

Horticultural Entomology

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

Hanna M. Kahl,^{1,4} Tobias G. Mueller,¹ Bodil N. Cass,¹ Xinqiang Xi,² Emma Cluff,¹ Elizabeth E. Grafton-Cardwell,³ and Jay A. Rosenheim¹

¹Department of Entomology and Nematology, University of California, Davis, CA 95616, USA, ²Department of Ecology, Nanjing University, Nanjing 210093, China, ³Department of Entomology, University of California, Riverside, CA 92521, USA, and ⁴Corresponding author, e-mail: hkahl@ucdavis.edu

Subject Editor: Jana Lee

Received 16 February 2021; Editorial decision 19 May 2021

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: (1) whether earwigs damage young citrus fruit; (2) whether the amount of damage earwigs generate differs across developmental stage or sex of adult earwigs; (3) the window of time during which fruit are most sensitive to earwig damage; (4) whether damaged fruit are retained to harvest; and (5) the resulting damage morphology caused by earwigs relative to katydids. Earwigs, particularly nymphs, chewed deep holes in young citrus fruit from 0 to 3 wk 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.

Key words: earwig, citrus, herbivory, abscission, life stage

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 the 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 et al. 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 (*Scudderella 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 the 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 bite mark(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 et al. 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: (1) whether earwigs damage young citrus fruit; (2) whether the amount of damage earwigs generate differs across earwig developmental stage or the sex of adult earwigs; (3) what is the window of time during which fruit are sensitive to earwig damage; (4) whether damaged fruit are selectively abscised, or instead, retained to harvest;

(5) 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 29 April 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.

Katydid (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 × W75 × H115 cm, and two BugDorm-2021F Insect Tents L61 × W61 × 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 (1) no insects (control), (2) an earwig nymph (mixed instars), (3) an earwig adult female, (4) an earwig adult male, or (5) 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 the development of fruit damage and recorded whether each tagged fruit had abscised on four dates: June 13 (45 d post-petal fall), August 8 (113 d post-petal fall), and October 16 (169 d post-petal fall), 2019, and 3 February 2020 (harvest; 280 d post-petal fall). This allowed us to determine whether damaged fruits 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 (180° 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 (1) no earwigs (control) or (2) 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 was 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 the 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: (1) earwig (average of nymph, adult male, and adult female) vs. control treatments; (2) katydid vs. control treatments; (3) earwig nymph vs. earwig adults (average of male and female) treatments, and (4) 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 (Supp Methods: A1 [online only]).

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 $\times$ 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 (Supp Methods: A1 [online only]).

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 χ^2 tests (*Anova*; package *car*; Fox and 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 2021) 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 d post-petal fall, respectively); 62 d 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 χ^2 tests were used to assess model effects (*Anova*; package *car*; Fox and 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 χ^2 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)) (Figs. 1 and 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 smaller proportions with deep holes. There were also differences in the proportion of deep hole damage caused by earwig nymphs and adults (Fig. 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. 2) and the proportion of fruit surface damaged on damaged fruit (conditional component; $X^2 = 79.6$, $df = 4$, $P < 0.001$; Fig. 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; $\beta = 0.31$, $df = 753$, $t = 5.89$, $P < 0.001$) and earwig treatments ($\beta = 1.30$, $df = 753$, $t = 8.46$, $P < 0.001$).

In our study, the earwig nymphs tested ranged from 8 to 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 ($\beta = -2.00$, $t = -2.33$, $df = 78$, $P = 0.02$; Fig. 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 d 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 (Supp Table S1: Model 3 [online only]). Increasing the proportion of fruit removed decreased early fruit abscission ($\beta = -1.27$, $z = -2.27$, $P = 0.02$). Fruit exposed to katydids also abscised marginally more frequently compared fruit exposed to the control ($\beta = 1.07$, $z = 1.95$, $P = 0.052$; Fig. 5A; Supp Table S1 [online only]), 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 ($\beta = 2.39$, $z = 2.44$, $P = 0.01$; Supp Table S1: Model 6 [online only] and Fig. 5B). However, once treatment and proportion of fruit removed were included in the model, there was no additional impact of the proportion of fruit surface area damaged. There were relatively few fruits that abscised late and, none of the models examining impacts on late abscission contained significant effects. However, when considered with other effects, the proportion of fruit surface area damaged was marginally significant in many of the models (Supp Table S2 [online only]). When earwig-damaged fruit was considered alone, the 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 fruits 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

