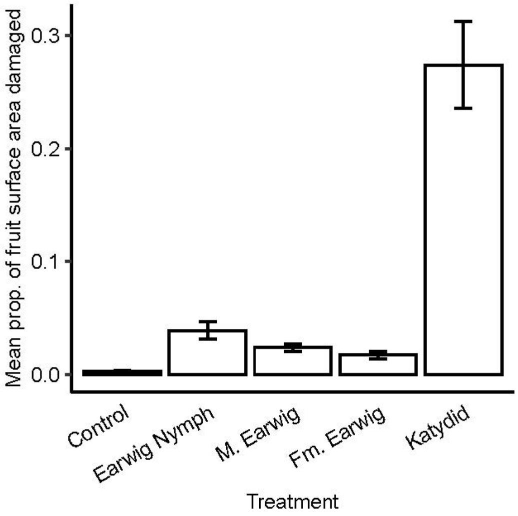

Figure 1.3. Mean and standard error of proportion of fruit surface area damaged across insect treatments (control, earwig nymph, male earwig adult, female earwig adult, and katydid) averaged first by cage then treatment at initial fruit evaluation in Experiment 1 (fruit with no damage, zeros, included).

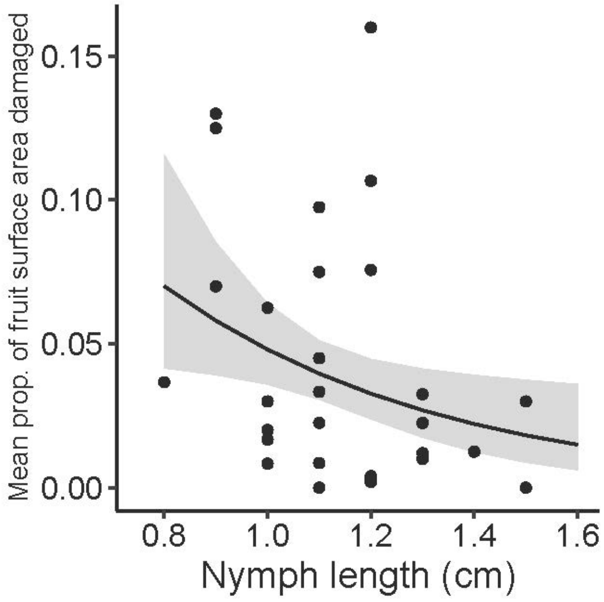

Figure 1.4. Influence of earwig nymph body length (cm) on the mean proportion of fruit surface area damaged after a six-day exposure to herbivory in Experiment 1. The line and confidence interval (shaded area) are predictions from the zero-inflated beta generalized linear mixed-effect model.

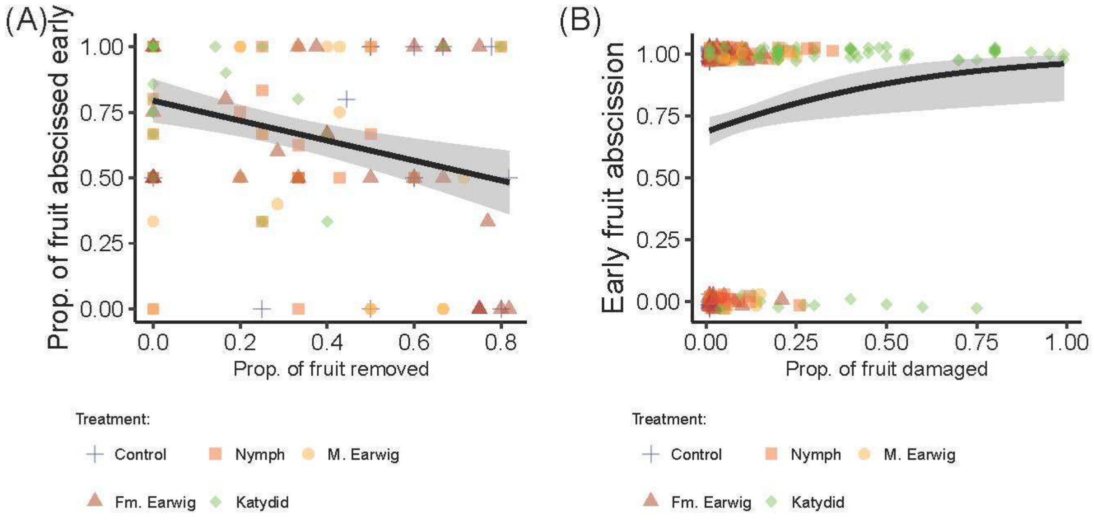

Figure 1.5. Factors influencing fruit abscission in Experiment 1. A) Influence of the proportion of fruit removed from each cage (because they had no damage) on the likelihood of early fruit

abscission. The line and confidence interval are linear predictions. B) Influence of proportion of fruit surface area damaged by herbivory on early (before 62 days post-petal fall) fruit abscission (0: did not abscise; 1: abscised). The line and confidence interval are predictions from the binomial generalized linear model.

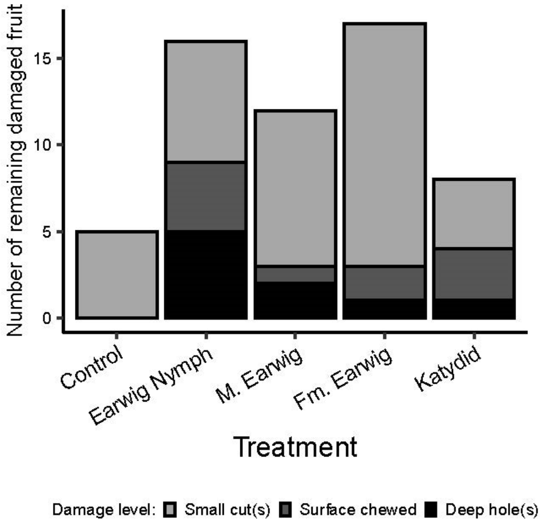

Figure 1.6. Numbers of fruit remaining to harvest, categorized by initial damage levels (small cut(s), surface chewed, and deep hole(s)) across insect treatment (control, earwig nymph, male earwig, female earwig, and katydid).

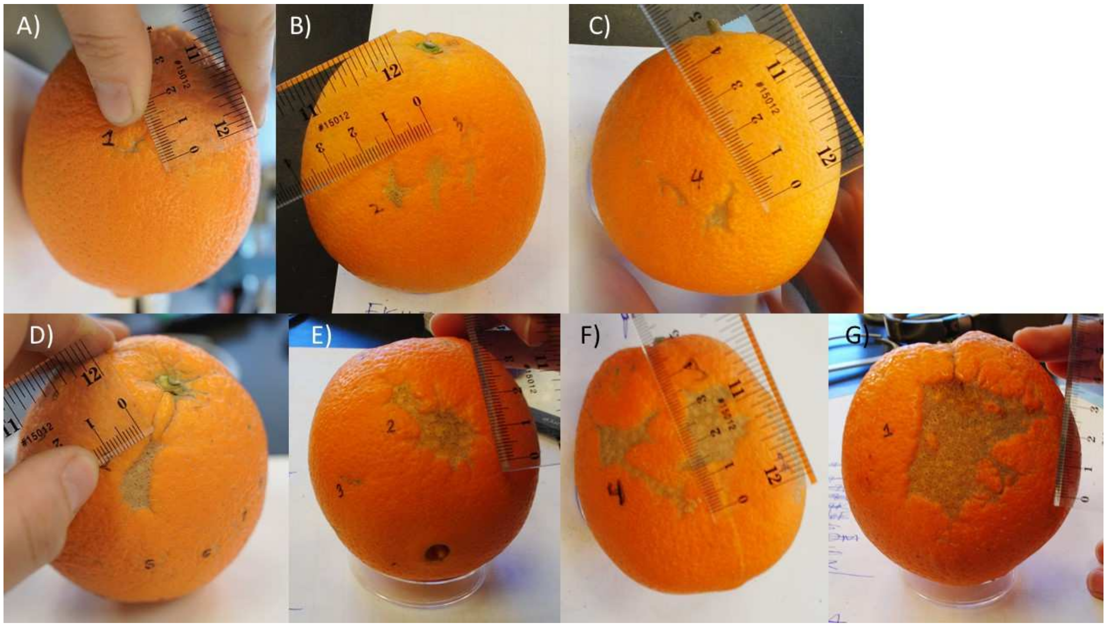

Figure 1.7. Examples of fruit damage at harvest and descriptions of initial damage evaluations in order of increasing severity in Experiment 1. Figures A-E are fruit exposed to earwigs, and figures F and G are fruit severely damaged by katydids. A) Fruit initially had 3% small cut damage. B) Fruit initially had 1% small cuts and 2% surface chewed damage. C) Fruit initially had 1% small cuts, 5% surface chewed, and 3% deep hole damage. D) Fruit initially had 1% small cuts, 3% surface chewed, and 10% deep hole damage. E) Fruit initially had 5% surface chewed and 10% deep hole damage. F) Fruit initially had 30% surface chewed. G) Fruit initially had 60% surface chewed.

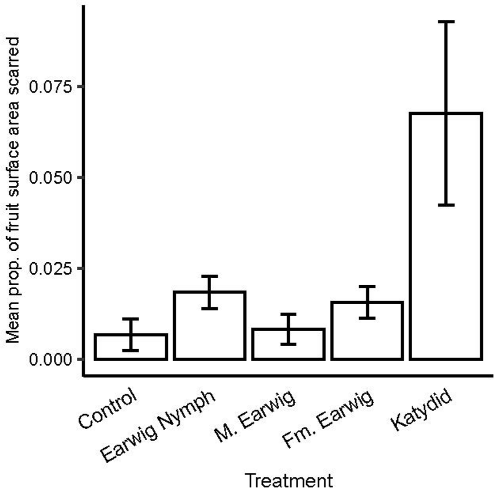

Figure 1.8. Experiment 1: Mean and standard error of proportion of fruit surface area scarred at harvest across insect treatments (control, earwig nymph, male earwig adult, female earwig adult, and katydid) averaged first by cage then treatment (fruit that healed and had no scarring, zeros, included).

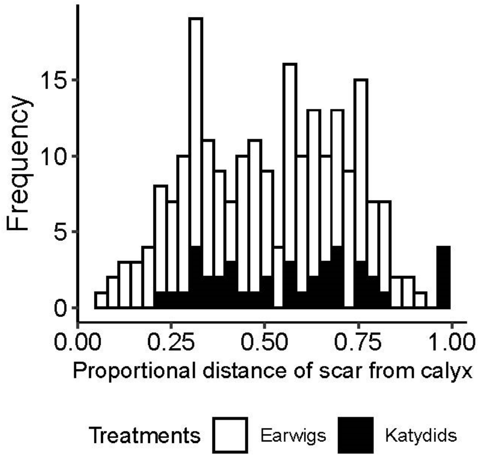

Figure 1.9. Distribution of the proportional distance of scars from the calyx for earwig and katydid damaged fruit. A proportional distance of 0 indicates feeding adjacent to the calyx, whereas a proportional distance of 1 indicates feeding directly adjacent to the style.

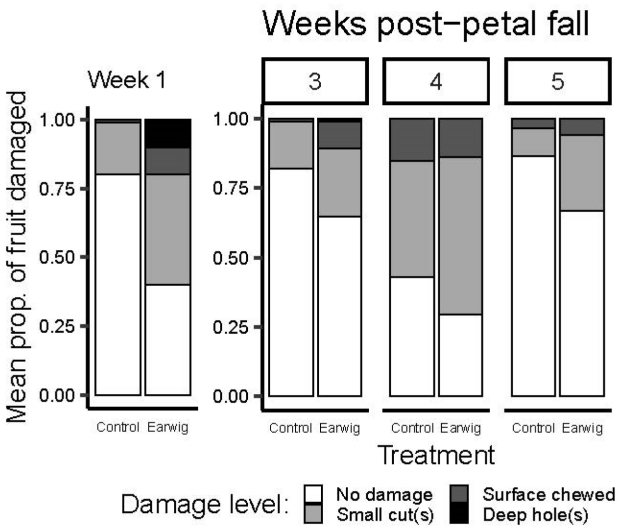

Figure 1.10. Experiment 2: Mean proportion of fruit that had each damage level (no damage, small cut(s), surface chewed, and deep hole(s)) across treatment (control and four adult earwigs) and weeks post-petal fall (3, 4, and 5) averaged first by cage and then treatment. Mean proportion damage level of fruit exposed to a single adult in Experiment 1, which was run during the 1st week post-petal fall is also shown for reference.

Appendix: Supplementary Material

Supplementary methods A1.1

Details of Bayesian (brms) analyses

Samples were drawn using No-U-Turn Sampler via rstan (Stan Development Team, 2020). All models were fit with continuing-ratio (cratio) distributions with a probit transformation. With continuing-ratio distributions ordered categories represent passing through the categories from lowest to highest, with each individual progressing through all lower categories before they go on to higher categories (Mcgowan 2000). We used weakly informative priors for all models (see model specification section below). We also ran all models with slightly different priors to confirm that model parameter estimates were not heavily influenced by prior choice. For each analysis, four models with and without category-specific effects (cs) and unequal variance were compared using Pareto smoothed importance-sampling with approximate leave-one-out cross-validation based on the posterior likelihood (“loo”; package brms; Bürkner, 2017) with (reloo=TRUE) and without (reloo=FALSE) exact cross-validation for problematic observations. We used Bürkner & Vuorre 2019 for general guidance in fitting category-specific and unequal variance models. The model with the highest average pointwise out-of-sample predictive accuracy was chosen. We confirmed chain convergence was met and that chains mixed well by examining model rhat values and trace plots.

Model specifications:

Damage after initial insect exposure in Experiment 1.

Category of worst damage: 0-no fruit damage; 1-small cut(s): distinct individual bitemark(s) chewed into fruits; 2-surface chewed: extensive and overlapping shallow chewing of the surface of the fruit; 3-deep hole(s) - a crater in the fruit from extensive feeding in one location

Treatments: no insects (control); an earwig nymph; an earwig adult female; an earwig adult male; a katydid nymph

Category-specific model:

brm(Category of worst damage[0,1,2,3]~1+cs(Treatment)+(1|Cage)+(1|Tree), family=cratio("probit"), chains=4, prior= c(set_prior("normal(0, 3)", class = "b") + set_prior("normal(0, 3)", class = "Intercept")))

Note: default prior for class=(“sd”): student_t(3, 0, 2.5)

Damage after initial insect exposure in Experiment 2.

Category of worst damage: 0-no fruit damage; 1-small cut(s): distinct individual bitemark(s) chewed into fruits; 2-surface chewed: extensive and overlapping shallow chewing of the surface of the fruit; 3-deep hole(s) - a crater in the fruit from extensive feeding in one location

Treatment: no insects (control); four earwig adults (earwig)

Week of exposure: third week post-petal fall; fourth week post-petal fall; fifth week post-petal fall

Basic model (no category-specific effects and no unequal variance)

```
brm(Category of worst damage[0,1,2,3]~1+Treatment*Week of exposure+(1|Cage)+(1|Tree),
family=cratio("probit"), chains=4, prior= c(set_prior("normal(0, 3)", class = "b") +
set_prior("normal(0, 3)", class = "Intercept")))
```

Note: default prior for class=(“sd”): student_t(3, 0, 2.5)

Calculating Custom contrasts:

Expected parameter values for proportion of each damage type for each treatment or treatment by week (for Experiment 2) were drawn 1,000 times from each model’s posterior predictive distribution. For Experiment 1, custom contrasts were made by calculating the mean posterior differences between parameters to compare damage in the combined earwig (male, female, and nymph) vs. control treatments, katydid vs. control treatments, earwig nymph vs. earwig adults (male and female) treatments, and earwig adult female vs. earwig adult male treatments for each damage type. For Experiment 2, custom contrasts compared the control and earwig treatment for each week post-petal fall. The 95% mean quantile interval for mean contrast differences were computed for each comparison. Comparisons in which quantile intervals did not contain 0 were interpreted as suggesting differences.

Table S1.1 Summary statistics of models used to analyze early fruit abscission.

	Model 1		**Model 2**		**Model 3**		**Model 4**		**Model 5**		**Model 6**		**Model 7**	
Predictors	*Statistic*	*p*	*Statistic*	*p*	*Statistic*	*p*	*Statistic*	*p*	*Statistic*	*p*	*Statistic*	*p*	*Statistic*	*p*
Intercept	2.06	**0.040**	0.97	0.334	2.09	**0.037**	5.65	**<0.001**	0.98	0.327	5.30	**<0.001**	7.62	**<0.001**
Treatment[Nymph]	-0.15	0.877	0.51	0.611	-0.15	0.883			0.55	0.581				
Treatment[Male]	0.13	0.900	0.74	0.461	0.13	0.898			0.76	0.445				
Treatment[Female]	-0.08	0.933	0.36	0.719	-0.08	0.935			0.38	0.705				
Treatment[Katydid]	1.79	0.074	2.69	**0.007**	1.95	0.052			3.14	**0.002**				
Prop. of fruit damaged	0.16	0.869	0.47	0.641			1.57	0.116			2.44	**0.015**		
Prop. of fruit removed	-2.22	**0.026**			-2.27	**0.023**	-3.09	**0.002**					-3.80	**<0.001**
Observations	372		372		372		372		372		372		372	
Marginal R^2 / Conditional R^2	0.127 / 0.129		0.112 / 0.122		0.126 / 0.129		0.085 / 0.114		0.110 / 0.123		0.053 / 0.108		0.061 / 0.106	
AIC	420.328		423.383		418.356		421.623		421.609		429.471		422.514	

Test statistic (z-value) and p-value for each included model coefficient, the number of observations, marginal and conditional R^2 values, and AIC (Akaike information criterion) for each model. Prop.: Proportion. The model within the box had the lowest AIC and was selected as the most parsimonious, informative model.

Table S1.2. Summary statistics of models used to analyze late fruit abscission.

