

Plant Resistance

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

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Abstract

Agricultural plant 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 are based upon research conducted on navel oranges [*Citrus sinensis* (L.) Osbeck; Sapindales: Rutaceae]. A recent study has established European earwigs (*Forficula auricularia* L.; Dermaptera: Forficulidae) as herbivores of young navel orange fruit, causing damage ranging from small bite marks to large chewed holes. It is unknown whether earwigs damage fruit of other citrus species. We conducted field experiments in which we caged earwigs to branch terminals bearing young fruit to explore potential differences in susceptibility of *Citrus* species to European earwigs. Specifically, we tested whether three species, navel oranges, clementines (*C. clementina* hort. ex Tanaka), and true mandarins (*C. reticulata* Blanco) 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. Earwigs caused heavy damage on navel orange and clementine fruit, whereas heavy damage was rare on true mandarin fruit. There was little evidence of preferential abscission of damaged fruit or healing of seriously damaged fruit. Consequently, several heavily damaged navel orange and one clementine fruit were retained to harvest and developed large scars. Overall, we found that *Citrus* fruit vary in their susceptibility to earwigs, and pest management strategies for earwigs should be refined to consider their varying effects on different *Citrus* species.

Key words: earwig, citrus cultivar, herbivory, resistance

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 that plants 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, Mitchell et al. 2016, War et al. 2012). Plants can resist herbivory through natural defenses that can deter pests, reduce pest survival, or reduce pest reproduction (Chakraborti et al. 2009, Duffey and Stout 1996, Felton 2005). 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). In California there are at least seven cultivated citrus species, but citrus species and cultivars have complex, debated phylogenies (Wu et al. 2014, 2018) 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) based on research conducted mainly in navel oranges, which historically dominated acreage. However, clementines and true mandarins have been increasing in acreage in California (CDFA and CASS 2020). If these citrus species are more or less susceptible to arthropod pests, or pests behave differently on 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 across species.

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, finding that damage by several herbivores was lower in ‘Tango’ and ‘Afourer’ mandarins compared to navel oranges (Cass et al. 2019a, 2020). 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 (navel oranges, clementines, and true mandarins). 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 before harvest in clementines (Cass et al. 2021), and early in the growing season in navel oranges (Kahl et al. 2021), but not in true mandarins (Cass 2019b). These species also differ in the fruit scarring patterns produced in response to early-season feeding by katydids, with navel orange fruit fed on by katydids usually exhibiting distinctive round scars, and clementine fruit exhibiting more weblike and diffuse scars (Cass et al. 2021). These studies indicate that pest management approaches that were based on navel oranges 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, Espadaler, et al. 2012). Although earwigs are generally understood to be either pests or predators in some crop systems, the role of earwigs in citrus systems is understudied (Orpet et al. 2019). Over approximately the last fifteen years, earwigs have been reported to be increasing in numbers, and damage suspected to be caused by earwigs has become a growing concern (Kallsen 2006, Logan et al. 2011). Recently, it was found that earwigs confined on citrus branch terminals severely damaged young navel orange fruit; fruit that sustained extensive earwig damage either abscised or developed prominent scars as they matured (Kahl et al. 2021), likely resulting in downgrading of fruit at the packinghouse and reduced grower profits. However, we do not yet know whether earwigs damage young true mandarin and clementine 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 to earwig fruit feeding differ across common cultivars of three citrus species (navel oranges, clementines, and true mandarins) grown in California. Specifically, we asked the following questions: (1) What are the characteristics and extent of feeding by earwigs on young fruit across the citrus species? (2) Are some citrus species an unsuitable food source for earwigs, resulting in earwig death? (3) Do trees preferentially abscise damaged

fruit, and does this vary across species? (4) Can some citrus species ‘heal’ damaged fruit, such that damage visible on young fruit disappears by the time of harvest?