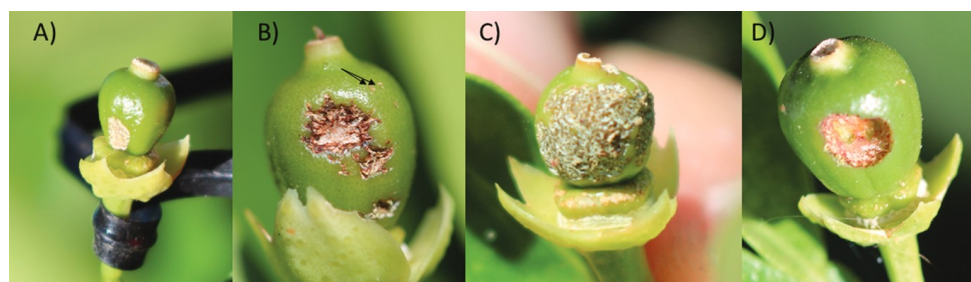


Fig. 1. Examples of initial fruit damage. A) surface chewed on earwig-exposed fruit. B) deep holes and small cuts on earwig-exposed fruit. The arrows point at examples of small cuts. C) surface chewed on katydid-exposed fruit. D) deep hole on katydid-exposed fruit. Damage category definitions: small 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.

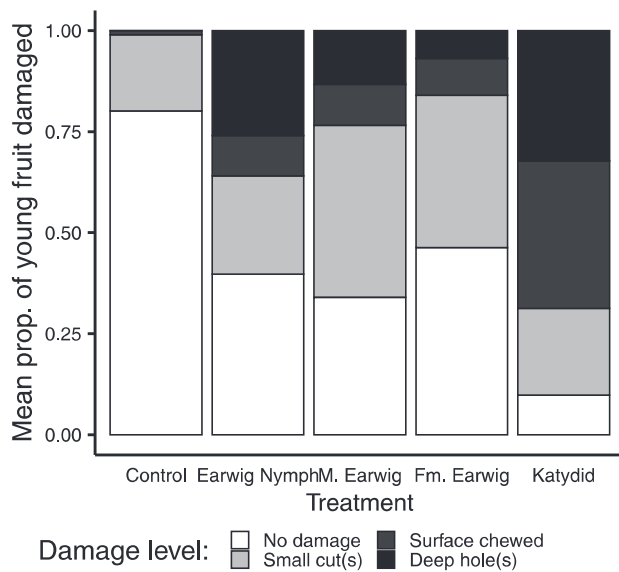


Fig. 2. Mean proportion of fruit that had each damage level (no damage, small cut(s), surface chewed, and deep hole(s)) across insect treatments (control, earwig nymph, male earwig adult, female earwig adult, and katydid) in Experiment 1 averaged first by cage and then treatment.

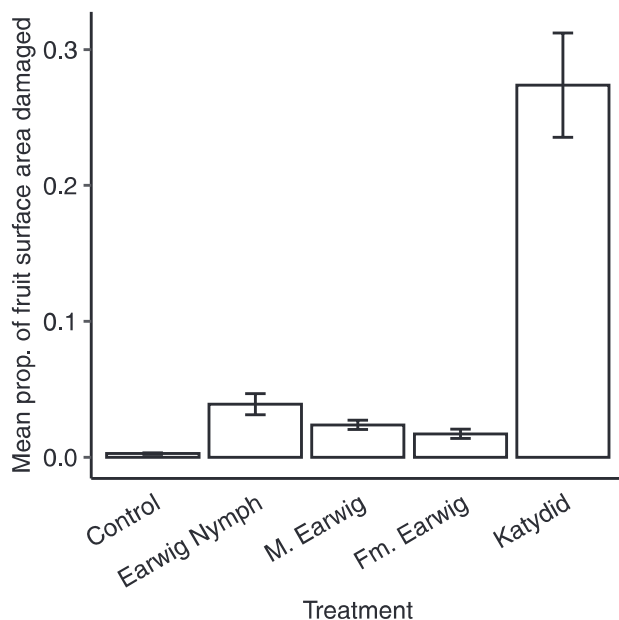


Fig. 3. Mean and standard error of proportion of fruit surface area damaged across insect treatments (control, earwig nymph, male earwig adult, female earwig adult, and katydid) averaged first by cage then treatment at initial fruit evaluation in Experiment 1 (fruit with no damage, zeros, included).