	Model 1		Model 2		Model 3		Model 4		Model 5		Model 6		Model 7	
Predictors	*Statistic*	*p*	*Statistic*	*p*	*Statistic*	*p*	*Statistic*	*p*	*Statistic*	*p*	*Statistic*	*p*	*Statistic*	*p*
Intercept	-0.58	0.562	-0.10	0.923	-0.34	0.732	-1.95	0.052	-0.00	1.000	-2.01	**0.044**	-1.32	0.187
Treatment[Nymph]	-0.61	0.540	-0.85	0.397	-0.46	0.648			-0.63	0.531				
Treatment[Male]	-0.11	0.916	-0.25	0.803	-0.01	0.990			-0.11	0.909				
Treatment[Female]	-0.92	0.356	-0.96	0.339	-0.81	0.417			-0.84	0.400				
Treatment[Katydid]	-0.94	0.346	-1.12	0.261	0.03	0.975			-0.16	0.870				
Prop. of fruit damaged	1.84	0.066	1.75	0.080			1.73	0.083			1.57	0.116		
Prop. of fruit removed	0.91	0.360			0.64	0.520	1.01	0.313					0.51	0.610
Observations	100		100		100		100		100		100		100	
Marginal R^2 / Conditional R^2	0.085 / 0.099		0.074 / 0.077		0.024 / 0.029		0.057 / 0.086		0.018 / NA		0.043 / 0.059		0.003 / 0.027	
AIC	145.809		144.695		148.195		139.894		146.620		138.974		141.778	

Test statistic (z-value) and p-value for each included model coefficient, the number of observations, marginal and conditional R^2 values, and AIC (Akaike information criterion) for each model. Prop.: Proportion. The model within the box had the lowest AIC and was selected as the most parsimonious, informative model.

Fig. S1. The influence of damage on fruit deformity.

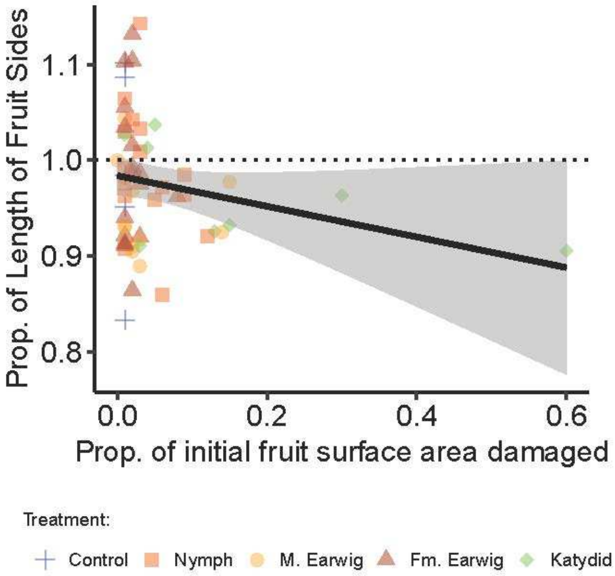

Figure S1. Ratio of the semi-perimeter (distance from calyx to style) of the side of the fruit with the most scarring damage to the semi-perimeter of the side with the least scarring damage. The line and confidence interval are linear predictions. A proportion of 1 indicates equal semi-perimeters or no clear deformity and is represented by a dashed line. Proportions significantly less than or greater than 1 indicate fruit deformity. A proportion of less than 1 indicates that the semi-perimeter for the side of the fruit with the most scarring is shorter than the semi-perimeter for the side of the fruit with the least scarring.

Chapter 2

Herbivory by European Earwigs (*Forficula auricularia*; Dermaptera: Forficulidae) on Commonly Cultivated California *Citrus* Species

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Abstract

Agricultural cultivars and species differ in susceptibility to herbivores; therefore, identifying natural resistances or tolerances to pests can be leveraged to develop preventative, integrated pest management approaches. While many *Citrus* species are grown in California, most pest management guidelines for California citrus are based upon research conducted on *Citrus sinensis* (L.) Osbeck. Previous work, however, has suggested that *Citrus* species vary in susceptibility to insect pests. Recent research has established European earwigs (*Forficula auricularia* L.; Dermaptera: Forficulidae) as herbivores of young *C. sinensis* fruit. We used field experiments to identify differences in susceptibility of *Citrus* species to European earwigs. Specifically, we tested whether three species (*C. sinensis*, *C. clementina* hort. ex Tanaka, and *C. reticulata* Blanco; Sapindales: Rutaceae) exhibit differences in: 1) feeding deterrence to earwigs; 2) suitability as food for earwigs; 3) preferential abscission of damaged fruit; and 4) healing of damaged fruit. We observed that earwigs caused heavy damage on young *C. sinensis* and *C. clementina* fruit, whereas heavy damage was rare on young *C. reticulata* fruit. A higher proportion of earwigs died when confined on *C. clementina* compared to *C. sinensis* and *C. reticulata*. There was little evidence of preferential abscission of damaged fruit and healing of seriously damaged fruit prior to harvest. Consequently, several heavily damaged *C. sinensis* and one *C. clementina* fruit were retained to harvest and developed large scars. Overall, we found that *Citrus* species vary in their susceptibility to earwigs, and pest management for earwigs should be tailored to specific *Citrus* species.

KEYWORDS: earwig, citrus cultivar, herbivory, resistance, abscission

Introduction

Plants can defend themselves against herbivory with a myriad of tactics. Natural plant resistance and tolerance to insect herbivores are two main types of strategies plant can utilize for defense, and these strategies can be leveraged to sustainably prevent economic losses due to herbivory in agriculture (Ehi-Eromosele et al. 2013, Gimenez et al. 2018). Plants can resist herbivory through natural defenses that can deter pests, reduce pest survival, or reduce pest reproduction. For instance, in response to herbivory by tobacco hornworm (*Manduca sexta* L.; Lepidoptera: Sphingidae) larvae, tomatoes have chemical arsenals that acts as antifeedants for the hornworm, reducing hornworm growth and development (Ryan 2000, Felton 2005, War et al. 2012). Lectins are produced by cowpeas as antifeedants to cowpea aphids (*Aphis craccivora*; Hemiptera: Aphididae), leading to reduced aphid survival and fecundity (Chakraborti et al. 2009). Alternatively, plants can express tolerance to herbivory by producing more tissue than is needed to maximize reproductive success or yield and selectively abscising damaged tissue, by high growth rates, by healing damaged tissue, by compensatory photosynthesis and increased growth after damage, or by having high levels carbon in the roots and shunting carbon from roots to shoots (Strauss and Agrawal 1999, Tiffin 2000, Mitchell et al. 2016). Citrus trees abscise young, developing fruit in response to damage generated by Kelly's citrus thrips (*Pezothrips kellyanus* Bagnall; Thysanoptera: Thripidae), perhaps to escape reduced fruit viability due to herbivory by reinvesting resources into nondamaged fruit (Planes et al. 2014). These strategies of resistance and tolerance often vary across crop species (Leimu and Koricheva 2006). Identifying and utilizing differences in resistance or tolerance to herbivory across crop species is an important preventative pest management strategy.

Citrus is a major agricultural crop, particularly in California, which produces 58% of the nation's citrus, contributing 72% of the national citrus value (CDFA and CASS 2020). There are several cultivated citrus species with complex, debated phylogenies (Wu et al. 2014) and chemical and morphological differences (Bocco et al. 1998, Zhang et al. 2017). Navel oranges (*Citrus sinensis* (L.) Osbeck; Sapindales: Rutaceae) and mandarins are the most common citrus crops grown in California. Mandarins are mostly composed of clementine mandarins (*Citrus clementina* hort. ex Tanaka), primarily cultivar 'Clemenules (or 'de Nules'), and "true mandarins" (*Citrus reticulata* Blanco), primarily cultivars 'Tango' and 'W. Murcott Afourer' (CDFA and CASS 2020). Citrus hosts a wide diversity of herbivores, and detailed integrated pest management guidelines have been developed for many of these herbivores in California (Grafton-Cardwell et al. 2020). However, *C. reticulata* and *C. clementina* have been increasing in acreage in California (CDFA and CASS 2020), but management guidelines are generally based on research conducted mainly in sweet oranges (*C. sinensis*), which historically dominated acreage. If other citrus species are more or less susceptible to arthropod pests, or pests behave differently in different citrus hosts, then it is possible that growers could be omitting important management practices or applying unnecessary interventions by assuming similar risk of damage by herbivores.

Recently, observational data from commercial citrus production in California's San Joaquin Valley have been used to explore differences in susceptibility to arthropod herbivores across citrus species (Cass et al. 2019a; Cass et al. 2020), finding that damage by several herbivores was lower in 'Tango' and 'Afourer' mandarins (*C. reticulata*) compared to navel oranges (*C. sinsensis*). Experiments following these observational studies confirmed substantial variation in damage by both fork-tailed bush katydids (*Scudderia furcata* Brunner von Wattenwyl; Orthoptera: Tettigoniidae) (Cass 2019b, Cass et al. 2020) and citrus thrips (*Scirtothrips citri* Moulton; Thysanoptera: Thripidae) (Mueller et al. 2019) across the three most prevalent citrus species (*C. sinensis*, *C. clementina*, and *C. reticulata*).

Responses to herbivory also appear to differ across citrus species. Selective abscission of fruit that were heavily damaged by katydids was observed to occur late in the growing season prior to harvest in *C. clementina* (Cass et al. 2021), and early in the growing season in *C. sinensis* (Kahl et al. 2021), but not in *C. reticulata*. These species also differ in the fruit scarring patterns produced in response to early-season feeding by katydids, with *C. sinensis* fruit fed on by katydids exhibiting distinctive round scars, and *C. clementina* fruit exhibiting more weblike and diffuse scars (Cass et al. 2021). This indicates that pest management approaches that were based on *C. sinensis* need to be refined for mandarins.

European earwigs (*Forficula auricularia*; Dermaptera: Forficulidae) are abundant omnivores in agricultural systems (Carroll and Hoyt 1984, Kallsen 2006, Romeu-Dalmau et al. 2012). Earwigs damage young *Citrus sinensis* fruit; fruit that sustained extensive earwig damage either abscised or developed prominent scars as they matured (Kahl et al. 2021), a likely cause of downgrading at the packinghouse and reduced grower profits. However, we do not yet know whether earwigs damage young *C. reticulata* and *C. clementina* fruit, and how that damage might manifest at harvest across these citrus species.

In this study, we conducted a series of field experiments to evaluate whether levels of resistance or tolerance differ across common cultivars of three citrus species (*C. sinensis*, *C. clementina*, and *C. reticulata*) grown in California. Specifically, we asked the following questions: (i) What are the characteristics and extent of feeding by earwigs on young fruit across the citrus species? (ii) Are some citrus species unsuitable to earwigs, resulting in earwig death? (iii) Do some species preferentially abscise damaged fruit, and does this vary across species? (iv) Can some citrus species "heal" damaged fruit, such that damage on young fruit disappears by the time of harvest?

Materials and Methods

General Background

Experiments in 2018 and 2019 were conducted to test all above questions, but all heavily damaged fruit abscised in 2018 so the experiments in 2018 only tested questions (i) and (ii). In 2018, two separate experiments were set up in a *C. sinensis* planting ("Parent Washington") and a *C. reticulata* planting (cv. "Tango") at Lindcove Research and Extension Center (LREC) in Lindcove (36.360895, -119.062348), Tulare County, CA. In 2019, three separate experiments were set up in *C. sinensis* (cv. "Old Line Washington"), *C. clementina* (cv. "de Nules" and "Fina sodea"), and *C. reticulata* (cv. "Tango") plantings at LREC. Petal fall is the time at which ~75% of petals have dropped from citrus flowers in the region, and is used as the date of the beginning of fruit development in these experiments; petal fall was declared on April 24th, 2018 and April 29th, 2019 by the Tulare County Agricultural Commissioner.

Earwig collection and rearing

Earwigs were collected from wraps on young citrus trees of mixed species at LREC. In 2018 we collected earwigs directly before experimental setup on May 8th, and in 2019, we collected from March 27th to April 19th. In 2019, earwigs were subsequently reared in plastic containers with mesh lids lined with potting soil and fed lettuce and ground dry dogfood (Purina

ALPO Come & Get It! Cookout Classics, Vevey, Switzerland), as described in Kahl et al. (2021), until experimental setup.

Damage initiation

In 2018, the experiments in *C. sinensis* and *C. reticulata* were initiated on May 8th (14 days post-petal fall), and in 2019 the experiments in *C. sinensis* and *C. reticulata* were initiated on May 2nd (three days post-petal fall) and the experiment in *C. clementina* was initiated on May 3rd (four days post-petal fall). In 2018, we choose three ~20 cm long branch terminals with 4 to 20 fruit on each of 10 trees, totaling 172 *C. sinensis* and 334 *C. reticulata* fruit. In 2019, we choose four ~20 cm long branch terminals with 3-20 young fruit on each of 12 trees, totaling 267 *C. sinensis*, 268 *C. clementina*, and 649 *C. reticulata* fruit. In the *C. clementina* block, six trees were cultivar “de Nules” and six were cultivar “Fina sodea”. “Fina sodea” and “de Nules” are common *C. clementina* cultivars and were used in a previous study involving katydid feeding on *C. clementina* (Cass et al., 2020). For both years in all blocks, we recorded the number of fruit on each branch terminal and attached a 19-liter (5 gallon) mesh paint strainer bag enclosure to contain the treatment to each branch terminal. In 2018, each tree received one replicate of each of three treatments: a (i) no insects (control), (ii) an earwig nymph (mixed instars), or (iii) an earwig adult (mixed sexes). In 2019, we established two replicates of two treatments on each tree: either (i) control (no insect) or (ii) earwigs (two earwig nymphs). In 2018, earwig nymphs were observed to cause more damage than earwig adults. Thus, in 2019 two earwig nymphs were chosen to produce realistic but high levels of damage, in the hopes of increasing the number of damaged fruit at harvest and obtaining a better representation of fruit damage morphology.

Damage assessment

On May 15th in 2018 (seven days after insects were caged), and on May 8th-9th in 2019 (six days after insects were caged), bags and enclosed insects were removed from branch terminals and the numbers of fruit abscised (lying at the bottom of the bag) and still present on terminals were recorded. In 2018, 80 *C. sinensis* and 95 *C. reticulata* fruit and in 2019, 72 *C. sinensis*, 51 *C. clementina*, and 147 *C. reticulata* fruit abscised during treatment exposure or abscised during handling and were excluded from analysis. In 2018 in both the *C. sinensis* and the *C. reticulata* experiment one earwig nymph was accidentally not released into the enclosure; these were treated as control treatments. The numbers of earwigs alive, dead, or missing in the bag were recorded. To assess earwig survival, proportions of earwigs dead out of total earwigs found (dead or alive) after the trial were calculated for each species and year. We then measured the proportion of each of three increasingly severe damage categories of fruit damage: (1) small cut(s) - distinct individual bitemark(s) chewed into fruits, (2) surface chewed - extensive and overlapping surface-level chewing on fruit, and (3) deep hole(s) - a crater in the fruit from extensive feeding in one location. These damage categories have been used in other studies of katydid and earwig damage in citrus (Cass et al. 2019b, Cass et al. 2021, Kahl et al. 2021). We found that when herbivores chew small cuts the resulting damage is often not noticeable at harvest, but surface chewing and deep holes are serious damage types leading to scarring at harvest (Cass et al. 2019b, Cass et al. 2020; Kahl et al. 2021). We also calculated each fruit's total proportion of surface area damaged by summing proportions across all damage categories.

Monitoring & Harvest

It can be challenging to follow citrus fruit to harvest, because often >90% of undamaged immature citrus fruit abscise shortly after fruit set (Goren 1993, Cass et al. 2019b). In 2018 all heavily damaged fruit abscised; the lightly damaged remaining fruit were not monitored to harvest. Our previous work with herbivory on *C. sinensis* showed that removal of undamaged fruit decreases the abscission of damaged fruit, thereby improving our ability to evaluate fruit scarring at harvest in *C. sinensis* (Kahl et al. 2021). Therefore in 2019 for half (six) of the selected trees in each plot we removed all non-damaged fruit on the experimental branch terminals after bags were removed, so that we could retain more damaged fruit to harvest. On the remaining six trees we did not remove any fruit, allowing us to quantify the natural rate of abscission. For *C. clementina*, three trees for each of the two cultivars had all non-damaged fruit removed. We affixed a numbered tag to the stem of each fruit to track the fruit across the growing season.

In 2019, on June 13 (45 days post-petal fall), August 8 (113 days post-petal fall), October 16, 2019 (169 days post-petal fall), and February 3, 2020 (harvest; 280 days post-petal fall) we checked whether each fruit remained on the branch terminal or had abscised. At harvest, all remaining fruit were removed from the tree, and we measured the maximum length and width of every scar using digital calipers to calculate the surface area of each scar (estimated as a rectangle). To calculate fruit surface area (estimated as a spheroid), we measured the polar and equatorial diameters using wide-arm calipers. The proportion of fruit surface area scarred was calculated by summing the area of all scars on each fruit and then dividing by the total fruit surface area. To estimate the potential of fruit to heal early-season damage, we derived the proportion of fruit with a particular category of damage present immediately after cages were removed that did not have any scarring at harvest.

Statistical Analyses

All analysis was done using R version 4.0.2 (R Core Team 2020); we used the package *tidyverse* to manipulate and summarize data (Wickham et al. 2019). Statistical analyses were used to compare insect treatments and controls, but comparisons across species were not statistically assessed because different citrus species were in different blocks managed differently.

Initial Damage Category. To assess the severity of damage caused by earwigs on young fruit, we analyzed treatment impacts on the most severe initial damage category present on a given fruit (small cut(s), surface chewed, and deep hole(s)) for both the 2018 and 2019 experiments. Data were analyzed with Bayesian regression models using *Stan* to capitalize on its versatility in fitting multilevel models (*brm*; package brms; Bürkner 2017, Bürkner and Vuorre 2019). Separate models were fit for the experiments in *C. sinensis*, *C. clementina*, and *C. reticulata* for each year. A continuing ratio (cratio) family was used with a probit transformation, because each individual fruit can be considered to have passed through damage types from lower to higher categories (Mcgowan 2000). Treatment was a fixed effect in all models, and cultivar was included as a fixed effect in the models for *C. clementina*. For the 2018 experiments, only tree was a random effect due to the smaller sample size, but for the 2019 experiments, tree and cage were random effects. For each experiment, we fit four models with and without category-specific effects and with and without unequal variance. We compared the models using Pareto smoothed importance-sampling with approximate leave-one-out cross-validation based on the posterior likelihood (*loo*; package brms; Bürkner 2017). Models with the highest expected log predictive density (elpd_diff=0) were selected as the best model (Vehtari et al. 2017). For all models weakly informative priors were used (p(α)=N(0,3), p(β)=N(0,3), and p(*disc*, β)=N(0,1) for unequal variance models) to improve model convergence (Supp. Methods A2.1). Expected parameter values were obtained by extracting 1,000 posterior parameter values for the earwig and control treatments, taking the difference, and calculating the 95% Mean Quantile Intervals (95% QI) of the mean differences. Quantile intervals are an effect size estimate based on each models' posterior parameter distributions. Quantile intervals that exclude 0 suggest a difference between the earwig and control treatments.