Materials and Methods

2018 Experiments

Experiment in Navel Oranges

In 2018 an experiment was set up in a navel orange planting (‘Parent Washington’; 26 yr old; 3.87 acres) at the Lindcove Research and Extension Center (LREC) in Lindcove (36.360895, -119.062348), Tulare County, CA on 8 May 2018 (14 d after petal fall). 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 (California Citrus Mutual 2019); petal fall was declared on 24 April 2018 by the Tulare County Agricultural Commissioner. Only ant bait (Clinch, Syngenta; Basel, Switzerland) was applied to this field on 3 May 2018. We choose three ~20 cm long branch terminals with 4–20 fruit on each of ten trees, bearing 172 navel orange fruit total. Fruit length, measured from calyx to style, averaged 7.4 mm (range: 4–11 mm). We recorded the number of fruit on each branch terminal and used 19-liter (5 gallon) mesh paint strainer bag enclosures (Brand: HDX; mesh size of 0.6 mm or less) to cage released earwigs on branch terminals while excluding other herbivores. Each tree received one replicate of each of three treatments: 1) no earwig (control), 2) an earwig nymph (mixed instars), or 3) an earwig adult (mixed sexes). Earwigs were collected from black foam trunk shields (‘Sprout Saver’; 46 cm in length) on young citrus trees of mixed species at LREC on 8 May and were directly used in the experiment.

Bags and caged 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 7 d after the bags were installed (15 May 2018); 80 navel orange fruit abscised during treatment exposure or during handling and were excluded from analysis. Status (alive, dead, or missing) of caged earwigs was recorded. The proportion of earwigs dead out of total earwigs recovered (dead or alive) after the trial was calculated. One replicate was reassigned as a control treatment as the earwig nymph was accidentally not released into the cage. We then evaluated each fruit for three increasingly severe categories of fruit damage: 1) small cut(s) – distinct individual bitemark(s) chewed into fruits, 2) surface chewing damage—extensive and overlapping superficial chewing on fruit, and 3) deep hole(s) – a crater in the fruit from extensive feeding in one location (Fig. 1A and B). These damage categories have been used in other studies of katydid and earwig damage in citrus (Cass et al. 2019b, 2021; Kahl et al. 2021). We found that when herbivores make small cuts in young fruit 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, 2020; Kahl et al. 2021). We also calculated each fruit’s total proportion of surface area damaged by summing proportions across all damage categories. Fruit were not monitored until harvest in 2018, and thus questions of differential abscission, healing, and damage at harvest were not examined.

Experiment in True Mandarins

This experiment was set up in a true mandarin planting (cv. ‘Tango’; 4 yr old; 1.39 acres) at LREC on 8 May 2018. Only ant bait (Clinch, Syngenta; Basel, Switzerland) was applied to this field on 3 May 2018. We chose three ~20 cm long branch terminals with 4–20