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. 6). All fruit with more than 75% of the surface damaged were from the katydid treatment and all of these fruits abscised. Because the abscission rate was selectively higher for these heavily-damaged katydid-exposed fruits, fewer fruits 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 (Figs. 5B and 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. 7B–E), whereas katydid scars were often irregularly shaped and branching (Fig. 7F and 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. 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 ($\beta = 1.86$, $df = 45$, $t = 2.84$, $P = 0.03$) or earwig treatments ($\beta = 1.35$, $df = 45$, $t = 3.84$, $P = 0.002$).

Scarring damage caused fruit to grow asymmetrically, resulting in mildly deformed fruit at harvest: the relationship between initial surface area damaged and the 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 ($\beta = -0.002$, $t = -2.0$ 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. 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. 9).

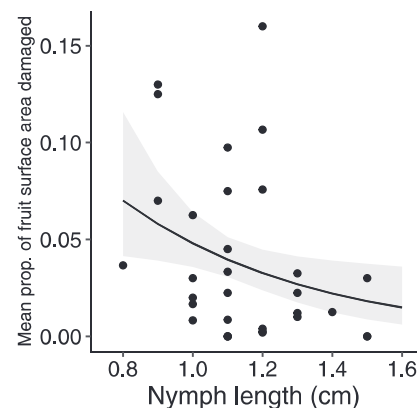


Fig. 4. Influence of earwig nymph body length (cm) on the mean proportion of fruit surface area damaged after a six-day exposure to herbivory in Experiment 1. The line and confidence interval (shaded area) are predictions from the zero-inflated beta generalized linear mixed-effect model.

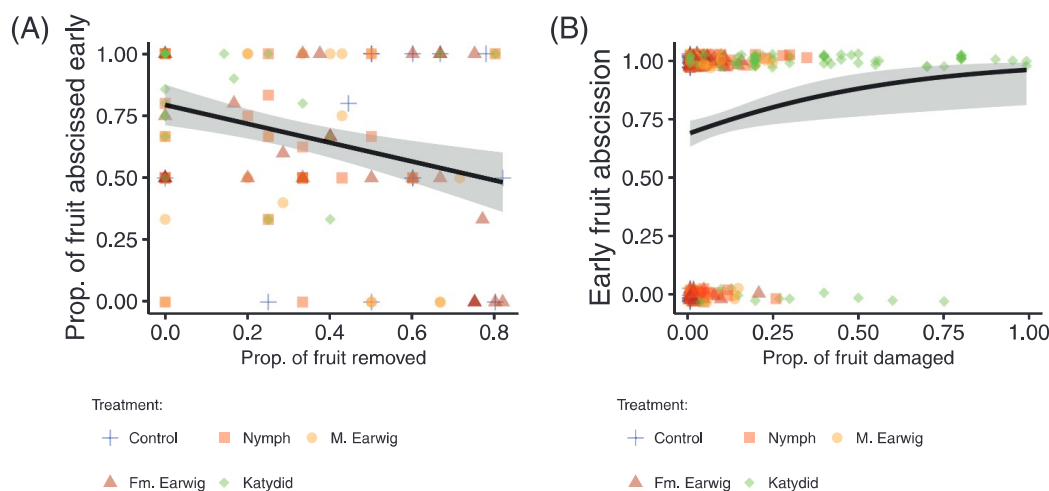


Fig. 5. Factors influencing fruit abscission in Experiment 1. A) Influence of the proportion of fruit removed from each cage (because they had no damage) on the likelihood of early fruit abscission. The line and confidence interval are linear predictions. B) Influence of proportion of fruit surface area damaged by herbivory on early (before 62 d post-petal fall) fruit abscission (0: did not abscise; 1: abscised). The line and confidence interval are predictions from the binomial generalized linear model.