Initial Damage Size. Treatment impacts on the total proportion of initial fruit surface area damaged was modeled with generalized linear mixed models (GLMM) using template model builder (*glmmTMB*; package glmmTMB; Brooks et al. 2017) for each experiment for both 2018 and 2019 experiments. Treatment was a fixed effect, and cage and tree were treated as random effects. Cultivar was included as a fixed effect in the model for the *C. clementina* experiment. Because the responses were proportions, models were fit with beta distributions. Typically, beta distributions do not include 0 or 1, and in this case every experiment had more than 50% of fruit with no damage. Thus, we fit these models with a zero-inflation component with treatment as a fixed effect, and assessed: 1) if treatments differ in whether feeding occurred ("zi"; zero-inflated component) and 2) if feeding did occur, whether there were differences in extent of feeding across treatments ("cond"; conditional component). This first question is also assessed in the analysis of the initial damage category above. The significance of model effects was determined using analysis of deviance Type II Wald Chi-square tests (*Anova*; package car; Fox & Weisberg, 2019) for both the continuous and zero-inflated model components.

Fruit abscission. To test whether the amount of fruit removal impacted fruit abscission for the 2019 experiments we only analyzed trees in which undamaged fruit were removed and we used mixed effects Cox models (*coxme*; package coxme; Therneau 2019) with proportion of fruit removed from the terminal as a fixed effect and tree and cage as random effects. To test whether damage extent and insect-exposure impacted fruit abscission for the 2019 experiments, we only analyzed trees without fruit removal and we used mixed effects cox models (*coxme*; package coxme; Therneau 2019) with initial fruit surface area damaged per fruit and treatment as fixed effects and tree and cage as random effects. Cultivar was included as a fixed effect for the model for the experiments with *C. clementina*. Cox mixed effect models also explicitly consider the time of abscission. Since treatment and damage extent are correlated, we calculated the Generalized Variance Inflation Factors (GVIFs) using *vif* (package car; Fox & Weisberg, 2019, Fox and Monette 1992). Only low collinearity was detected ($\mathrm{GVIF}^{\frac{1}{2*df}} < 3.3$), thus we could interpret all factors together in the model (Kock and Lynn 2012). We again used Type II Wald Chi-square tests (*Anova*; package car; Fox & Weisberg, 2019) to assess the significance of model effects.

Damage at harvest. The area of fruit surface scarred at harvest was analyzed using Wilcoxon rank sum nonparametric tests (*wilcox.test*; package stats; R Core Team 2020) for each experiment, because the distributions of scar size were non-normal.

Results

2018 Experiments

Early Damage in *Citrus sinensis*.

After seven days of exposure to earwigs (at initial fruit evaluation), there was considerable serious damage (surface chewed and deep holes) on the fruit in the earwig treatment (Fig. 2.1A-B; Fig. 2.2A). Averaging branches exposed to earwig nymphs and adults, ~19% of fruit were damaged. Only 3.3% of fruit in the control treatment were damaged, likely due to branch rubbing and rare events of background herbivory. The basic (without damage category-specific effects and without unequal variance) ordinal model was selected as the best model. The earwig nymph treatment had smaller proportions of fruit with no damage (95% Mean Quantile Interval (95% QI): 0.15-0.32) and slightly larger proportions of fruit with serious damage (95% QI: 0-0.06 and 0.01-0.26 for fruit with surface chewed and deep hole damage, respectively) than the control treatment (Fig. 2.2). The earwig adult treatment produced intermediate levels of damage compared to the control and nymphal earwig treatments, but did not differ from either (95% QIs overlapped 0).

Fruit with small cuts had an average of ~2% damage (range: 1-2%), fruit with surface area chewed had an average of ~2.5% damage (range: 2-3%), and fruit with deep holes had an average of ~14.4% damage (range: 4-40%). Proportion of fruit surface area damaged significantly differed between treatments because whether fruit were fed on differed across treatment; the zero-inflated component was marginally significant (X^2=5.83, df=1, *P*=0.05; Fig. 2.2A, Fig. 2.3A) but the conditional component was not significant (X^2=1.26, df=2, *P*=0.53). The control treatment had marginally more fruit with no damage than the earwig nymph treatment (β=2.4, df=83, t=2.19, *P*=0.08).

Early Damage in *Citrus reticulata*

In the 2018 experiments, there were few *C. reticulata* fruit with serious damage (Fig. 2.2B). In *C. reticulata*, only ~3% of fruit in the control were damaged; whereas in the earwig treatments (average of earwig nymphs and adults) ~6% of fruit were damaged. Only two fruit exposed to earwig nymphs had surface chewed damage and none had deep holes. The damage category-specific model was the best fit. Fruit from the earwig nymph treatment had more extreme damage than those exposed to earwig adults and the control. Compared to the no insect control, the earwig nymph treatment had slightly smaller proportions of fruit with no damage

(95% QI: 0.01-0.16) and slightly larger proportions of fruit with small cuts (95% QI: 0.02-0.14). Compared to the earwig adult treatment, the earwig nymph treatment had slightly smaller proportions of fruit with no damage (95% QI: 0.02-0.17), and slightly larger proportions of fruit with small cuts (95% QI: 0-0.13), and slightly larger proportions of fruit with surface chewed (95% QI: 0-0.07).

Fruit with small cuts had an average of 1.5% damage (range 1-5%). Fruit with surface chewed had an average of ~7.7% damage (range 3-10%). Only one fruit had a deep hole. That fruit was from the control treatment and had 10% damage. Treatments differed in whether fruit were fed on and the amount of feeding; there were significant treatment differences for both the zero-inflated component (X^2=6.17, df=2, *P*=0.05; Fig. 2.2B, Fig. 2.3B) and the conditional (X^2=19.79, df=2, *P*<0.001; Fig. 2.3B). While there was no significant pairwise differences for whether feeding occurred (zero-inflated component), the control had more damaged area than the earwig nymph (β=1.51, df=230, t=4.08, *P*=0.0002) and adult treatment (β=1.95, df=230, t=3.15, *P*=0.005); this was due to two fruit with high levels of background damage.

2019 Experiments

Early Damage in *Citrus sinensis*

After six days of exposure to earwigs, several fruit had serious damage (Fig. 2.1A-B; Fig. 2.4A). Less than 15% of fruit in the control treatment were damaged, whereas 80% of fruit in the earwig treatment had some damage. The basic model had the best fit. Compared with the control treatment, the earwig treatment had smaller proportions of fruit with no damage (95% QI: 0.55-0.84), and larger proportions of fruit with small cuts (95% QI: 0.02-0.29), surface chewed (95% QI: 0.08-0.28), and deep holes (95% QI: 0.19-0.56).

Fruit with small cuts had an average of ~1% damage (range: 1-5%). Fruit with surface chewed had an average of ~9% damage (range: 2-40%). Fruit with deep holes had an average of ~16% damage (range: 2-55%). Fruit in the earwig treatment were both more frequently damaged and had higher proportions of surface area damaged compared to the control. There were significant differences between the control and earwig treatment for both the conditional component (X^2=4.1, df=1, P=0.04; Fig. 2.5A) and the zero-inflated component (X^2=66.92, df=1, P<0.001).

Early Damage in *Citrus clementina*

At initial fruit evaluation, more serious damage to the fruit was observed in the earwig treatment than the control (Fig. 2.1C-D; Fig 4B). In the control treatment ~8% fruit were damaged, whereas ~60% of fruit in the earwig treatment had some damage. The model with the best fit contained category-specific effects. Compared with the control treatment, the earwig treatment had smaller proportions of fruit with no damage (95% QI: 0.32-0.78) and larger proportions of fruit with small cuts (95% QI: 0.19-0.56), surface chewed (95% QI: 0.01-0.33), and deep holes (95% QI: 0-0.28). Cultivar had minimal effect on proportions of fruit in each damage category (QIs overlapped 0).

Fruit with small cuts had an average of ~2% damage (range: 1-10%), fruit with surface area averaged ~12% damage (range: 2-30%), and fruit with deep holes averaged ~39% damage (range: 10-98%). Fruit in the earwig treatment had more fruit damaged but not higher proportions of surface area damaged compared to the control. There was a significant difference the zero-inflated component (X^2=50.5, df=1, P<0.001; Fig. 2.5B), but not in the conditional component (P=0.20). Cultivar was not significant for the conditional (X^2=0.81, df=1, P=0.37) or zero-inflated comp (X^2=0.68, df=1, P=0.68).

Early Damage in *Citrus reticulata*

In the control treatment ~12% of fruit were damaged, whereas ~46% of fruit in the earwig treatment had some damage (Fig. 2.4C). Only a small proportion, ~9%, of evaluated fruit sustained serious damage (surface chewed and deep hole(s)), and the deep holes on five *C. reticulata* fruit were relatively small (Fig. 2.1E-F). The basic model had the best fit. Compared with the control treatment, the earwig treatment had smaller proportions of fruit with no damage (95% QI: 0.25-0.52), larger proportions of fruit with small cuts (95% QI: 0.21-0.43), and slightly larger proportions of fruit with surface chewed (95% QI: 0.02-0.09) and deep holes (95% QI: 0-0.03).

Fruit with small cuts had the least damage with an average of ~2% damage (range: 1-25%), fruit with surface chewed averaged ~15% damage (range: 2-70%), and fruit with deep holes averaged ~12% damage (range: 7-20%). Fruit in the earwig treatment were both more frequently damaged and had slightly higher proportions of surface area damaged compared to the control. There was a significant treatment difference for the zero-inflated component (X^2=62.30, df=1, P<0.001), and marginally significant difference for the conditional component (X^2=2.92, df=1, P=0.09; Fig. 2.5C).

Earwig Death

In 2018 during the 7-day caging treatment, 25% (two out of eight) nymphs died in *C. sinensis*, and ~11% (one out of nine) nymphs died in *C. reticulata*. Earwig adults did not die in either species. In 2019 during the 6-day caging treatment, death of earwig nymphs was relatively low in *C. sinensis* and *C. reticulata* with only ~3% (1 out of 39), and ~5% (2 out of 43) found dead, respectively. However, in *C. clementina* ~24%, 10 out of 41 earwigs, were found dead at the end of the treatment exposure period.

Abscission

In 2019 abscission of fruit was high for all citrus species, with 82.2% of *C. sinensis*, 88.9% of *C. clementina*, and 95.3% of *C. reticulata* fruit abscising overall between the removal of cages and harvest. For all experiments, across all predictors (treatment, proportion of initial total fruit surface damaged, proportion of fruit removed, and cultivar for the *C. clementina* models) only the proportion of fruit removed from branch terminals for *C. reticulata* was a significant predictor of abscission rate (X^2=4.91, df=1, *P*=0.03). High fruit removal (defined here as removal of ≥50%) reduced the risk of abscission in comparison to low or moderate fruit removal (Fig. S2.1). Without any fruit removal (under natural abscission), abscission of fruit with deep holes was actually lower than abscission of undamaged fruit for *C. sinensis* (deep holes: ~71% vs. undamaged: 89%). While for *C. clementina* all fruit with deep holes abscised compared to 88% of fruit without damage, but there were only three *C. clementina* fruit with deep holes.

Damage and Healing Assessment at Harvest for *Citrus sinensis*

When the 2019 experiment was harvested in February of 2020, more than half of the remaining *C. sinensis* fruit from the earwig treatment initially had deep holes, whereas the remaining fruit from the control initially had small cuts or no damage (Fig. 2.6A). *C. sinensis* fruit that initially had small cuts had hardly noticeable scarring at harvest (Fig. 2.7A) or had no evident scarring (for one of eight fruit that initially had small cuts). Scarring was evident on the one fruit remaining that initially had surface chewed. All *C. sinensis* fruit that initially had deep holes developed large scars at harvest that were often rectangular and sometimes had branching edges (Fig. 2.7D). There was a marginal difference in total proportion of fruit surface scarred between the earwig and control treatments (W = 88.5, *P* = 0.07; Fig. 2.9A;).

Damage at Harvest and Healing Assessment at Harvest for *Citrus clementina*

No *C. clementina* fruit that initially had deep holes were retained to harvest. The earwig treatment but not the control retained fruit that initially had surface chewed damage (Fig. 2.7B). Similar to what was found for *C. sinensis*, *C. clementina* fruit that initially had small cuts only had small scars that were hardly noticeable at harvest (Fig. 2.7B) or no noticeable scarring (for two out of the five fruit). One out the three *C. clementina* fruit that initially had surface chewed had no scarring present at harvest, and two out of three with surface chewed developed scars. One of them developed a large, crescent-shaped and branching scar (Fig. 2.7E). The other only had small scars at harvest. There was no significant difference in the proportion of fruit scarred between the earwig and control treatments (W=36, *P*=0.18; Fig. 2.9B;).

Damage and Healing Assessment at Harvest at Harvest for *Citrus reticulata*

Only one *C. reticulata* fruit that initially had deep holes and one that had surface chewed were retained to harvest from the earwig treatment (Fig. 2.6C). All *C. reticulata* fruit, no matter the initial damage on fruit, had only small (Fig. 2.7C&F) or no scarring. Out of the eight fruit that initially had small cuts at harvest, three had no clear scarring. There was no significant difference in the proportion of fruit surface area scarred between the earwig and control treatment (W=16, *P*=0.39; Fig. 2.8C).

Discussion

In this study, earwigs fed extensively on *C. sinensis*, producing damage in the form of fruit surface chewing and deep holes. Earwig-damaged *C. sinensis* fruit developed scars and several remained at harvest. In contrast, few *C. reticulata* fruit were seriously damaged by earwigs, leading to minimal fruit scarring at harvest. On *C. clementina*, earwigs caused intermediate damage, and many earwigs died when confined onto *C. clementina* fruit in comparison to earwigs confined on *C. reticulata* and *C. sinensis.* There was only one *C. clementina* fruit exposed to earwigs with severe scarring at harvest. There was no evidence for selective abscission of damaged fruit, and most fruit with serious damage caused by earwigs were not able to heal for any of the citrus species. Because the different citrus species were located in different blocks, these descriptive species comparisons should be interpreted with caution. However, findings from this study are generally supported by other studies (Cass, Grafton-Cardwell, et al. 2019b, Mueller et al. 2019, Cass et al. 2021 unpubl. ms.).

Our current findings reinforce a previous study that also concluded that earwigs can severely damage *C. sinensis* fruit soon after petal fall, leading to scars on fruit at harvest (Kahl et al. 2021). In both studies nymphs were more damaging than adults to *C. sinensis* fruit. This present study confirms that earwigs damage *C. sinensis* fruit, and suggests that herbivory by earwigs varies considerably across citrus species. *Citrus reticulata* fruit had generally minimal damage at harvest. Previously, it was also found that fork-tailed bush katydids also chew into and heavily damage *C. sinensis* fruit but left mostly only small bite marks on *C. reticulata* fruit (Cass et al. 2019b). These studies suggest that herbivores are tasting but not ingesting and then rejecting *C. reticulata* fruit, leading to only minimal damage. Fewer *C. reticulata* fruit were scarred by thrips compared to *C. sinensis* fruit as well (Mueller et al. 2019).

The present study found moderate levels of damage caused by earwigs on *C. clementina* fruit. Thrips scarring was also found to be intermediate on *C. clementina* in comparison to *C. sinensis* and *C. reticulata* (Mueller et al. 2019). Katydids, in contrast, were found to cause high proportions of serious damage to *C. clementina* fruit (Cass et al. 2021). In this current study, fruit damage by earwigs did not differ across *C. clementina* cultivar. A previous study found that fruit damage by katydids also did not differ across *C. clementina* cultivar (Cass et al. 2021). In the present study we found that many earwigs died when confined on *C. clementina* in comparison to *C. reticulata* and *C. sinensis*. Fork-tailed bush katydids also died faster when feeding on *C. clementina* in comparison to *C. sinensis*, although the death rate was fastest and survival lowest on *C. reticulata* (Cass et al., unpubl. ms.). It may be that, unlike with *C. reticulata*, earwigs do not avoid feeding on *C. clementina*, but that *C. clementina* is a poor food source or toxic for earwigs. However, because *C. clementina* only had a moderate proportion of earwig-damaged fruit initially and abscission of *C. clementina* fruit was high, only one fruit with a large, prominent scar was retained to harvest. Thus, more research on *C. clementina* is needed to determine whether *C. clementina* is truly toxic to herbivores and to get a better representation of the morphology of earwig-generated scars on *C. clementina* fruit.

Feeding deterrence and toxicity to herbivores of some citrus species could be due to chemical or morphological differences between these species. The volatile chemical profiles of mature fruit of these species have been shown to differ, with loose-skin mandarins (including *C. reticulata* and *C. clementina*) containing more terpenoids that often play a role in plant defense against herbivory (Wink 1988). There may also be differences in rind morphology, including hardness or density of oil glands. Previous research has shown significant differences in rind morphology and oil gland eruption in mature fruit across citrus species and cultivar (Montero et al. 2012). Although these studies on the chemistry of citrus fruit rind and fruit rind morphology were done on mature fruit, these differences may also be present in developing fruit. More research is needed to assess which factors moderate feeding by herbivores on young citrus fruit.

There was no evidence for preferential abscission of damaged fruit or in response to earwig treatment. This is consistent with a previous study in which abscission was not increased for *C. sinensis* fruit exposed to earwigs (Kahl et al. 2021). We expected fruit removal to increase the retention of the remaining fruit as the tree redirected resources, but this was only observed for *C. reticulata*. In contrast to the present study, the proportion of fruit removed was shown to have a strong effect on *C. sinensis* fruit retention (Kahl et al. 2021). The variable effects of fruit removal on abscission of *C. sinensis* fruit seen between studies could possibly be explained by differences in statistical power (the previous study had a higher sample size). Alternatively, the damage may not be extreme enough (in size or depth) to trigger fruit abscission by the plant. Katydids that caused more extreme damage were included in Kahl et al. 2021. Nonetheless, both studies suggest that on *C. sinensis* earwigs chew deep holes into fruit that can cause economically significant damage. *C. clementina* fruit with deep holes chewed by earwigs may preferentially abscise as all *C. clementina* fruit with deep holes abscised, but more research is needed because there were only three *C. clementina* fruit with deep holes. Tolerance to earwig damage through selective fruit abscission is not strongly supported in this study for any of the citrus species.