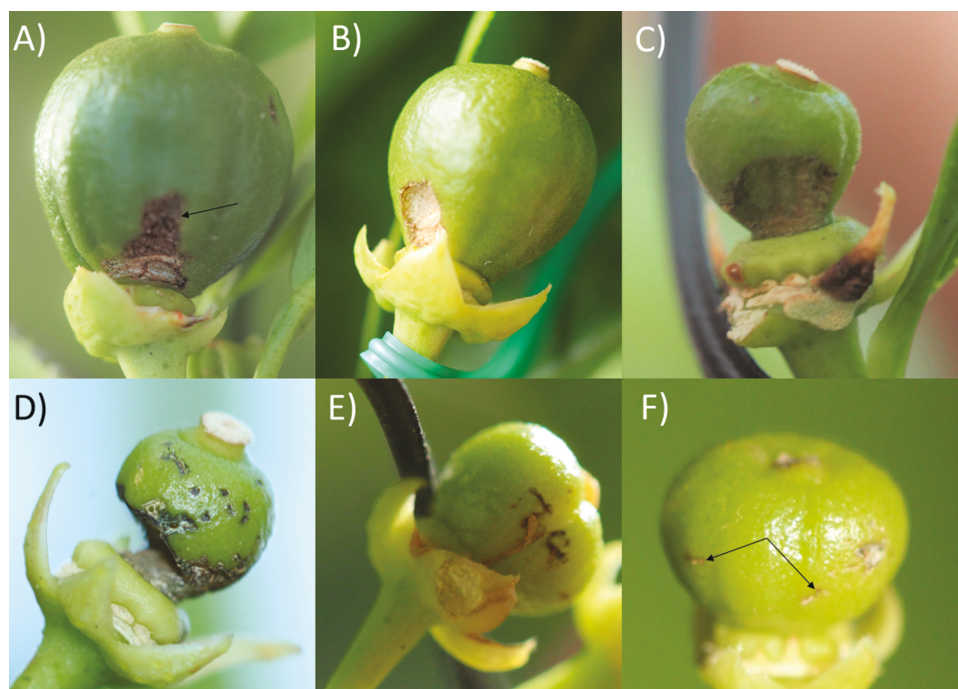


Fig. 1. Examples of deep holes chewed into navel orange (*Citrus sinensis*) (A–B), clementine (*Citrus clementina*) (C–D), and true mandarin (*Citrus reticulata*) (E–F) fruit after exposure to two earwig nymphs for 6 d. Arrows also point out surface chewing damage (A; above deep hole) and small cuts (F).

fruit on each of 10 trees, totaling 334 fruit (average length 4.26 mm [range: 3–8 mm]). All methods followed those described for the 2018 navel orange experiment. One earwig nymph was accidentally not released into the enclosure; this replicate was reassigned as a control treatment. Fruit were not monitored until harvest, and thus questions of differential abscission, healing, and damage at harvest were not examined.

2019 Experiments

Experiment in Navel Oranges

Petal fall was declared on 29 April 2019. A field experiment was set up in a navel orange planting (cv. ‘Old Line Washington’; 30 yr old; 4.57 acres) at LREC on 2 May 2019 (3 d postpetal fall). We collected earwigs from 27 March to 19 April. Earwigs were subsequently reared in plastic containers with mesh lids lined with potting soil and fed lettuce and ground dry dog food (Purina ALPO Come & Get It! Cookout Classics, Vevey, Switzerland), as described in Kahl et al. (2021). Fertilizer (17-0-0) was applied on 24 June, 30 July, and 27 August, a spray (Actara, Syngenta) was applied on 18 September, and a spray (Copper, Lime, Urea, Nitrate, Zinc, and Manganese) was applied on 22 November in the navel orange planting. In this experiment, we choose four ~20 cm long branch terminals with 3–20 young fruit on each of 12 trees, totaling 267 navel orange fruit. Fruit length, measured from calyx to style, averaged ~6.88 mm (range: 4–12 mm). We recorded the number of fruit on each branch terminal and used mesh bag enclosures to establish treatments as described above. We established two replicates of two treatments on each tree: 1) control (no earwig) or 2) 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. Bags and enclosed insects were removed from branch terminals and the numbers of fruit abscised and still present on terminals and the status of the earwigs were

recorded 6 d after mesh bags were installed (8 May 2019); 72 navel orange fruit abscised during treatment exposure or during handling and were excluded from analysis. As above, we then assessed the damage category and proportion of fruit surface area damaged for every remaining fruit.

It is 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). Our previous work with herbivory on navel oranges showed that removal of undamaged fruit decreases the abscission of remaining damaged fruit, thereby improving our ability to evaluate fruit scarring at harvest (Kahl et al. 2021). Therefore, in 2019 for half (six) of the selected trees in each plot, we removed all nondamaged 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. We affixed a numbered tag to the stem of each fruit to track the fruit across the growing season. We checked whether each fruit remained on the branch terminal or had abscised on 13 June, 8 August, and 16 October 2019, and 3 February 2020, when fruit were harvested (i.e., 45, 113, 169, and 280 d postpetal fall).