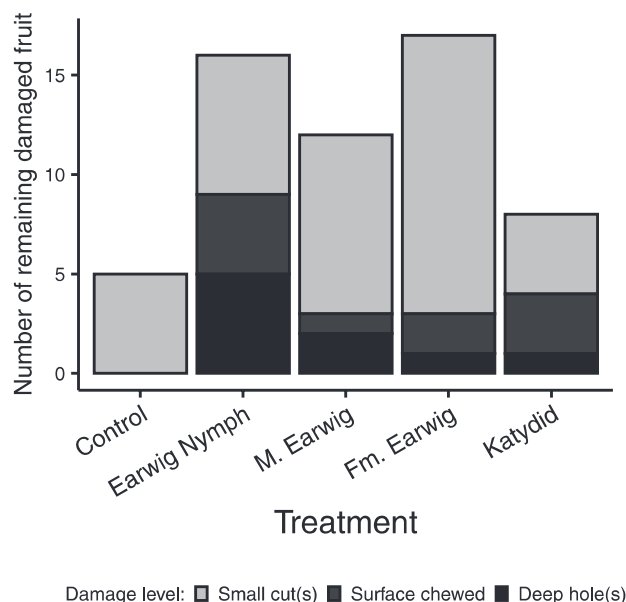


Fig. 6. Numbers of fruit remaining to harvest, categorized by initial damage levels (small cut(s), surface chewed, and deep hole(s)) across insect treatment (control, earwig nymph, male earwig, female earwig, and katydid).

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. 10); in the earwig treatment, there was 0.01–0.43 (95% mean quantile interval (QI)) smaller proportions of fruit with no damage, 0.01–0.35 larger proportions with small cuts, 0–0.12 larger proportions 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. 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.

Katydid are recognized as notorious early-season citrus pests, and damage caused by katydids has been carefully studied (Cass et al. 2019a, b, c; Cass et al. 2021). Thus, it is not surprising that initial damage severity and intensity caused by katydids surpassed

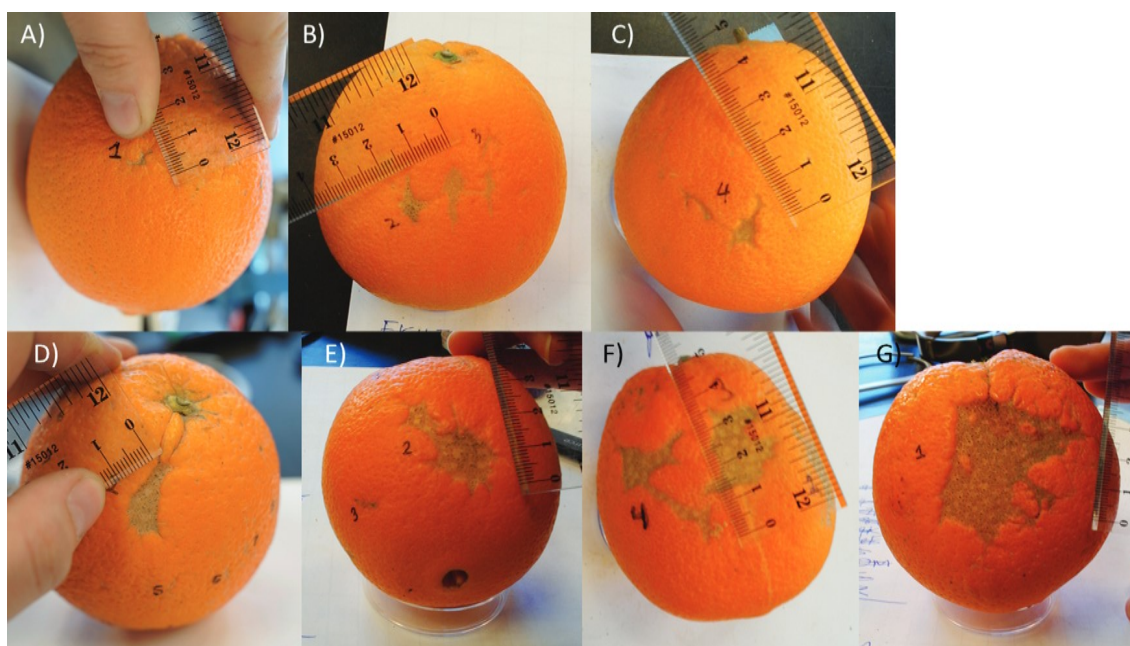


Fig. 7. Examples of fruit damage at harvest and descriptions of initial damage evaluations in order of increasing severity in Experiment 1. Figures (A–E) are fruit exposed to earwigs, and figures (F) and (G) are fruit severely damaged by katydids. A) Fruit initially had 3% small cut damage. B) Fruit 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.