Our study produced little evidence that fruit of any of the tested *Citrus* species can heal serious damage generated by earwigs. Citrus fruit can completely recover from small bite marks by herbivores, and in one case recovered from surface chewed damage. However, when exposed to extensive damage, if retained, the fruit typically develops large scars. If *C. sinensis* and *C. clementina* fruit are exposed to earwig herbivory early in the growing season, because selective abscission and healing likely does not occur, the generated damage will likely lead to downgrading of fruit at the packinghouse.

Damage caused by earwigs differed across citrus species. Earwigs appear to be important herbivores on *C. sinensis* fruit. Earwigs caused moderate damage on *C. clementina* fruit as well, suggesting that earwigs are likely pests of *C. clementina* fruit. However, very few *C. clementina* fruit remained to harvest and more research is needed on the impacts of earwigs on *C. clementina* fruit. In contrast, earwigs mostly only generated small scars on *C. reticulata* fruit, making earwigs non-pests on *C. reticulata*. This work advances knowledge of differential susceptibility to herbivores across citrus species and complements previous research that found that *C. reticulata* can resist herbivory by katydids (Cass et al. 2019b) and, to some degree, citrus thrips (Mueller et al. 2019). This study suggests that species-specific management guidelines are needed for earwigs in citrus. A species-specific management approach would allow growers to avoid unnecessary pesticide sprays, as pesticides are likely not needed for earwigs on *C. reticulata*.

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Figures

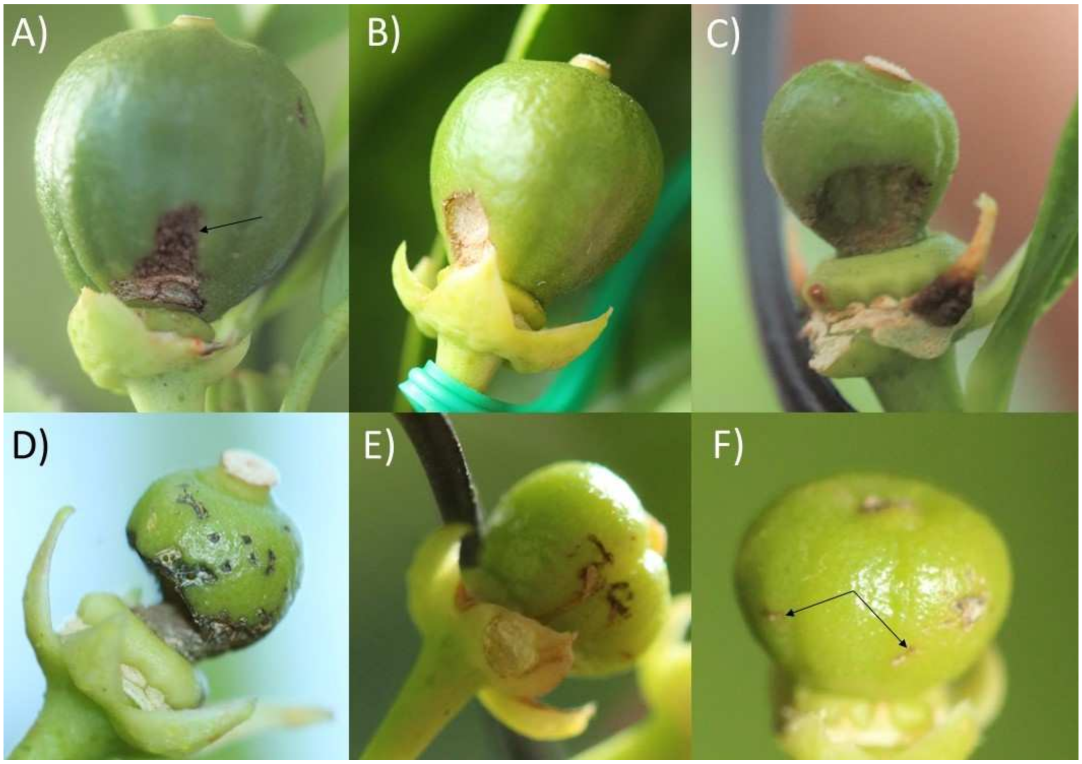

Figure 2.1. Examples of deep holes chewed into *Citrus sinensis* (A-B), *Citrus clementina* (C-D), and *Citrus reticulata* (E-F) fruit after exposure to two earwig nymphs for six days. Arrows also point out surface chewed damage (A; above deep hole) and small cuts (F).

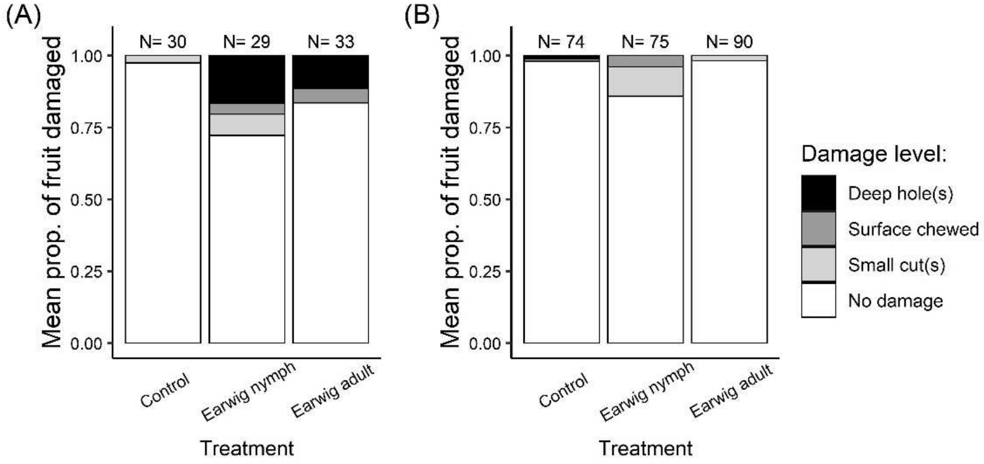

Figure 2.2. 2018: Mean proportion of fruit at each damage level (none, small cut(s), surface chewed, and deep hole(s)) across insect treatments (Control: no earwig; Earwig nymph: one earwig nymph; Earwig adult: one earwig adult) in A) *Citrus sinensis* and B) *Citrus reticulata*. Means were calculated by averaging first by cage and then by treatment. Treatment sample sizes are given above each bar.

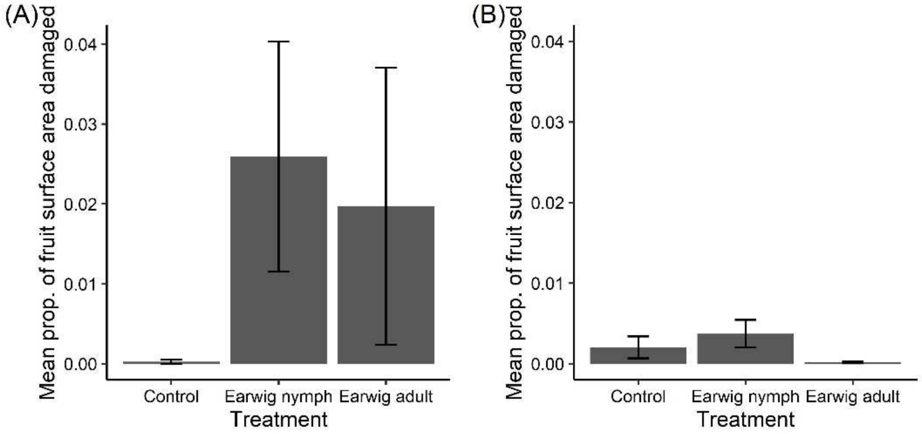

Figure 2.3. 2018: Mean and standard error of proportion of total fruit surface damaged across treatments (Control: no earwig; Earwig nymph: one earwig nymph; Earwig adult: one earwig adult) at initial fruit evaluation in A) *Citrus sinensis* and B) *Citrus reticulata*. Means were calculated by averaging first by cage, and then by treatment (fruit with no damage, zeros, included in mean calculations).

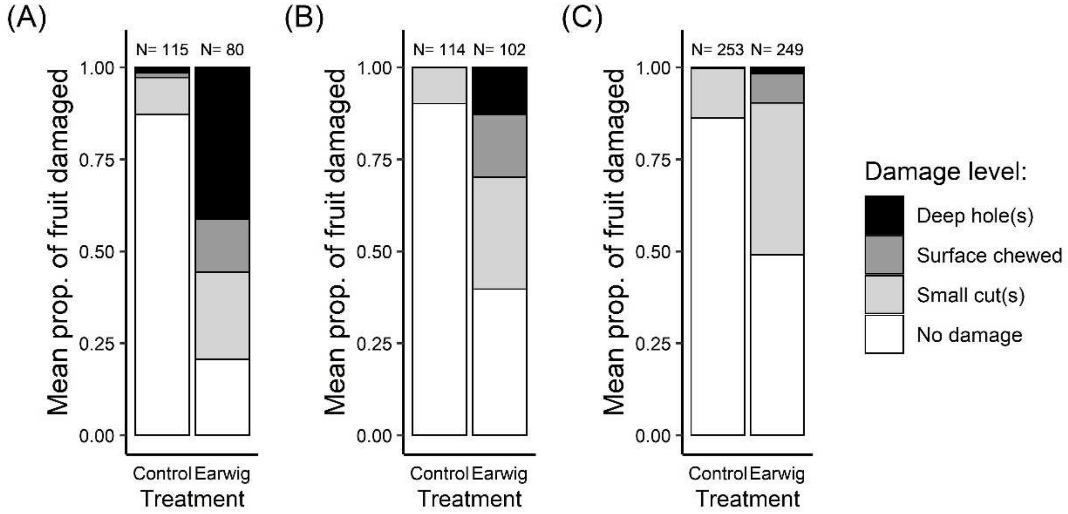

Figure 2.4. 2019: Mean proportion of fruit at each damage level (none, small cut(s), surface chewed, and deep hole(s)) across insect treatments (Control: no earwig; Earwig: two earwig nymphs) in A) *Citrus sinensis*, B) *Citrus clementina*, and C) *Citrus reticulata*. Means were calculated by averaging first by cage then across replicates within tree and then by treatment. Treatment sample sizes are given above each bar.

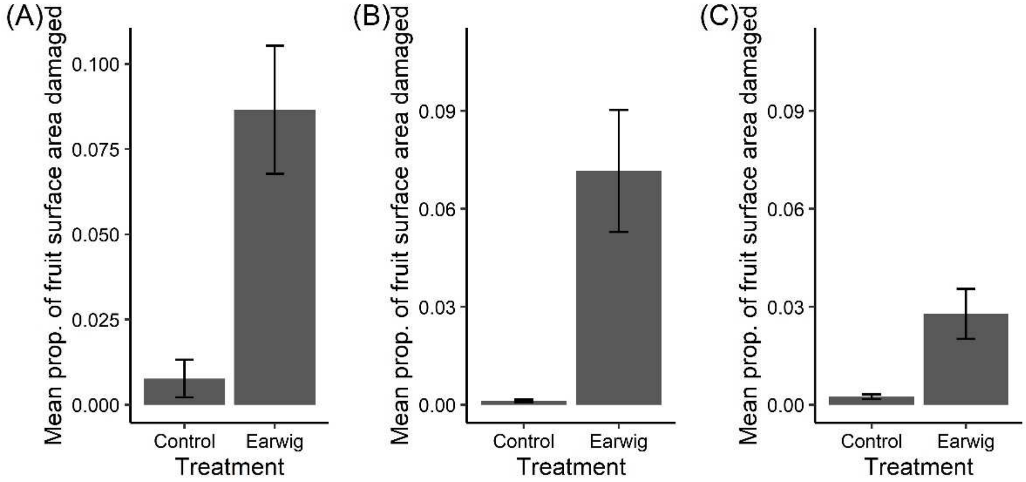

Figure 2.5. 2019. Mean and standard error of proportion of total fruit surface damaged across treatments (Control: no earwig; Earwig: two earwig nymphs) at initial fruit evaluation in A) *Citrus sinensis*, B) *Citrus clementina*, and C) *Citrus reticulata*. Means were calculated by averaging first by cage, then across replicates within tree and then by treatment (fruit with no damage, zeros, included in mean calculations).

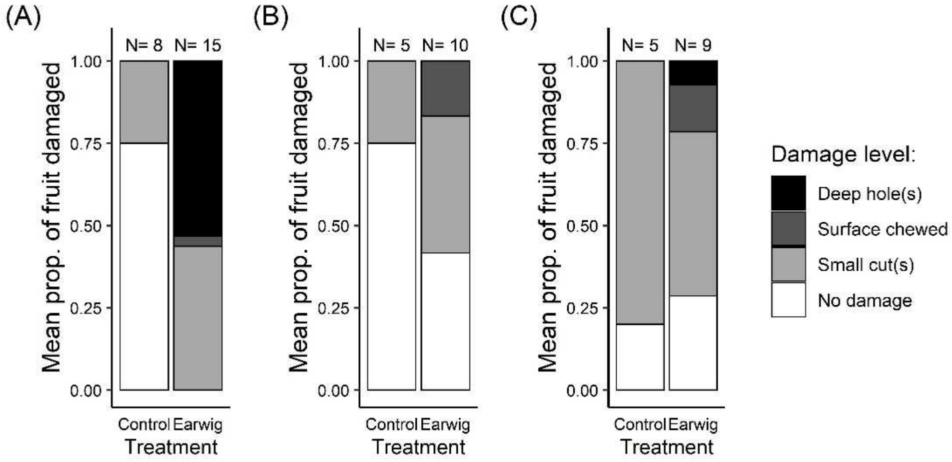

Figure 2.6. Mean proportion of fruit remaining to harvest of each initial damage level category (none, small cut(s), surface chewed, and deep hole(s)) across treatment (Earwig: two earwig nymphs; Control: no earwig) for A) *Citrus sinensis*, B) *Citrus clementina*, and C) *Citrus reticulata*. Means were calculated by averaging first by cage then across replicates within tree and then by treatment. Treatment sample sizes are given above each bar.

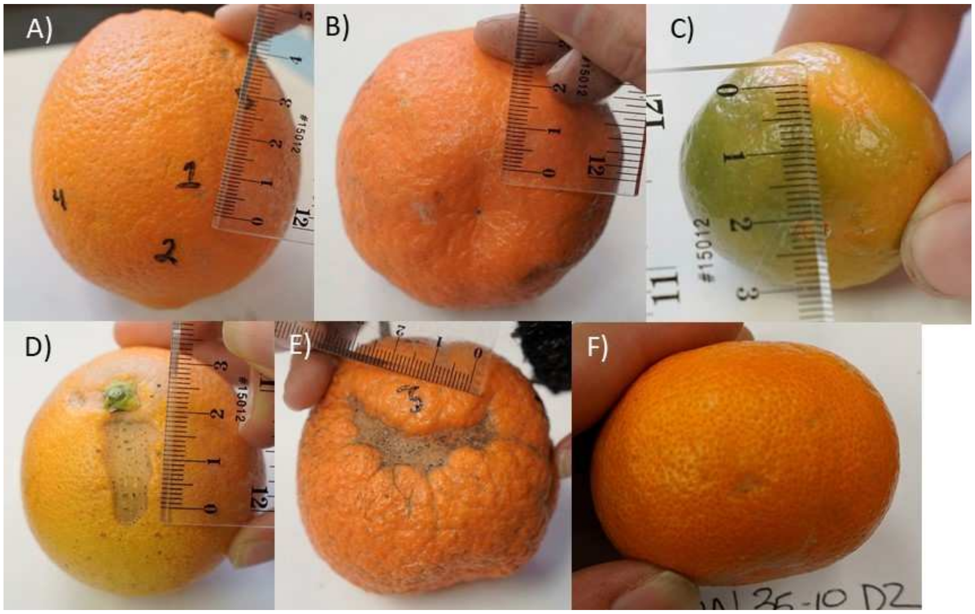

Figure 2.7. Examples of the appearance of damaged fruit at harvest and descriptions of initial damage evaluations. A-C represent fruit that originally had only small cuts. D-F represent fruit that initially had some serious damage (surface chewed or deep holes). A) *Citrus sinensis* fruit that initially had 1% small cut damage. B) *Citrus clementina* fruit that initially had 2% small cuts. C) *Citrus reticulata* fruit that initially had 5% small cut damage. D) *Citrus sinensis* fruit that initially had 2% surface chewed and 2% deep hole damage. This fruit is the same fruit displayed in Figure 1A, matured. E) *Citrus clementina* fruit that initially had 10% small cuts and 20% surface area damage. F) *Citrus reticulata* fruit that initially had 5% small cuts and 2% deep hole damage.

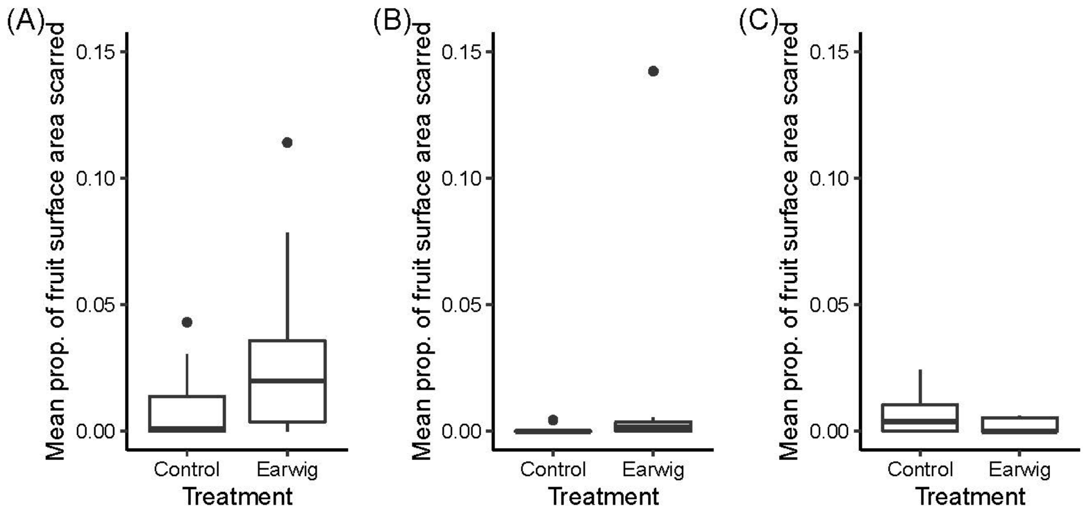

Figure 2.8. Boxplot showing median and interquartile range of proportion of fruit scarred at harvest across treatment (Control: no earwig; Earwig: two earwig nymphs) for A) *Citrus sinensis*, B) *Citrus clementina*, and C) *Citrus reticulata*.

Supplementary Methods A2.1

Details of Bayesian (brms) analyses

Samples were drawn using No-U-Turn Sampler (NUTS) No U-Turn extension and the Hamiltonian Monte Carlo algorithm via rstan (Stan Development Team, 2020).

<u>*Model specifications:*</u>

Category of worst damage: 1-no fruit damage; 2-small cut(s): distinct individual bitemark(s) chewed into fruits; 3-surface chewed: extensive and overlapping shallow chewing of the surface of the fruit; 4-deep hole(s) - a crater in the fruit from extensive feeding in one location

Treatments: no insects (control); an earwig nymph; an earwig adult

Damage on C. sinensis fruit 2018.

Basic model:

```
brm(Category of worst damage[1, 2, 3, 4]~1+ Treatment+(1|Tree), family=cratio("probit"), chains=4, prior= c(set_prior("normal(0, 3)", class = "b") + set_prior("normal(0, 3)", class = "Intercept")))
```

Damage on C. reticulata fruit 2018.

Category-specific model:

```
brm(Category of worst damage[1, 2, 3, 4]~1+ cs(Treatment)+(1|Tree), family=cratio("probit"), chains=4, prior= c(set_prior("normal(0, 3)", class = "b") + set_prior("normal(0, 3)", class = "Intercept")))
```

Damage on C. sinensis fruit 2019.

```
brm(Category of worst damage[1, 2, 3, 4]~1+ cs(Treatment)+(1|Tree), family=cratio("probit"), chains=4, prior= c(set_prior("normal(0, 3)", class = "b") + set_prior("normal(0, 3)", class = "Intercept")))
```

Damage on C. clementina fruit 2019.

```
brm(dam~1+cs(treat+cultivar)+(1|cage)+(1|tree_num), data=clem.ear.fix, family=cratio("probit"), cores=parallel::detectCores(), prior= c(set_prior("normal(0, 3)", class = "b") + set_prior("normal(0, 3)", class = "Intercept")))
```

Damage on C. reticulata fruit 2019.

```
brm(dam~1+treat+(1|cage)+(1|tree_num), data=ret.ear.fix, control = list(adapt_delta = 0.95), family=cratio("probit"), cores=parallel::detectCores(), prior= c(set_prior("normal(0, 3)", class = "b") + set_prior("normal(0, 3)", class = "Intercept")))
```

Note: default prior with brms for class=“sd” is student_t(3, 0, 2.5)

The prior we used centers on 0 and is skeptical but inclusive of extreme values and differences. One standard deviation of the intercept and slope differences is 3 meaning ~68% of the expected differences are contained between -3 and 3. We assessed the appropriateness of the prior used by visualizing simulations of the expected values from only the prior predictive distribution (Fig. 2.2.1). Expected values from the prior were reasonable and varied showing that the prior used was not tightly constraining. Plots of prior parameter estimates also showed that the prior used encompassed realistic parameter estimates and centered on 0 (Fig. 2.2). We conducted a sensitivity analyses comparing our prior with the default brms prior (Table 1). For the analyses of fruit damage in 2018, our prior was generally more conservative, including 0 in the 95% QI more frequently than the default prior, but changing the prior did not change our conclusions. Yet, our prior improved convergence; while the *C. reticulata* 2018 damage analysis failed to converge with the default prior even at high target average proposal acceptance probability (adapt_delta) values, our prior allowed for model convergence. For the fruit damage analyses in 2019, our prior usually produced similar estimates to the default prior and did not drastically change posterior estimates. We also confirmed chain convergence was met and that chains mixed well by examining model rhat values and trace plots (Fig. 2.2).

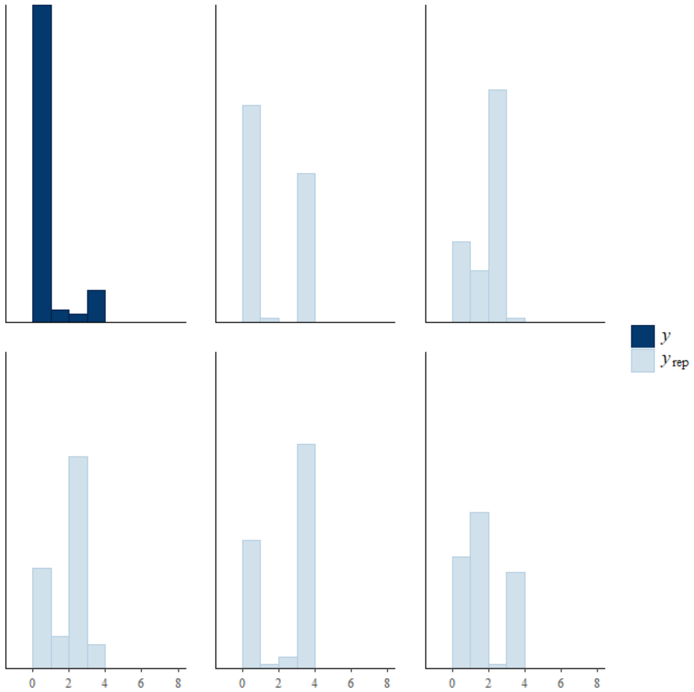

Figure A2.1.1. Histogram of actual data in upper left graph followed by five simulations of the expected values from the prior predictive distribution.

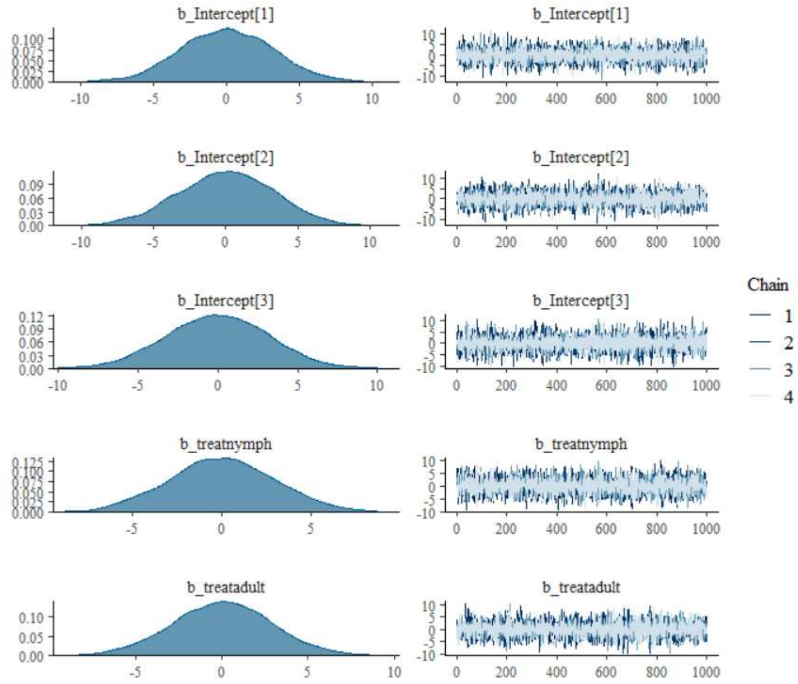

Figure A2.1.2. Density plots on the left and trace plots on the right for some model parameters for the 2018 *C. sinensis* fruit damage assessments.

Table A2.1. Table of 95% quantile interval estimates for each contrast with priors used in this study compared to default priors.

Experiment		Damage category	Prior Type	
			Chosen prior: p(α)=N(0,3), p(β)=N(0,3)	Default: p(α)= student_t(3, 0, 2.5), p(β)=flat
C. sinensis 2018	Nymph vs. Control	No damage	[-0.317, -0.0150]	[-0.506, -0.0551]
		Small cuts	[-0.00272, 0.0609]	[0.00289, 0.112]
		Surface chewed	[0.000318, 0.0646]	[0.00275, 0.119]
		Deep holes	[0.00793, 0.262]	[0.0112, 0.441]
C. sinensis 2018	Adult vs. Control	No damage	[-0.167, 0.0592]	[-0.258, -0.00463]
		Small cuts	[-0.0136, 0.0411]	[0.00189, 0.0779]
		Surface chewed	[-0.00851, 0.0391]	[0.000436 0.0737]
		Deep holes	[-0.0388, 0.114]	[0.000139, 0.164]
C. sinensis 2018	Nymph vs. Adult	No damage	[-0.263, 0.0606]	[-0.381, 0.0100]
		Small cuts	[-0.00802, 0.0449]	[-0.0139, 0.0691]
		Surface chewed	[-0.00491, 0.0446]	[-0.00520, 0.0751]
		Deep holes	[-0.0481, 0.235]	[-0.00436, 0.371]
C. sinensis 2019	Earwig vs. Control	No damage	[-0.836, -0.554]	[-0.837, -0.558]
		Small cuts	[0.0187, 0.293]	[0.0101, 0.304]
		Surface chewed	[0.0840, 0.283]	[0.0827, 0.269]
		Deep holes	[0.186, 0.564]	[0.202, 0.595]

C. clementina 2019	Earwig vs. Control	No damage	[-0.777, -0.319]	[-0.812, -0.365]
		Small cuts	[0.194, 0.557]	[0.240, 0.526]
		Surface chewed	[0.0106, 0.327]	[0.0433, 0.268]
		Deep holes	[0.000820, 0.283]	[0.00495, 0.246]
C. clementina 2019	fina sodea vs. de nules	No damage	[-0.254, 0.226]	[-0.355, 0.135]
		Small cuts	[-0.144, 0.218]	[-0.0698, 0.130]
		Surface chewed	[-0.282, 0.0130]	[-0.0591, 0.153]
		Deep holes	[-0.0177, 0.254]	[-0.0510, 0.166]
C. clementina 2019	Earwig vs. Control	No damage	[-0.519, -0.245]	[-0.535, -0.244]
		Small cuts	[0.211, 0.432]	[0.210, 0.444]
		Surface chewed	[0.0195, 0.0900]	[0.0194, 0.0994]
		Deep holes	[0.00105, 0.0279]	[0.00103, 0.0296]

Supplementary Figure

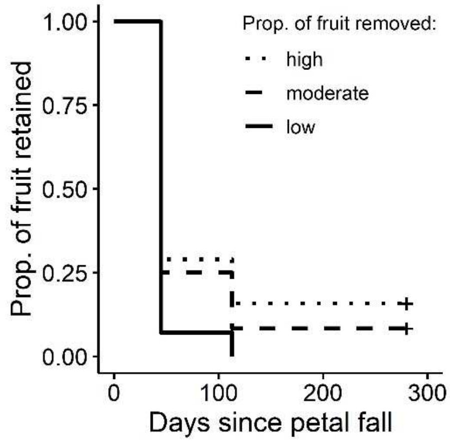

Figure S2.1. Proportion of fruit that did not abscise across the growing season up to harvest for different levels of undamaged fruit initially removed from the citrus terminal (low: 0-20%; moderate: 20-50%; and high: >50% fruit removal) for *Citrus reticulata* trees with fruit removal.

Chapter 3

Effect of Trunk Barriers on European Earwigs, Fuller Rose Beetles, Ants, and Fruit Quality and Yield in Navel Oranges

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Abstract

As an omnivore, the European earwig (*Forficula auricularia*; Dermaptera: Forficulidae) can function both as natural enemy and as a pest in citrus systems. Few studies have examined the net impacts of earwigs in citrus, and particularly not in navel oranges, *Citrus sinensis* (Sapindales: Rutaceae). Trunk barriers may block the movement of earwigs, Fuller rose beetles (*Naupactus godmani*; Coleoptera: Curculionidae), and other crawling arthropod pests into citrus canopies. This study tests the degree to which sticky barriers or bifenthrin chemical barriers applied to trunks: 1) prevent the movement of earwigs into canopies, 2) impact other crawling arthropods pests and predators, 3) disrupt biological control of aphid and scale insects that may be preyed upon by earwigs, and 4) influence citrus fruit damage or infestation, fruit size, and total yield in commercial *C. sinensis* in California. We found that trunk barriers reduced canopy densities of earwigs, Fuller rose beetles, and ants, but did not influence densities of spiders. Sticky barriers were more effective at reducing densities of earwigs and Fuller rose beetles, but chemical barriers were more effective against ants. We did not find evidence that the reduction in densities of earwigs resulted in increased densities of aphids or scales. Barriers also reduced fruit scarring, likely by earwigs, and infestation of mature citrus fruit by Fuller rose beetle eggs. Overall, trunk barriers appear to show promise as a tactic that can simultaneously manage several arthropod pests of citrus.

KEYWORDS: earwigs, citrus, barriers, omnivory, Fuller rose beetles, ants

Introduction

Omnivorous arthropods can play multiple, sometimes contrasting, roles in agricultural ecosystems. Some omnivores act primarily as natural enemies, primarily consuming herbivores, including pest species. Others are primarily herbivorous, mostly consuming plant tissue. Still others play a complex ecological role as they commonly consume both herbivore prey and plant tissue. The net effect of omnivores can be perplexing if they consume an economically important part of the crop, such as the marketed fruit produced by a fruit tree, but also consume herbivore prey that can cause serious crop damage (Coll and Guershon 2002, Krimmel 2011). These omnivores may have net negative, positive, or balancing neutral effects on agricultural quality and yield.

European earwigs (*Forficula auricularia*; Dermaptera: Forficulidae) are known as omnivores and, as such, can be considered both pests and natural enemies; whether earwigs act primarily as pests or natural enemies in citrus is in question (Orpet et al. 2019). Several studies, mostly conducted in organic clementines (*Citrus clementina* hort. ex Tanaka; Sapindales: Rutaceae) grown in Spain (Piñol et al. 2009a,b, Piñol et al. 2012, Romeu-Dalmau et al. 2012a,b,c), highlight earwigs functioning as predators in citrus. However, earwigs are considered pests in California, and are listed in the state's pest management guidelines (Grafton-Cardwell et al. 2003, 2020). Earwigs can defoliate young citrus trees, and have been found to feed on young fruit developing on mature trees (Kahl et al. 2021, Kahl 2021 et al. in review). Fruit scarring can cause downgrading at harvest and loss of fruit value. Thus, growers often try to tightly control chewing herbivores that can cause fruit scarring (Grafton-Cardwell et al. 2003, 2020). Earwig damage to fruit is most extreme on navel oranges (*Citrus sinensis*), moderate on clementines (*Citrus clementina*), and infrequent on certain mandarins (*Citrus reticulata*). The relationship between earwig densities and fruit scarring has not yet been resolved. Earwig damage appears morphologically similar to damage caused by katydids (Kahl et al. 2021). Thus, post-harvest assessments of damaged fruit are likely misclassifying damage caused by earwigs as “katydid damage,” and earwig damage is likely underestimated in commercial production. Earwig densities have increased, and growers have become increasing concerned with managing earwigs (Kallsen 2006, Romeu-Dalmau et al. 2012d).

Citrus growers have few effective management options available for earwigs. In laboratory trials with an array of diverse insecticides, only chlorpyrifos (Lorsban Advanced) was able to kill earwigs rapidly (within two days; Romeu-Dalmau et al. 2012d). However, chlorpyrifos has been banned recently in California citrus for use against all insect pests other than ants (California Department of Pesticide Regulation 2019). Bifenthrin trunk and ground applications are used by some growers to treat earwigs (pers. communication 2020), but to our knowledge there have been no studies testing the field efficacy of bifenthrin sprays for earwigs in citrus. Furthermore, there are currently no organic-compatible management options listed as effective for earwigs in California citrus (Grafton-Cardwell et al. 2020). Thus, there is a need for both conventional and organic-compatible management options for earwigs in California citrus. Furthermore, management should be economically feasible and practical for growers to apply.

Managing multiple pests simultaneously can be more economically feasible for growers and less disruptive to agroecosystems. Earwigs lay their eggs during the spring in nests excavated in the soil, earwig nymphs can not fly, and adult earwigs rarely fly. Thus, barriers that prevent movement of earwigs from the floor of a citrus grove into the tree canopy could potentially exclude earwigs, along with a suite of flightless, damaging herbivores such as Fuller rose beetles (*Naupactus godmani*; Coleoptera: Curculionidae), ants (Hymenoptera: Formicidae), and brown garden snails (*Cornu aspersum*; Stylommatophora: Helicidae). Fuller rose beetles generally do not damage citrus fruit. However, they may lay their eggs under the sepals of fruit. Recently some countries that are important markets for citrus fruit exported from California (e.g. Korea) have placed strict quarantine restrictions on citrus contaminated with Fuller rose beetle eggs. Several insecticides are applied yearly to citrus to eliminate Fuller rose beetle eggs from exported fruit (Houtby 2016, Grafton-Cardwell et al. 2020). Argentine ants (*Linepithema humile* Mayr; Hymenoptera: Formicidae) and native gray ants (*Formica aerata* Francoeur; Hymenoptera: Formicidae) are problematic in citrus orchards, particularly in the spring, because they protect several citrus pests such as scales and aphids. In addition, ant management is becoming increasingly critical, because ants protect Asian citrus psyllids (*Diaphorina citri*; Kuwayama; Hemiptera: Liviidae). Asian citrus psyllid is a vector of the devastating Huanglongbing disease (*Liberibacter americanus*; Alphaproteobacteria: Rhizobiales: Phyllobacteriaceae), a disease that has no cure and kills citrus trees (Navarette et al. 2013). Brown garden snails feed on ripening citrus fruit causing circular craters in fruit, and also feed on leaves (Grafton-Cardwell et al. 2020).