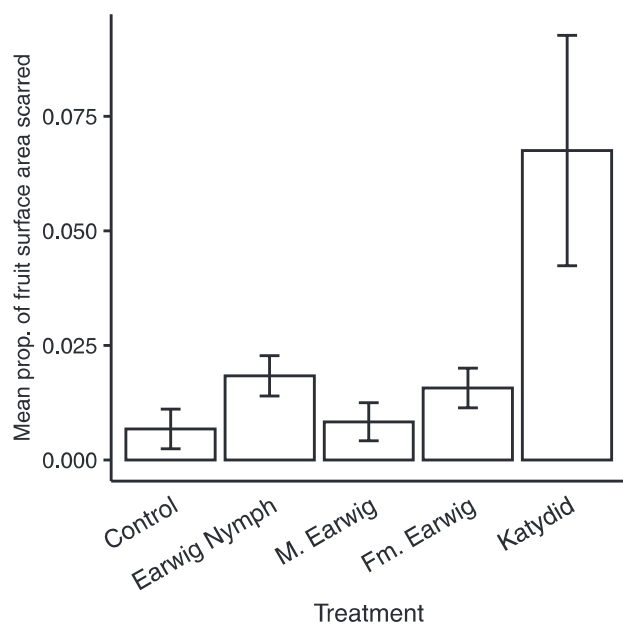


Fig. 8. Experiment 1: Mean and standard error of proportion of fruit surface area scarred at harvest across insect treatments (control, earwig nymph, male earwig adult, female earwig adult, and katydid) averaged first by cage then treatment (fruit that healed and had no scarring, zeros, included).

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

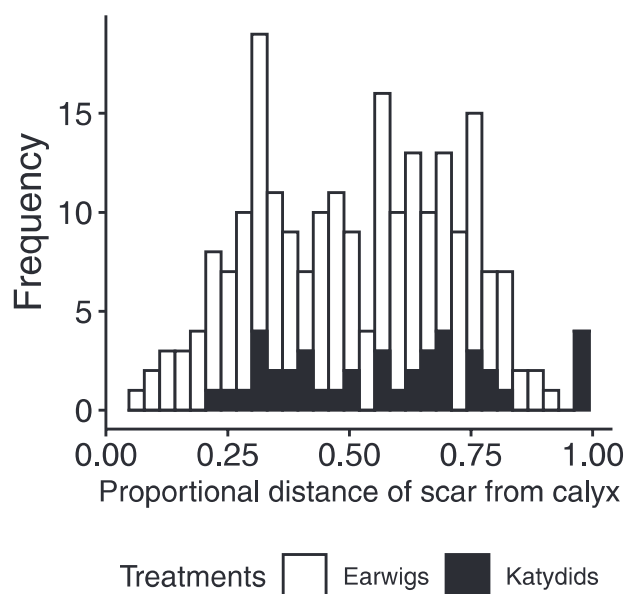


Fig. 9. Distribution of the proportional distance of scars from the calyx for earwig and katydid damaged fruit. A proportional distance of 0 indicates feeding adjacent to the calyx, whereas a proportional distance of 1 indicates feeding directly adjacent to the style.

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.

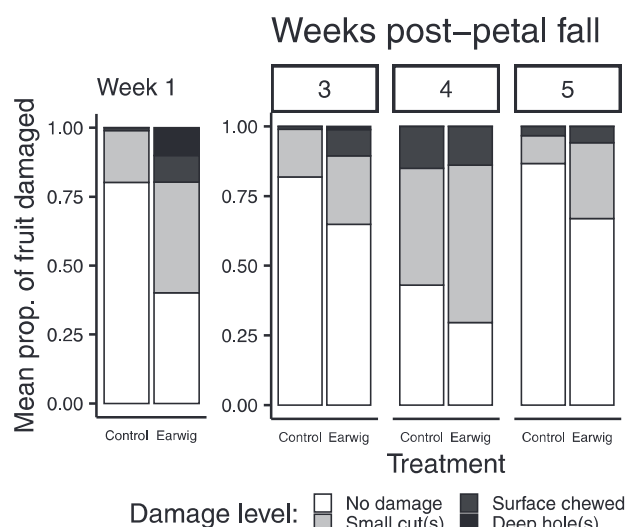


Fig. 10. Experiment 2: Mean proportion of fruit that had each damage level (no damage, small cut(s), surface chewed, and deep hole(s)) across treatment (control and four adult earwigs) and weeks post-petal fall (3, 4, and 5) averaged first by cage and then treatment. Mean proportion damage level of fruit exposed to a single adult in Experiment 1, which was run during the 1st week post-petal fall is also shown for reference.