A barrier tactic that can simultaneously exclude several damaging pests from the tree canopy can reduce overall insecticide use in California citrus and efficiently sustain fruit yield and quality. Several studies determined that sticky barriers excluded earwigs from the canopies of clementine trees in Spain (Piñol 2009a, Piñol et al. 2010, 2012, Romeu-Dalmau et al. 2012c,d). Sticky barriers also successfully reduced ants in clementine orchards in Spain (Juan-Blasco et al. 2011). Furthermore, sticky and insecticide barriers have been shown to reduce densities of Fuller rose beetles in citrus canopies (Haney and Morse 1988, Morse et al. 1988, Magarey et al. 1993). Sticky barriers are compatible with organic production and may manage several arthropod pests while having minimal impacts on the environment and on most arthropod natural enemies operating in tree canopies. We suspect that pesticide barriers that are selectively applied on the trunk and soil would be more compatible with conventional systems and would be less likely to kill bees or be destructive to beneficial arthropods, such as predators and parasitoids that forage in the canopy, than foliar sprays (Davis and Williams 1990, Frank and Sadof 2011).

Trunk barriers may, however, also have unintended consequences. Pesticide trunk barriers may have negative impacts on ground-dwelling beneficial arthropods and can contaminate the soil, air, and water. Sticky barriers may exclude beneficial arthropods from citrus canopies. For example, earwigs are effective aphid (Hemiptera: Aphididae) predators (Piñol et al. 2009a,b, Piñol et al. 2012, Romeu-Dalmau et al. 2012a,b,c); thus, the exclusion of earwigs from the canopy can actually lead to a rise in aphid densities (Cañellas et al. 2005, Piñol et al. 2009a, Piñol et al. 2010, Romeu-Dalmau et al. 2012c). Aphids can transmit citrus tristeza virus (Martellivirales: Closteroviridae), which can kill citrus trees. Thus, growers can actually benefit from earwigs if predation of aphids by earwigs is enough to prevent the establishment or spread of citrus tristeza. As earwigs also consume California red scale (*Aonidiella aurantia*; Hemiptera: Diaspididae) (Romeu-Dalmau et al. 2012d) and may consume citricola scale (*Coccus pseudomagnoliarum*; Hemiptera: Coccidae), densities of these scale insects may also increase when earwigs are excluded. Trunk barriers could possibly prevent the movement into citrus canopies of other generalist predators that primarily crawl, such as spiders. However, if barriers exclude ants, this might promote spider densities by relaxing the often-antagonistic relationship between ants and spiders (Marras et al. 2008, Piñol et al. 2010, Mestre et al. 2012). In sum, although trunk barriers have been shown to be effective in preventing earwigs, Fuller rose beetles, and ants from accessing the canopy, the impacts of barriers on other important arthropods in the canopy, and the effects of barriers on citrus harvest quality and quantity have not been well examined.

Broadly, this study aims to improve the understanding of the role of earwigs in California citrus and design a comprehensive management tool for earwigs and other crawling insect pests. Our main questions were: 1) Can trunk barriers be used to reduce earwig densities in citrus canopies? 2) Do trunk barriers simultaneously reduce densities of other crawling pest arthropod species? 3) Are there unintended effects of trunk barriers resulting from exclusion of earwigs and other predators that offer pest control in the canopies? 4) What are the net effects of trunk barriers on fruit quality and yield?

Methods

Treatment setup

The experiment was established in 2020 in a *C. sinensis* planting at Lindcove Research and Extension Center (LREC) (36.360895, -119.062348) in Lindcove, Tulare County, CA. Most earwig young do not start leaving the nest until April, when offspring reach the second instar (Crumb et al. 1941, Orpet et al. 2019). Thus, citrus plantings were prepared early in the spring to prevent earwigs and other crawling herbivores from accessing the canopy using routes other than the trunk. On March 25th, 2020, the foliar skirts of 90 trees in our experimental block were pruned to 0.60-0.75 m above the ground. The sides of the trees were pruned back 1.5-2 m from neighboring tree foliage to prevent movement of crawling arthropods between trees. Tree foliage was maintained as needed across the season. Weeds were controlled across the season by hand hoeing and using clippers.

Three treatments, each applied to single trees and replicated 30 times, were then established: (i) a sticky barrier, applied on 31 March 2020, (ii) an insecticide barrier, applied on 1 April 2020, and (iii) a no barrier (control). The treatments were randomly assigned to trees, but we avoided having adjacent trees with the same treatment. The sticky banding (Sticky Stuff, Olsen Products Inc., Medina OH) was prefabricated with an even layer of sticky material applied to a paper backing. We set up sticky barriers by tightly tying fiberglass insulation batting to the trunk with a string and then wrapping the banding around the batting. The banding was secured tightly to the batting by wrapping saran wrap strips across the top and the bottom and tightening the saran wrap seals with string (see Fig. 3.1 for more details and step-by-step instructions). The sticky banding was ~18 cm wide (~16 cm of sticky surface). This barrier was similar to those used in previous studies and to barriers recommended for Fuller rose beetle management (Juan-Blasco et al. 2011, Grafton-Cardwell et al. 2020). Insecticide barriers (bifenthrin, Brigade®, FMC Corporation, Philadelphia, PA) were applied with an atomizing hand wand using a 200 gallon mechanical agitation diaphragm pump spraying at 400 psi (Spring Devices Inc.) with a 80-02 Teejet flat fan nozzle. Bifenthrin was applied as a directed spray at 16 oz/acre onto the soil from the drip line to the base of the tree and 0.45 m up the tree trunks following label guidelines (FMC Corporation 2019). Because only individual trees, rather than the whole block, were treated, this application is likely to underestimate of the true potential of bifenthrin to reduce target arthropod densities. Pest control advisors working in California citrus have observed effective plot-level control of earwigs with bifenthrin (pers. communication 2020). Nothing except the skirt pruning and weed control was done to control trees.

Sampling

We used a series of methods to sample arthropods of interest. First, following other research (Piñol et al. 2009b, Romeu-Dalmau et al. 2012a, Romeu-Dalmau et al. 2012c), to sample earwigs and other foliar arthropods, we beat a ~50 cm long branch terminal with a wooden rod three times over a 0.5 x 0.5 m beating sheet (Bioquip). We recorded the numbers, sex, and lifestage of dislodged earwigs, along with the numbers of Fuller rose beetles, ants, aphids, spiders, and other insects that can cause chewing damage that could be mistaken for earwig damage (katydids and caterpillars). This was repeated for each of the four sides of each tree. We sampled foliage approximately weekly in April and May and then approximately monthly through September. Subsamples of spiders were identified to family, and ants were identified to species. Although, we originally planned to survey snails, we observed that snails easily cross sticky barriers and bifenthrin is not listed as an option for snail management (Grafton-Cardwell et al. 2020), so we did not anticipate that trunk barriers would influence snail densities and did not monitor snails.

Second, we used a trapping method to sample earwigs and spiders in the tree canopies following Burnip et al. (2002) and Suckling et al. (2006). Cardboard sheets, each 10 x 85 cm, were rolled lengthwise (making the rolls ~6 cm in diameter) and stuffed into black plastic drinking cups (Creative Converting 28134081B 16 oz) to create a dark environment (Fig. 3.2). We oriented cups vertically in the canopy, with the bottom of the cups forming the roofs of the traps, and secured them in trees using a wire inserted through the center of the roll and wrapped around the branch. On 13 April 2020, we set up two cardboard rolls per tree, one on the north side and another on the south side of the tree. Cardboard rolls were sampled on 7-8 May, 23 June, 15 July, and 25 September 2020. Arthropods were extracted from the roll, and the numbers of nymphal and adult male and female earwigs and earwig exuviae were recorded, along with counts of spiders. We returned extracted arthropods to the roll or foliage near the roll when possible. We identified subsamples of spiders to family-level.

Finally, we inspected leaves to quantify the densities of scale insects. On 24 June 2020, we examined 14 leaves per tree in the field using a hand lens to count California red scale and citricola scale. We recorded whether each scale was alive, dead (blackened), chewed (partially consumed), or parasitized (parasitoid meconial pellets or exit holes seen).

Chewing damage to young fruit was evaluated on 25-26 May 2020 after the period when citrus fruit are vulnerable to herbivory from earwigs (Kahl et al. 2021). We visually scored ninety haphazardly chosen fruit per tree for the presence or absence of deep holes or surface chewing damage. Fruit damage was again quantified at harvest on 1-2 February 2021 using visual assessments and packline evaluation. Fruit from each tree were kept in separate lots at harvest and processed with an automated packline equipment (Compac Sorting Equipment, Aukland, New Zealand). The packline provided an estimate of fruit surface area (mm^2) scarred using AI software trained on images of what was thought to be katydid damaged fruit (Supp Fig. 3.1). We calculated the surface area of the fruit using the formula for a spheroid, and the proportion of the fruit surface scarred was calculated by dividing area with scarring by total fruit surface area. The packline also measured the area of dark scars (using primarily an assessment of the percent of black coloring on the fruit), the weight of each individual fruit, and the number of fruit harvested per tree. After packline evaluation, we visually inspected the first 50 fruit harvested from each tree to estimate the percent of fruit area covered by scars from chewing herbivores. We only counted scars that were concave and had at least some dark scabby tissue, which is characteristic of scars produced by earwigs, katydids, and caterpillars.

To quantify infestation of fruit with Fuller rose beetle eggs, we removed the sepal from each of the first 50 harvested fruit using laboratory spatulas and searched the sepal and the exposed fruit surface for the presence of eggs. We recorded whether each fruit was infested or uninfested.

Sticky barriers were removed from trees after fruit harvest and the numbers of European earwigs, Fuller rose beetles, and ants trapped on sticky barriers were counted. European earwigs were further classified as nymphs or adult males or females.

Statistical Analyses

We used R for all analyses and *tidyverse* (Wickham et al. 2019) was used to manipulate data. The proportions of non-zero counts for each arthropod taxon on each date were calculated to compare the efficacy of different sampling methods. Arthropod counts from foliage beating and cardboard rolls were analyzed with Bayesian models specified in R using package *brms* (Bürkner 2017), which utilizes Hamiltonian Monte Carlo and its extension, the No-U-Turn Sampler (NUTS). For most arthropod taxa, Poisson distributions and zero-inflation were used, because for the majority of samples no arthropods were recorded. Bayesian Generalized Linear Mixed Models (GLMMs) produced better model convergence than frequentist GLMMs, especially in cases when counts were low. For models analyzing arthropods found in foliage beating and cardboard rolls, treatment, date, and treatment by date were included as fixed effects, and tree was included as a random effect. The side of the canopy sampled was also included as a fixed effect to see if we could refine future sampling methods for these taxa in citrus. Because of the rarity of earwigs, counts of earwig nymphs and male and female adults were combined for analyses of earwigs. We also built a Bayesian GLMM model with a zero-inflated Poisson family with tree as a random effect to examine the influence of earwig or ant densities on aphid densities. California red scale densities were analyzed using a Bayesian linear model (LM), and a Bayesian LM was also used to examine the influence of earwig and ant densities on scale densities.

The maximum numbers of earwig exuviae across all dates found in each cardboard roll were compared across treatment and side of the tree sampled. Maximum numbers across all dates were used, because most earwig exuviae were found on the first sampling date (by this point most nymphs had already molted into adults) and remained in cardboard rolls thereafter. A Bayesian Generalized Linear Model (GLM) with a zero-inflated Poisson family with tree as a random effect was used to test whether maximum earwig exuvia counts predicted maximum earwig adults across all dates found in rolls.

For Bayesian modeling, we used weakly informative priors based on estimated maximum mean values of each taxon found in previous studies using similar sampling methods (Supp Table 3.1). For each arthropod taxon, we compared a model with a date by treatment interaction (interaction model) with a model with date and treatment included as only main effects (main effect model) with approximate leave-one-out cross-validation based on the posterior likelihood and exact cross-validation for problematic observations (*loo*; package brms; Bürkner 2017). Models with the highest expected log predictive density (elpd_diff=0) were selected as the best model (Vehtari et al. 2017). We used package *emmeans* (Lenth 2020), which, when used with Bayesian models, provided 95% Highest Posterior Density Intervals (HPDIs) for every treatment contrast. Intervals that exclude zero suggest statistically meaningful treatment differences.

A Cumulative Link Mixed Model (CLMM) computed using package *ordinal* (Christensen 2019) was used to assess the severity of early fruit damage across treatment with tree as a random effect; damage categories were modeled as an ordered variable (minimal damage or no damage<surface chewed<deep holes). *Anova.clmm* from the *RVAideMemoire* package was used to test treatment significance (Hervé 2021). For assessments of proportions of fruit scarred, fruit samples for six trees were mislabeled and were omitted from the analysis. Proportions of harvested fruit surface scarred calculated from visual estimates and packline equipment (katydid and dark scarring) were averaged by tree. Because normality assumptions were violated, we analyzed mean proportions of fruit scarred from visual estimates with a Kruskal-Wallis rank sum test using the *stats* package (R Core Team 2021). A Dunn test with the Holm method was used for testing pairwise treatment comparisons when the rank sum test was significant (package *FSA*; Ogle et al. 2021). Mean proportions of katydid and dark scarring measured by the packline were analyzed with LMs using package *lme4* (Bates et al. 2015). For assessments of Fuller rose beetle eggs underneath fruit sepals, two mislabeled trees were omitted from the analysis. Fuller rose beetle egg counts were analyzed with a binomial GLM using package *lme4* (Bates et al. 2015). A GLM with a quasi-Poisson family (due to overdispersion) was used to analyze differences in fruit number per tree across treatment. A Linear Mixed-effect Model (LMM) with tree as a random effect was computed using package *lme4* to analyze differences in individual fruit weight across treatments, and total fruit weight per tree across treatments was analyzed with an LM using *lme4*. For all linear models analyzed using *lme4*, *Anova* from the *car* package was used for testing treatment significance (Fox and Weisberg 2019).

Results

From foliage beating, several spider families were found (Supp Table 3.2). All collected ant specimen were identified as *Brachymyrmex patagonicus* (Hymenoptera: Formicidae). Most spiders observed in cardboard roll traps were identified as Sparassidae. Nymphal and male and female adult European earwigs, ring-legged earwigs, ants, and Fuller rose beetles were found caught on sticky barriers (Supp Table 3.3). Adult European earwigs were the most abundant and common (present in the highest percentage) arthropods trapped. Fuller rose beetles were also abundant and common. Spiders were not observed on sticky barriers. Other chewing herbivores such as katydids and caterpillars were very rare in foliage beating samples; only five katydids and ten caterpillars were observed across all sampling dates.

Pest densities

Earwig densities in citrus canopies were reduced by barriers. Earwigs were only captured from foliage beating from 10 April to 29 May, and only in ~0.8% of samples. To test the effects of treatment and date on earwig densities measured with foliage beating the main effects model was selected. Although there was a trend towards higher densities in control (mean ± SE: 0.011±0.003) vs. barrier treatments (bifenthrin: 0.008±0.003; sticky: 0.005±0.002), statistical support for a difference was weak (Supp Table 3.4), likely due to low capture rates. Earwigs were captured in cardboard roll traps on all sampling dates, and from ~6.3% of samples. Earwig counts were highest on May 7th and June 23rd. For the effect of treatment and date on earwigs from cardboard roll traps the date by treatment interaction model was selected, and the treatments differed on some dates (Fig. 3.3; Supp Table 3.4). Both sticky and bifenthrin barriers reduced earwig densities, but earwigs were particularly reduced by sticky barriers on 7 May and 23 June. Earwigs caught in the North and South sides of trees did not clearly differ (Supp Table

3.4). Earwig exuviae were found in ~5.6% of samples and counts of exuviae differed across treatments (Fig. 3.4): more exuviae were found in cardboard roll traps in control trees compared to trees with sticky barriers (HPDI: [0.75, 3.17]) and bifenthrin barriers (HPDI: [0.11, 1.74]). Counts of exuviae did not differ across the tree side sampled (HPDI: [-0.54, 0.80]). Earwig exuviae counts were not strongly correlated with the number of earwig adults found in traps (HPDI: [-29.8, 25.4]; HPDI crossed 0).

Fuller rose beetle densities were also reduced by trunk barriers. Fuller rose beetles from foliage beating were captured on all sampling dates except 24 April and 15 May, and were found in ~1.7% of samples. Fuller rose beetle numbers were highest on the first sampling date (10 April). The main effects model was selected. Numbers of Fuller rose beetles differed across treatment, with more beetles found in the control than in the sticky barrier (HPDI: [0.64, 2.09]) or bifenthrin barrier (HPDI: [0.11, 1.28]) treatments (Fig. 3.5). Sampling side also differed for Fuller rose beetles, with fewer beetles found on the east side of the tree compared to the north (HPDI: [0.01, 1.64]) and the south (HPDI: [0.25, 1.83]) sides.

Ant densities were also reduced by barriers. Ants were detected from foliage beating on all sampling dates except 17 April and 24 April; ants were found in ~3.0% of samples. The main effects model was selected. Numbers of ants differed across treatment, with more ants found in the control than in the bifenthrin barrier (HPDI: [0.78, 3.08]) or the sticky barrier (HPDI: [0.23, 2.47]) treatments (Fig. 3.6). There were no clear differences in ant counts across the side of the tree sampled.

Exclusion of predators or disruption of biological control

Treatments had no influence on spider densities in citrus canopies. Spiders from foliage beating were found on every sampling date and in 11.3% of samples. The main effects model was selected. Spider densities were very similar across treatments (control: 0.12±0.01; bifenthrin: 0.12±0.01; sticky: 0.13±0.01; HPDIs included 0). The side of the tree sampled also did not reveal significant differences in spider densities (Supp Table 3.4). Similarly, spiders were sampled in cardboard roll traps on every sampling date and in ~6.8% of all samples. The interaction model was selected, but there were no differences in spider numbers across treatment for any date or across side sampled (HPDIs include 0; Supp Table 3.4).

Aphid densities did not differ across trunk treatments. Aphids were found in ~2.0% of all foliage beating samples. The main effects model was selected, and, while there was a trend towards more aphids in the barrier treatments (control: 0.017±0.005; bifenthrin: 0.031±0.007; sticky: 0.029±0.007), the support for differences across treatment or side sampled was weak (HPDIs include 0; Supp Table 3.4). Further, earwig and ant numbers were not strongly correlated with aphid numbers (earwigs: β= -1.42 [-5.37, 2.64]; ants: β=0.48 [-0.14, 1.03]; HPDIs include 0).

California red scale densities also did not differ statistically across treatments. California red scale were found in ~51.1% of leaf samples. Across all samples, only four citricola scales were found, so only California red scale data were analyzed. Red scale densities did not differ across treatment (HPDI includes 0; Supp Table 3.4). Earwig and ant densities did not strongly influence California red scale numbers (earwigs: β= -0.25 [-2.38, 1.77]; ants: β= -0.10 [-0.90, 0.66]).

Fruit damage and infestation by Fuller rose beetle eggs

We found some evidence for reduced fruit scarring in barrier treatment trees. Damage categories on young fruit were very similar and did not significantly differ across treatment (P=0.25). Packline assessments of dark scars (control: 0.011±0.001; bifenthrin: 0.011±0.001;

sticky: 0.010±0.001; *P*=0.48) and scars recognized by AI (control: 0.004±0.0002; bifenthrin: 0.004±0.0002; sticky: 0.004±0.0002; *P*=0.59) did not vary significantly across treatment. Scarring on mature fruit from visual assessments significantly differed (X^2=7.31, df=2, *P*=0.03) with more on control compared to sticky barrier trees (*z*=2.60, *P*=0.03, Fig. 3.7; Fig. 3.8).

Barriers, in particular sticky barriers, reduced Fuller rose beetle egg infestations of harvested fruit. Percent of fruit with fuller rose beetle eggs differed across treatment (X^2=9.58, df=2, *P*=0.008). Fruit harvested from control trees had marginally higher proportions of Fuller rose beetle eggs than fruit harvested from trees with sticky barriers (*P*=0.07; Fig. 3.8; Supp Fig. 3.2).

Effects on fruit number, size, and yield

Yield did not differ across treatments. There were no significant differences across treatments in either: (i) numbers of fruit harvested per tree (control: 541±19.3; bifenthrin: 564±16.7; sticky: 571±19.3; *P*=0.42), (ii) mean fruit size (control: 259±3.32 g/fruit; bifenthrin: 262±2.96 g/fruit; sticky: 264±3.41 g/fruit; *P*=0.54), or (iii) total weight of fruit harvested per tree (control: 140±3.71 kg/tree; bifenthrin: 147±4.53 kg/tree; sticky: 150±4.35 kg/tree; *P*=0.21) (*P*>0.20 in all cases).

Discussion

Trunk barriers, particularly sticky barriers, reduced densities of earwigs in the tree canopies. Trunk barriers also reduced counts of earwig exuviae, serving as an additional indicator of reduced earwig populations by trunk barriers. In addition, densities of Fuller rose beetles and ants were successfully reduced by trunk barriers. Barriers did not produce any unintended consequences: spider densities were not reduced, and there were no increases of aphids or scale populations in trees with trunk barriers. Visual assessments of harvested fruit revealed more scarring on fruit in control compared to sticky barrier trees. In addition, fewer Fuller rose beetle eggs were detected on fruit harvested from trees with sticky barriers. Thus, our results suggest that trunk barriers reduce significant problems associated with several crawling insect pests, including earwigs, Fuller rose beetles, and ants, all without clear interruptions in biological control.

Citrus pests excluded by barriers

Our results mirror previous studies that also similarly found fewer densities of European earwigs in trees protected by sticky barriers (Piñol et al. 2009a, Piñol et al. 2010, 2012, Mestre et al. 2012, Romeu-Dalmau et al. 2012c,d). Our study is one of the only studies conducted in California; all prior studies, except Romeu-Dalmau et al. (2012d), were conducted in Spain. European earwig nymphs and adults were found stuck to sticky barriers, indicating that barriers reduced earwig densities in the canopy not only by blocking their ability to walk up the trunks but also by killing earwigs outright. Counts of earwig exuviae and adults were reduced in cardboard roll traps placed in trees with trunk barriers. Earwig exuviae indicate the presence of earwig nymphs, suggesting that earwig nymphs were also reduced in the tree canopies. Reduction of earwig nymph densities is particularly important, because earwig nymphs appear to generate more damage on developing citrus fruit per individual than adults do (Kahl 2021). However, the exclusion of earwigs in the present study was not as complete as that observed in previous studies. Due to their thigmotaxic nature, earwigs could have found ways to squeeze underneath the sticky banding. While likely infrequent, earwig adults could have flown to colonize canopies. Trunk barriers seem to be an effective way to reduce earwig densities in citrus canopies.

Earwigs were likely the only chewing herbivore of citrus fruit highly impacted by barriers in this study. We monitored other herbivores that cause damage that can be classified as chewing (snails, katydids, and caterpillars). Snails naturally secrete and travel over a sticky slime and, in this study, we discovered that snails easily crossed sticky barriers. Thus, sticky barriers do not seem to be a promising management option for snails in citrus. Katydids and caterpillars were very rare in this study. Thus, earwigs likely contributed to the majority of chewing damage observed in this study.

Densities of Fuller rose beetle adults and eggs were reduced by barriers, particularly sticky barriers, and adults were found stuck on the sticky barrier bandings. Reduction of Fuller rose beetles by sticky barriers is not surprising, as sticky barriers have been recommended as an ecologically less disruptive option for control of Fuller rose beetles since 1950 (Dickson 1950), but fewer studies have examined whether trunk barriers reduce numbers of Fuller rose beetle egg masses. Previous studies that examined many different trunk barrier treatments, including sticky barriers, found that only lambda-cyhalothrin reduced viable egg masses (Magarey et al. 1992). However, since then, improvements have been made to sticky barrier formulations (Olson Products, Inc., pers. communication). In this study, the infestation rates of fruit with Fuller rose beetle eggs were reduced below threshold (0.2% of fruit) on sticky barrier treatments, but were above threshold on control trees and trees with bifenthrin barriers (Grafton-Cardwell et al. 2020). While the UC IPM guideline on Fuller rose beetles reports peak emergence of beetles in August (Grafton-Cardwell et al. 2020), we observed the highest numbers of beetles on our first sampling date, 10 April. In addition, we found that the east side of the tree canopy had fewer Fuller rose beetles than the north and south side of the tree. We suggest sampling the south side of trees for

Fuller rose beetles. This study provides further evidence to support the effective of sticky barriers for Fuller rose beetle management in citrus.

Ants were also reduced by barriers, and ants were found stuck on sticky barriers. However, unlike with earwigs and Fuller rose beetles, ants were reduced to a greater degree by bifenthrin barriers than sticky barriers. Several studies have looked at the effect of sticky barriers on ants in citrus systems and demonstrated success (Marras et al. 2008, Piñol et al. 2009a, Piñol et al. 2010, 2012, Juan-Blasco et al. 2011, Mestre et al. 2012, Navarette et al. 2013, Kistner et al. 2016), and one study looked at trunk sprays of chlorpyrifos (James et al. 1998) and α-cypermethrin for ant control (Stevens et al. 1995). However, few studies have tested the use of bifenthrin as a control option for ants in citrus orchards. Instead, experiments with bifenthrin have been conducted on sand in the laboratory and in the field (Soeprono and Rust 2004), on soil in pots (Oi and Williams 1996), and as granules in the lab and in an urban circular gravel drive (Pranschke et al. 2009). While these studies have shown that bifenthrin could be used to reduce ants, this is one of the only studies demonstrating that ants can be reduced using bifenthrin barriers. Bifenthrin treatments may have been more effective than sticky barriers at reducing ants in this study because the spray was applied to the soil as well as the trunk; previous studies cited above have shown soil-directed bifenthrin applications to be very effective at reducing ant populations. Future studies could examine differences in effectiveness between trunk and soil-focused barriers used to treat ants. Ant peak activity from May to August was found in previous studies (Piñol et al. 2010, Juan-Blasco et al. 2011, Navarette et al. 2013) as well as our study. Trunk barriers, particularly bifenthrin barriers, seem to be a promising, timely option for managing ants in citrus canopies.

Exclusion of predators or disruption of biological control

Unintended negative consequences of trunk barriers were not detected in this study. Spider numbers from foliage beating and cardboard rolls were not reduced in trunk treatments. Although trunk treatments may impede movement of spiders into the canopy by crawling, many spiders likely have other ways of accessing the canopy such as jumping, ballooning, and traveling across silk lines. Other studies have actually found an increase of spider densities in the canopies of trees with barrier treatments due to the reduction of ant predators (Piñol et al. 2010, Mestre et al. 2012, Kistner et al. 2016). Negative impacts of ants on spiders and positive impacts of ants on aphids, and scales were not observed in this case. Negative impacts of earwigs on aphids and scales were also not observed. This could be because arthropod densities were low in this study.

Alternatively, earwigs may not have negatively impacted aphids because earwigs may not be effective predators of aphids or scales in conventional *Citrus sinensis* orchards in California. Most of the research done on earwigs as predators in citrus were conducted in organic *C. clementina* orchards. Previous work suggests that *C. clementina* fruit may not be a preferred or suitable food for earwigs compared to *C. sinensis* fruit (Kahl et al. in review). If this is the case, earwigs may be more likely to consume plant material and less likely to consume insects in *C. sinensis* compared to *C. clementina*. It is also possible that organic citrus systems may have a more consistent insect prey source available to earwigs than conventional systems, allowing earwigs to function more consistently as predators; whereas, in conventional systems, particularly in *C. sinensis*, it may be necessary to manage earwigs to reduce damage to fruit and foliage.

Comparison of sampling methods

To make more informed decisions about whether earwig management may be needed or timing of management, an effective sampling method for earwigs in citrus is needed. We found that cardboard rolls seem to be a more effective sampling method for earwigs in citrus foliage than foliage beating. Cardboard rolls captured earwigs almost eight times more frequently than foliage beating. Cardboard rolls also have the benefit of revealing more information about development of earwigs in the canopy as they also frequently contain earwig exuviae. In other studies earwig densities have been shown to peak from May to August (Piñol et al. 2009a, Piñol et al. 2010, Romeu-Dalmau et al. 2012a,c,d); we found that earwigs peaked in May and June, complementing previous studies' findings. This method, as well as information on peak earwig emergence, could be utilized by Pest Control Advisors and growers looking to assess earwig abundance in tree canopies.

Fruit damage

Even with low earwig abundance from both sampling methods, our visual assessments of harvested fruit revealed more scarring in the control compared to sticky barrier treatment. However, interestingly, we did not detect differences in damage on young fruit across treatment, or detect differences in packline assessments of scars due to chewing herbivores on harvested fruit. This is likely due to differences in measurements used. The difference in fruit damage between sticky barriers and control trees seems to be driven more by the amount of damage (which we only measured on mature fruit) than by whether the fruit was damaged or not, or by the severity of damage (which we only measured on young fruit). Visual scarring assessments may be more accurate than scarring assessments provided by the automated packline, despite the increased numbers of fruit evaluated by the packline, because we may be able to distinguish more effectively scars generated by arthropod herbivores versus scars generated by other sources of damage (eg. physical rubbing of fruit on branches). The packline likely needs to be trained on more images to reliably recognize chewing scars, or the AI algorithms used by the packline may need images of earwig-damaged fruit rather than katydid-damaged fruit to improve its ability to detect scars caused by earwigs. This study provides further evidence that earwigs can contribute to increased scarring on mature navel orange fruit at harvest.

Effects on fruit number, size, and yield

However, similar to what was found in a previous study (Romeu-Dalmau et al. 2012c), barriers did not significantly alter fruit number, size, or total yield (net fruit weight per tree). If citrus trees abscise damaged fruit and cannot compensate for the fruit abscised, then fruit damage could lead to yield losses. However, this was not observed for earwig-damaged C. sinensis fruit in previous studies (Kahl 2021, Kahl et al. in review). In years with higher pressure of ants, earwigs, or Fuller rose beetles and increased feeding on foliage, barriers might have effects on yield.

Overall, in this study we found that sticky barriers and bifenthrin barriers reduced densities of earwigs, Fuller rose beetles, and ants and led to reduced scarring and Fuller rose beetle eggs on fruit. We did not find any negative effects of barriers on spider densities, and we did not record any increases in the densities of aphids or California red scale due to losses of biological control contributions from earwigs in barrier treatments. While sticky barriers were found to be more effective than bifenthrin barriers for suppression of earwigs and Fuller rose beetles, bifenthrin was found to be more effective against ants. Using current application techniques, sticky barriers are very time-consuming to apply. Thirty sticky barriers took two people 5.5 hours to apply, compared to only two hours to apply the bifenthrin sprays to the 30 experimental trees. Furthermore, sticky barriers were physically difficult to apply, requiring the applicant to crouch under the canopy to access the tree trunk. However, sticky barriers have fewer negative impacts on human and environmental health and are an organic-compatible option. Future work focusing on finding ways to apply sticky barriers more efficiently and with greater ease through a mechanized application method would increase the feasibility of this method for adoption by growers of citrus and other tree or vine crops attacked by crawling herbivores.

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Figures/Tables

Figure 3.1. Sticky barrier treatment applied on tree trunks. Sticky barriers were constructed by: 1) wrapping fiberglass insulation batting around the trunk; 2) tightly securing the batting by tying padding to the trunk with a string; 3) wrapping the sticky, laminated banding with paper backing (Olson Products Inc.) around the tree with some extra to overlap the wrap; and attaching the sticky side to the laminated non-sticky side; 4) providing extra security for the banding and removing possible gaps by tightly wrapping saran wrap strips across the top and the bottom; and 6) tightening saran wrap seals with string.

Figure 3.2. Cardboard roll traps with black cup cover used as one method for sampling earwigs.

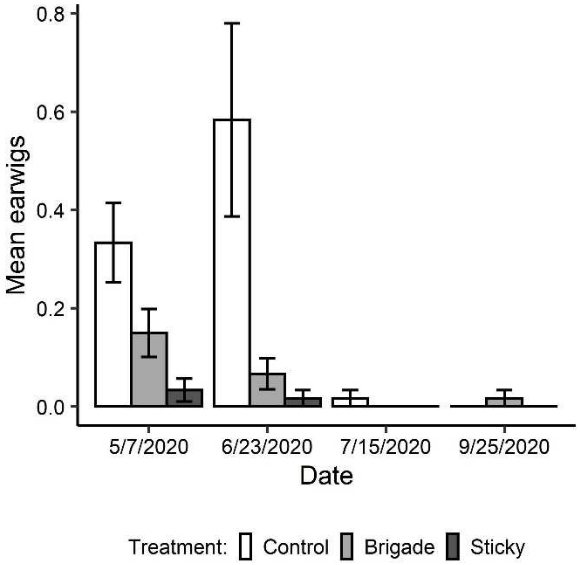


Figure 3.3. Number of earwigs (means ± SE) found in cardboard rolls over time. Means were calculated by averaging first by tree and then by treatment per each date. Standard errors are calculated from mean counts per tree, treatment, and date (averaging across sides sampled).

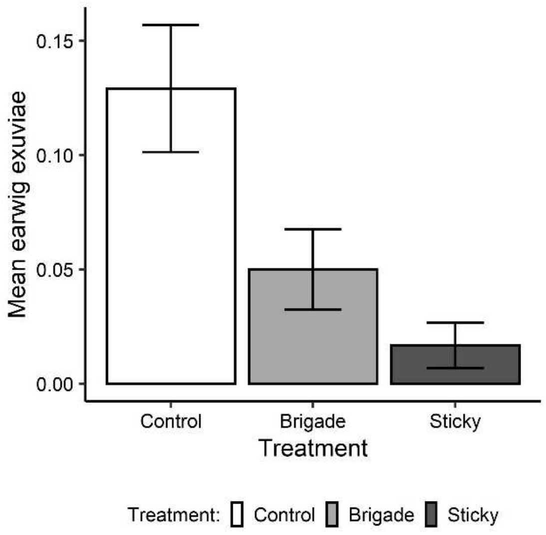


Figure 3.4. Maximum number of earwig exuviae (means ± SE) found in each cardboard roll traps. Means were calculated by averaging first by tree and then by treatment. Standard errors were calculated from mean counts by tree and treatment (averaging across sides sampled).

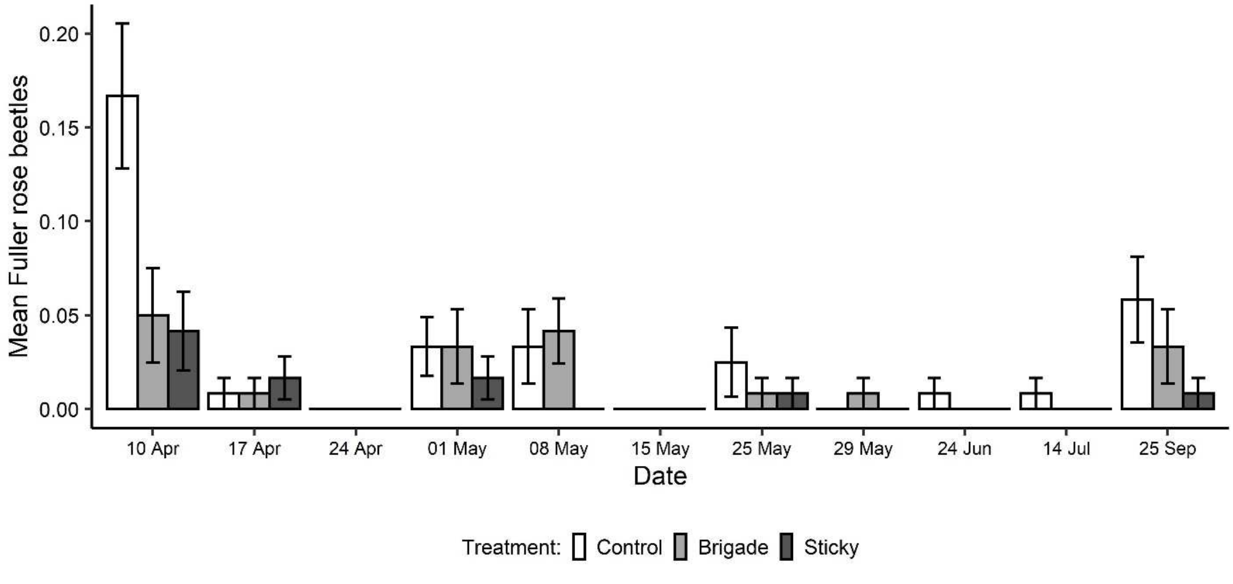


Figure 3.5. Number of Fuller rose beetles (means ± SE) from foliage beat samples across date. Means were calculated by averaging first by tree and then by treatment per each date. Standard

errors were calculated from mean counts by tree, date, and treatment (averaging across sides sampled).