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 and 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, the 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 the 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 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 the 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 the 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 the 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 the 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 recommendations 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 the 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.

Supplementary Data

Supplementary data are available at *Journal of Economic Entomology* online.

Acknowledgments

We thank Stephanie Doria-Kelly, Adrianna Oliver, Joshua Reger, Salvador Barcenás, and the LREC station staff for assistance with field work, and California citrus growers for helping us find katydids. We also thank Louie Yang and Ian Grettenberger for comments on the manuscript. This research was funded by the Citrus Research Board grants (5500-220 and 5500-501), California Department of Pesticide Regulation contracts 11-C0089 and 13-C0064 and grant 18-PML-R001, and an NSF Graduate Research Fellowship to HMK (1650042). XX was financially supported by the China Postdoctoral Exchange Fellowship Program.

References Cited

- Bates, D., M. Mächler, B. Bolker, and S. Walker. 2015. Fitting Linear Mixed-Effects Models Using lme4. *J. Stat. Softw.* 67: 1–48.
- Bottrell, D. R. 1979. Integrated pest management. Council on Environmental Quality, Washington, DC.
- Brooks, M. E., K. Kristensen, K. J. van Benthem, A. Magnusson, C. W. Berg, A. Nielsen, H. J. Skaug, M. Maechler, and B. M. Bolker. 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *R J.* 9: 378–400.
- Bürkner, P.-C. 2017. brms: an R package for Bayesian multilevel models using Stan. *J. Stat. Softw.* 80: 1–28.
- Bürkner, P.-C. 2018. Advanced Bayesian multilevel modeling with the R package brms. *R J.* 10: 395–411.
- Bürkner, P.-C., and M. Vuorre. 2019. ordinal Regression models in psychology: a tutorial. *Adv. Methods Pract. Psychol. Sci.* 2: 77–101.
- Carroll, D. P., J. T. S. Walker, and S. C. Hoyt. 1985. European earwigs (Dermaptera: Forficulidae) fail to control apple aphids on bearing apple trees and woolly apple aphids (Homoptera: Aphididae) in apple rootstock stool beds. *J. Econ. Entomol.* 78: 972–974.
- Cass, B. N., E. E. Grafton-Cardwell, and J. A. Rosenheim. 2019a. Resistance of fruits from a mandarin cultivar to feeding by fork-tailed Bush Katydid. *J. Econ. Entomol.* 112: 2861–2871.
- Cass, B., E. Grafton-Cardwell, and J. A. Rosenheim. 2019b. A ‘big data’ approach for pest management in mandarins. *Citrograph.* 10: 62–65.
- Cass, B. N., L. M. Hack, E. E. Grafton-Cardwell, and J. A. Rosenheim. 2019c. Impacts of fruit-feeding arthropod pests on oranges and mandarins in California. *J. Econ. Entomol.* 112: 2268–2277.
- Cass, B. N., H. M. Kahl, T. G. Mueller, X. Xi, E. E. Grafton-Cardwell, and J. A. Rosenheim. 2021. Profile of fork-tailed Bush Katydid (Orthoptera: Tettigoniidae) feeding on fruit of clementine mandarins. *J. Econ. Entomol.* 114: 215–224.

- (CDFA) California Department of Food and Agriculture. 2019. California agricultural statistics review 2018–2019. CDFA, Sacramento, CA.
- (CDFA) California Department of Food and Agriculture & (CASS) California Agricultural Statistics Service. 2018. 2018 California citrus acreage report. USDA's National Agricultural Statistics Service (NASS), Sacramento, CA.
- Chapman, J. C. 1984. Ethephon as a fruit thinning agent for 'Murcott' mandarins. *Sci. Hortic. (Amsterdam)*. 24: 135–141.
- Crumb, S. E., P. M. Eide, and A. E. Bonn. 1941. The European earwig. *USDA Tech. Bull.* 766: 1–76.
- Ehi-Eromosele, C. O., O. C. Nwinyi, and O. O. Ajani. 2013. Integrated pest management, pp. 105–115. *In* Soloneski, S., Larramendy, M. L. (eds.), *Weed and pest control*. InTech, London, UK.
- Flint, M. L., S. Daar, and R. Molinar. 2003. Establishing integrated pest management policies and programs: a guide for public agencies. *ANR Publ.* 8093: 1–13.
- Fox, J., and S. Weisberg. 2019. An {R} companion to applied regression, Third. ed. Sage, Thousand Oaks, CA.
- Gómez-Cadenas, A., J. Mehouchi, F. R. Tadeo, E. Primo-Millo, and M. Talon. 2000. Hormonal regulation of fruitlet abscission induced by carbohydrate shortage in citrus. *Planta*. 210: 636–643.
- Goren, R. 1993. Anatomical, physiological, and hormonal aspects of abscission in citrus. *Hortic. Rev.* 15: 145–182.
- Grafton-Cardwell, E. E., N. V. O'Connell, C. E. Kallsen, and J. G. Morse. 2003. Photographic guide to citrus fruit scarring. *ANR Publ.* 8090: 1–8.
- Grafton-Cardwell, E. E., R. A. Baldwin, J. O. Becker, A. Eskalen, C. J. Lovatt, S. Rios, J. E. Adaskaveg, B. A. Faber, D. R. Haviland, K. J. Hembre, *et al.* 2020. UC IPM pest management guidelines: citrus. UCANR Publ., Oakland, CA.
- Greenberg, J., S. Holtzman, M. Fainzack, Y. Egozi, B. Giladi, Y. Oren, and I. Kaplan. 2010. Effects of NAA and GA3 sprays on fruit size and the incidence of creasing of 'Washington' navel orange. *Acta Hortic.* 884: 273–280.
- He, X. Z., Q. Wang, and J. Xu. 2008. European earwig as a potential biological control agent of apple leaf-curling midge. *New Zeal. Plant Prot.* 61: 343–349.
- Headrick, D. 2000. Fork-tailed Katydid studies. *Citrus Research Board Annual Report*.
- Kallsen, C. 2006. Earwigs flying under the radar of many citrus pest control advisors. *West. Farm Press*. 1–3.
- Kekelidze, N. A., E. P. Lomidze, and M. I. Janikashvili. 1989. Analysis of terpene variation in leaves and fruits of Citrus unshiu Marc. during ontogenesis. *Flavour Fragr. J.* 4: 37–41.
- Korner-Nievergelt, F., T. Roth, S. von Felten, J. Guélat, B. Almasi, and P. Korner-Nievergelt. 2015. The Bayesian and the frequentist ways of analyzing data, pp. 19–31. *In* Bayesian data anal. ecol. using linear model. with R, bugs, Stan. Academic Press.
- Kostenyuk, I. A., and J. K. Burns. 2004. Mechanical wounding and abscission in citrus. *Physiol. Plant* 122: 354–361.
- Lenth, R. 2021. emmeans: estimated marginal means, aka least-squares means, R package version 1.6.0. <https://CRAN.R-project.org/package=emmeans>
- Logan, D. P., B. J. Maher, and P. G. Connolly. 2011. Increased numbers of earwigs (*Forficula auricularia*) in kiwifruit orchards are associated with fewer broad-spectrum sprays. *New Zeal. Plant Prot.* 64: 49–54.
- Malagnoux, L., Y. Capowicz, and M. Rault. 2015. Impact of insecticide exposure on the predation activity of the European earwig *Forficula auricularia*. *Environ. Sci. Pollut. Res. Int.* 22: 14116–14126.
- McElreath, R. 2020. Statistical rethinking, Second. ed. Stat. Rethink. Chapman and Hall/CRC, Boca Raton, FL.
- Mcgowan, M. J. 2000. Ordinal outcomes with the continuation ratio model, pp. 1–4. *In* Northeast SAS users Gr. Philadelphia, PA.