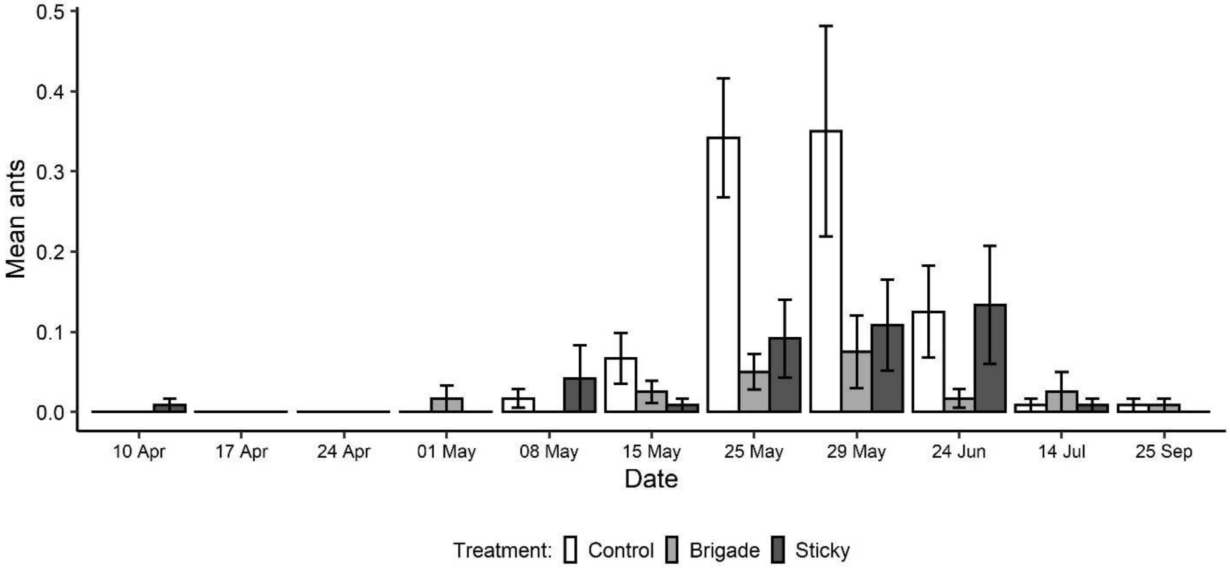


Figure 3.6. Number of ants (means ± SE) from foliage beat samples across date. Means were calculated by averaging first by tree and then by treatment per each date. Standard errors were calculated from mean counts by tree, date, and treatment (averaging across sides sampled).

Figure 3.7. Examples of scars observed on mature navel orange fruit at harvest.

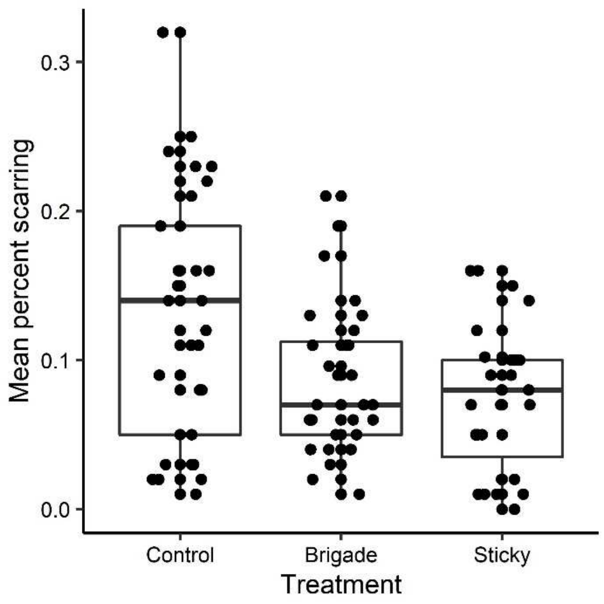


Figure 3.8. Median, interquartile range, and values of mean percent of surface area of mature navel orange fruit scarred per tree across treatment. The points were jittered along the x-axis to allow for visualization of every point.

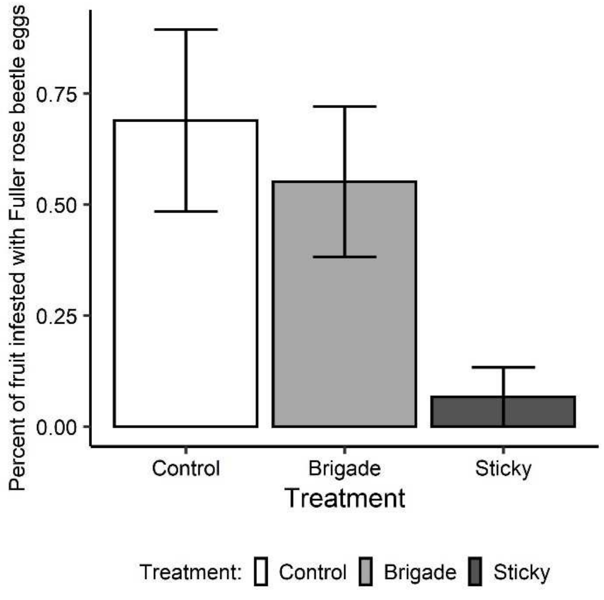


Figure 3.9. Percent of mature navel orange fruit infested with Fuller rose beetle eggs (means ± SE) underneath the sepal. Means were calculated as the percentage of fruit with Fuller rose

beetle eggs per tree, and then averaged by treatment. Standard errors were calculated by tree and treatment.

Supplementary Material

Supplementary Table 3.1. Studies used to establish priors. For each study, we approximated the maximum mean number of arthropods captured for each specific taxon of interest from published graphs. Studies in bold were those used to inform priors. Studies that took samples across multiple years and/or were more recent were preferred for each taxon. Priors for the slope and intercept of all models were set to have a mean of 0 and a standard deviation of one-third of the approximate maximum mean observed in the selected previous studies. This assigns maximum mean values found in prior studies some but little weight. Default *brms* priors were used for the standard deviation and zero-inflated parameters.

Publication	Species	Taxa	Location	Method	Approx. max. mean
Piñol et al. 2012	***C. clementina***	***Forficula auricularia***	**Tarragona, Spain**	**Foliage beating**	**9**
Piñol et al. 2012	***C. clementina***	**Formicidae**	**Tarragona, Spain**	**Foliage beating**	**18**
Piñol et al. 2012	***C. clementina***	**Aphididae**	**Tarragona, Spain**	**Foliage beating**	**7.5**
Piñol et al. 2012	***C. clementina***	**Araneae**	**Tarragona, Spain**	**Foliage beating**	**13.5**
Suckling et al. 2006	***M. domestica***	***Forficula auricularia***	**Canterbury, New Zealand**	**Cardboard rolls**	**42**
Dib et al. 2020	***M. domestica***	**Araneae**	**Avignon, France**	**Cardboard rolls**	**0.65**
Grafton-Cardwell et al. 2008	***C. sinensis***	***Aonidiella aurantii***	**McFarland, CA**	**Counts on leaves**	**3.6 (number/leaf)**
Romeu-Dalmau et al. 2012a	*C. sinensis*	*Forficula auricularia*	Lindcove, CA	Foliage beating	1.4
Piñol et al. 2009	*C. clementina*	*Forficula auricularia*	Tarragona, Spain	Foliage beating	2.3 (7 is the sum of three samples)
Romeu-Dalmau et al. 2012b	*C. clementina*	Aphididae	Tarragona, Spain	Foliage beating	300
Romeu-Dalmau et al. 2012b	*C. clementina*	*Forficula auricularia*	Tarragona, Spain	Foliage beating	1.25 (median)

Magarey et al. 1993	*C. sinensis*	*Naupactus godmani*	Colignan, Victoria	Foliage beating	14.8

Supplementary Table 3.2. Identification to family of spider samples collected from sampling with foliage beating.

Date	Family
8 May	Agelenidae
	Araneidae
	Segestriidae
	Oxyopidae
	Theridiidae
14 July	Agelenidae
	Sparassidae
	Anyphaenidae
	Oxyopidae
	Salticidae
	Theridiidae
	Dictynidae
25 Sep	Theridiidae
	Salticidae
	Sparassidae
	Theridiidae

Supplementary Table 3.3. Mean number and standard errors (SE) of each arthropod type found on sticky barriers and percentage of sticky barriers with each arthropod type.

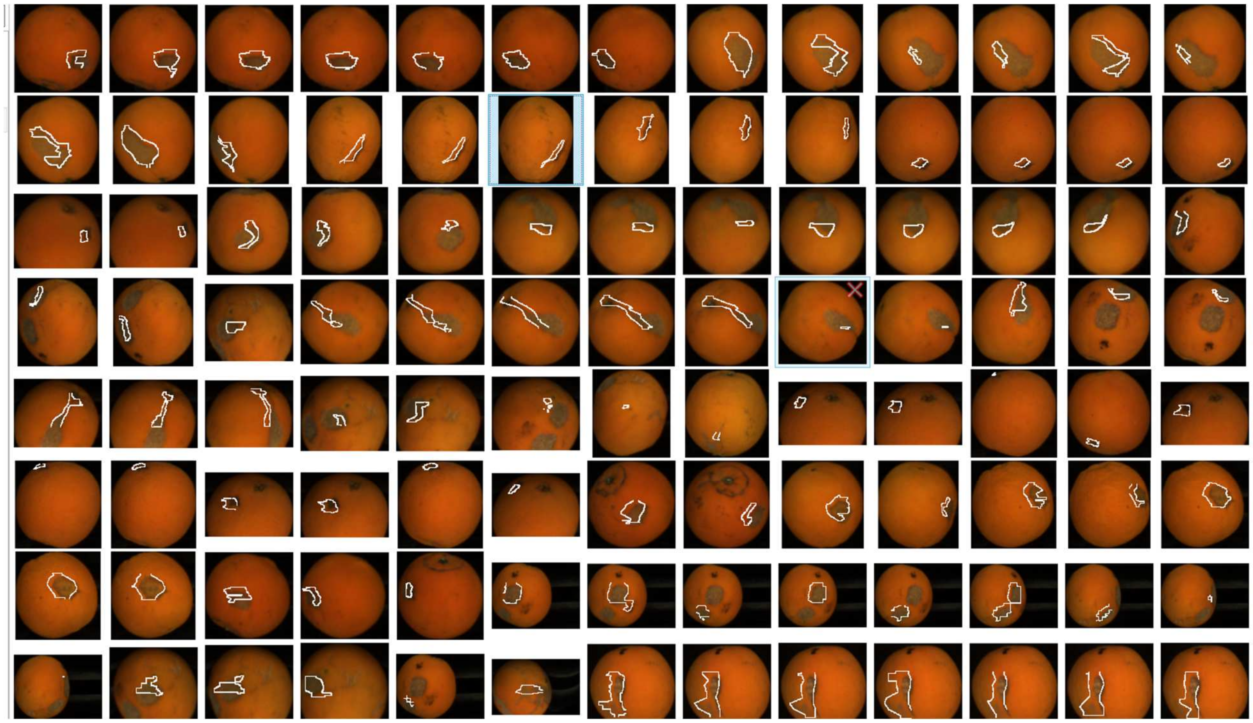
Taxa	Mean numbers	SE	Percent
European earwigs	3	0.58	80%
nymphs	0.13	0.06	13.3%
males	1.33	0.26	63.3%
females	1.53	0.36	60%
Ants	0.77	0.28	30%
Fuller rose beetles	2.07	0.32	76.7%

Supplementary Table 3.4. Median and lower and upper values of the Highest Probability Density (HPD) Interval for specific contrasts from the Bayesian models used to assess arthropod densities not already provided in the main text. Contrasts that suggest statistically meaningful differences (HPD intervals do not include zero) are bolded in the table or are discussed in the main text.

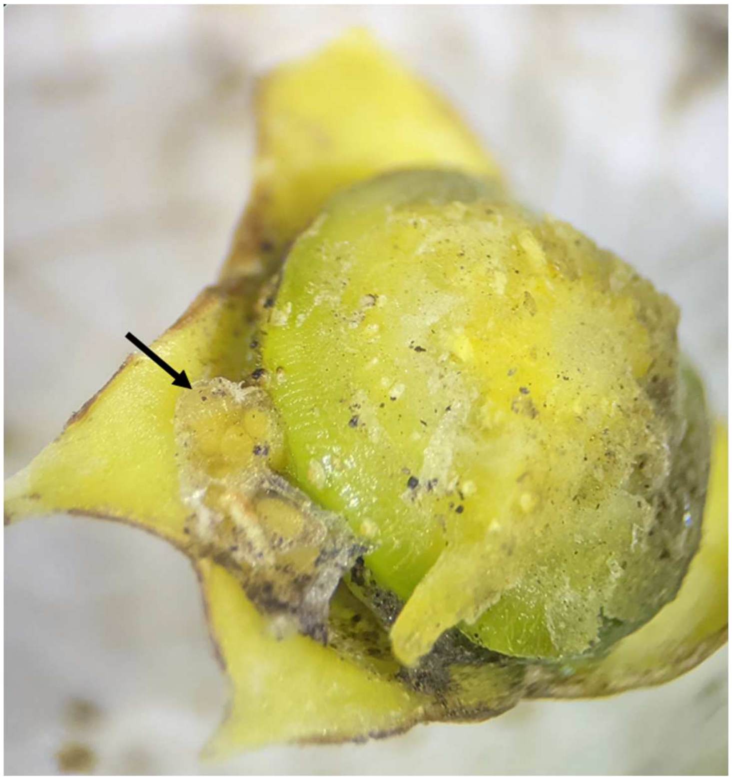
Total earwigs from foliage beating			
Contrast	*Median*	*Lower HPD*	*Upper HPD*
Control vs. Sticky barriers	0.77	-0.17	1.86

Control vs. Bifenthrin barriers	0.43	-0.52	1.41
Bifenthrin vs Sticky barriers	0.32	-0.73	1.55
North vs. East side	0.07	-0.99	1.13
North vs. South side	0.46	-0.76	1.62
North vs. West side	-0.48	-1.53	0.44
East vs. South side	0.38	-0.84	1.60
East vs. West side	-0.55	-1.56	0.39
South vs. West side	-0.96	-2.10	0.19
Total earwigs from cardboard rolls			
Contrast	*Median*	*Lower HPD*	*Upper HPD*
7-8 May: Control vs. Sticky barriers	**2.49**	**0.84**	**4.43**
7-8 May: Control vs. Bifenthrin barriers	0.70	-0.30	1.71
7-8 May: Bifenthrin vs. Sticky barriers	**1.77**	**0.08**	**3.83**
23 June: Control vs. Sticky barriers	**4.18**	**2.17**	**7.04**
23 June: Control vs. Bifenthrin barriers	**2.51**	**1.17**	**3.87**
23 June: Bifenthrin vs. Sticky barriers	1.66	-0.53	4.76
15 July: Control vs. Sticky barriers	10.26	-1.85	29.71
15 July: Control vs. Bifenthrin barriers	9.58	-2.18	29.00
15 July: Bifenthrin vs. Sticky barriers	0.59	-24.92	25.56
25 Sep: Control vs. Sticky barriers	7.19	-10.63	30.04
25 Sep: Control vs. Bifenthrin barriers	-7.00	-20.23	2.18
25 Sep: Bifenthrin vs. Sticky barriers	14.69	-1.89	37.52
North vs. South side	-0.26	-0.83	0.31
Ants from foliage beat samples			
Contrast	*Median*	*Lower HPD*	*Upper HPD*
North vs. East side	0.33	-0.10	0.77
North vs. South side	0.44	-0.06	0.87
North vs. West side	0.33	-0.12	0.79
East vs. South side	0.11	-0.37	0.58
East vs. West side	-0.001	-0.49	0.49
South vs. West side	-0.11	-0.61	0.40
Spiders from foliage beat samples			
Contrast	*Median*	*Lower HPD*	*Upper HPD*
Control vs. Sticky barriers	-0.07	-0.32	0.16
Control vs. Bifenthrin barriers	-0.02	-0.26	0.21
Bifenthrin vs. Sticky barriers	-0.05	-0.28	0.18
North vs. East side	-0.04	-0.29	0.19
North vs. South side	0.08	-0.17	0.33
North vs. West side	0.16	-0.11	0.42
East vs. South side	0.13	-0.11	0.38
East vs. West side	0.20	-0.05	0.47
South vs. West side	0.08	-0.21	0.33
Spiders from cardboard rolls			
7-8 May: Control vs. Sticky barriers	-0.03	-0.40	0.31
7-8 May: Control vs. Bifenthrin barriers	-0.02	-0.37	0.34

7-8 May: Bifenthrin vs. Sticky barriers	-0.02	-0.50	0.43
23 June: Control vs. Sticky barriers	-0.02	-0.51	0.51
23 June: Control vs. Bifenthrin barriers	0.06	-0.50	0.59
23 June: Bifenthrin vs. Sticky barriers	-0.08	-0.75	0.65
15 July: Control vs. Sticky barriers	0.06	-0.46	0.64
15 July: Control vs. Bifenthrin barriers	0.05	-0.50	0.56
15 July: Bifenthrin vs. Sticky barriers	0.02	-0.74	0.69
25 Sep: Control vs. Sticky barriers	0.01	-0.54	0.51
25 Sep: Control vs. Bifenthrin barriers	-0.10	-0.61	0.38
25 Sep: Bifenthrin vs. Sticky barriers	0.11	-0.56	0.81
North vs. South side	0.04	-0.28	0.39
Aphids from foliage beat samples			
Contrast	*Median*	*Lower HPD*	*Upper HPD*
Control vs. Sticky barriers	-0.59	-1.51	0.34
Control vs. Bifenthrin barriers	-0.77	-1.74	0.08
Bifenthrin vs. Sticky barriers	0.21	-0.73	1.05
North vs. East side	-0.34	-1.04	0.32
North vs. South side	-0.56	-1.22	0.08
North vs. West side	0.01	-0.68	0.78
East vs. South side	-0.23	-0.85	0.38
East vs. West side	0.35	-0.34	1.07
South vs. West side	0.58	-0.06	1.25
California red scale from leaf assessments			
Contrast	*Median*	*Lower HPD*	*Upper HPD*
Control vs. Sticky barriers	-0.02	-0.17	0.14
Control vs. Bifenthrin barriers	-0.13	-0.30	0.03
Bifenthrin vs. Sticky barriers	0.11	-0.06	0.26



Supplementary Figure 3.1. Images of navel orange fruit used to train the packline software to recognize chewing damage on fruit. This damage was assumed to be katydid damage and was used previously to assess levels of katydid fruit damage.



Supplementary Figure 3.2. Fuller rose beetle eggs in the crevice of the sepal. The black arrow points to an egg mass with yellow oval viable eggs.