- Mueller, T. G., H. M. Kahl, B. N. Cass, E. E. Grafton-Cardwell, and J. A. Rosenheim. 2019. Differential impacts of citrus thrips across sweet orange and mandarin species. *J. Econ. Entomol.* 112: 2767–2773.
- O'Connell, N. 2014. Citrus, earwigs, and tree wraps. *Top. Subtrop.* 1–6.
- Orpet, R. J., D. W. Crowder, and V. P. Jones. 2019. Biology and management of European earwig in orchards and vineyards. *J. Integr. Pest Manag.* 10: 1–9.
- Ouma, G. 2012. Fruit thinning with specific reference to citrus species : a review. *Agric. Biol. J. North Am.* 3: 175–191.
- Owen-Turner, J., D. Smith, P. Mayers, and N. Vock. 1997. Citrus information kit. Agrilink, your growing guide to better farming guide. Department of Primary Industries, Queensland Horticulture Institute, Brisbane, Queensland.
- Piñol, J., X. Espadaler, N. Cañellas, and N. Pérez. 2009a. Effects of the concurrent exclusion of ants and earwigs on aphid abundance in an organic citrus grove. *BioControl*. 54: 515–527.
- Piñol, J., X. Espadaler, N. Pérez, and K. Beven. 2009b. Testing a new model of aphid abundance with sedentary and non-sedentary predators. *Ecol. Modell.* 220: 2469–2480.
- Piñol, J., X. Espadaler, N. Cañellas, J. MartíNez-Vilalta, J. A. Barrientos, and D. Sol. 2010. Ant versus bird exclusion effects on the arthropod assemblage of an organic citrus grove. *Ecol. Entomol.* 35: 367–376.
- Piñol, J., X. Espadaler, and N. Cañellas. 2012. Eight years of ant-exclusion from citrus canopies: effects on the arthropod assemblage and on fruit yield. *Agric. For. Entomol.* 14: 49–57.
- Planes, L., J. Catalan, A. Urbaneja, and A. Tena. 2014. Within-tree and temporal distribution of *Pezothrips kellyanus* (Thysanoptera: Thripidae) nymphs in citrus canopies and their influence on premature fruit abscission. *Environ. Entomol.* 43: 689–695.
- R Core Team. 2020. R: a language and environment for statistical computing. R Found. Stat. Comput., Vienna, Austria.
- Radesäter, T., and H. Halldórsdóttir. 1993. Two male types of the common earwig: male-male competition and mating success. *Ethology*. 95: 89–96.
- Rodríguez, A., V. S. Andrés, M. Cervera, A. Redondo, B. Alquézar, T. Shimada, J. Gadea, M. Rodrigo, L. Zacarías, L. Palou, *et al.* 2011. The monoterpene limonene in orange peels attracts pests and microorganisms. *Plant Signal. Behav.* 6: 1820–1823.
- Romeu-Dalmau, C. 2012. Friend or foe? The relative role of earwigs as pests versus biocontrol agents in citrus canopies. Ph.D. dissertation, Universitat Autònoma de Barcelona.
- Romeu-Dalmau, C., P. Gu, S. Scott, and B. Grafton-Cardwell. 2012a. Earwigs: pests or beneficials in California citrus orchards? *Citrograph.* January/February: 18–22.
- Romeu-Dalmau, C., J. Piñol, and N. Agustí. 2012b. Detecting aphid predation by earwigs in organic citrus orchards using molecular markers. *Bull. Entomol. Res.* 102: 566–572.
- Romeu-Dalmau, C., J. Xinol, and X. Espadaler. 2012c. Friend or foe ? The relative role of earwigs as pests versus biocontrol agents in citrus canopies. *Biol. Control*. 63: 143–149.
- Simpson, S. J., and P. R. White. 1990. Associative learning and locust feeding: evidence for a "learned hunger" for protein. *Anim. Behav.* 40: 506–513.
- Tomkins, J. L., and L. W. Simmons. 1995. Patterns of fluctuating asymmetry in earwig forceps: No evidence for reliable signalling. *Proc. R. Soc. B Biol. Sci.* 259: 89–96.
- Wheeler, D. 1996. The role of nourishment in oogenesis. *Annu. Rev. Entomol.* 41: 407–431.
- Wickham, H., M. Averick, J. Bryan, W. Chang, M. D'Agostino, R. François, G. Grolemond, A. Hayes, L. Henry, J. Hester, *et al.* 2019. Welcome to the tidyverse. *J. Open Source Softw.* 4: 1686.