At harvest, all remaining fruit were removed from the tree, and, although scars were generally of irregular shape, we approximated the surface area of each scar by measuring the maximum length (widest length of scarring for each scar) and width (directly perpendicular to the length) of every scar using digital calipers (FineSource VC-HeiKa), and calculated the surface area of the shape as a rectangle (length multiplied by width). To calculate fruit surface area (estimated as a spheroid), we measured the polar and equatorial diameters using wide-arm calipers (iGaging Precision Instruments 6” digital electronic OD caliber gage, San Clemente, CA). 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 calculated the proportion of fruit with each category of damage

present immediately after mesh bags were removed that did not have any scarring at harvest.

Experiment in Clementines

A field experiment was set up in two cultivars (cv. 'de Nules' and 'Fina sodea') in a clementine planting (15 yr of age; 1.5 acres) at LREC on 3 May 2019 (4 d post petal-fall). Fertilizer (17-0-0) was applied on 24 June, 30 July, and 27 August, a pesticide (Weevilcide, UPL Europe Ltd.; Chadwick, United Kingdom) was applied on 18 September, and a spray (Copper, Lime, Urea, Nitrate, Zinc, and Manganese) was applied on 13 November. We choose four ~20 cm long branch terminals with 3–20 young fruit on each of 12 trees, totaling 268 clementine fruit. Fruit were an average 2.89 mm (range: 1 mm to 5 mm) in length. All methods followed those described for the 2019 navel orange experiment, except six trees were cultivar 'de Nules' and six were cultivar 'Fina sodea.' 'Fina sodea' and 'de Nules' are common clementine cultivars and were used in a previous study involving katydid feeding on clementines (Cass et al. 2020). Also, bags and enclosed insects were removed on 9 May 2019; 51 clementine fruit abscised during treatment exposure or abscised during handling and were excluded from analysis. Three trees for each of the two cultivars had all nondamaged fruit removed.

Experiment in True Mandarins

A field experiment was set up in a true mandarin planting (cv. 'Tango'; 9 yr of age; 3.77 acres) at LREC on 2 May 2019 (3 d postpetal fall). Ant bait (Altrevin, BASF; Ludwigshafen, Germany) was applied on 19 June, fertilizer (17-0-0) was applied on 28 June and 27 August, a spray (Centaur, Nichino America; Pike Creek Delaware) was applied on 16 September, and a spray (Copper, Lime, Urea, Nitrate, Zinc, and Manganese) was applied on 14 November. We choose four ~20 cm long branch terminals with 3–20 young fruit on each of 12 trees, totaling 649 true mandarin fruit. Fruit were on average 3.52 mm (range: 2–7 mm). All methods followed those described for the 2019 navel orange experiment; 147 true mandarin fruit abscised during treatment exposure or abscised during handling and were excluded from analysis.

Statistical Analyses

Throughout, analyses were done using R version 4.0.2 (R Core Team 2021); we used the package *tidyverse* to manipulate and summarize data (Wickham et al. 2019). To assess the severity and nature of damage caused by earwigs on young fruit, we analyzed treatment effects on the most severe initial damage category present on a given fruit (small cuts, surface chewed, and deep holes) for each experiment. Data were analyzed with Bayesian regression models using *Stan* because of its versatility in fitting multilevel, category-specific, and unequal variance ordinal models (*brm*; package *brms*; Bürkner 2017, Bürkner and Vuorre 2019); see Bürkner and Vuorre (2019) and Liddell and Kruschke (2018) for additional information on the advantages of using Bayesian models for analysis of ordinal data. 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 factor and tree id was a random effect factor. Cultivar was included as a fixed effect in all analyses for treatment differences in clementines. 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 ($\text{elpd_diff} = 0$) were selected as

the best model (Vehtari et al. 2017). For all models, weakly informative priors were used ($p(\alpha) = N(0,3)$, $p(\beta) = N(0,3)$, and $p(\text{disc}, \beta) = N(0,1)$ for unequal variance models) to improve model convergence (Supp Methods A1 [online only]). Expected parameter values were obtained by extracting 1,000 posterior parameter values for the earwig and control treatments and calculating the 95% Mean Quantile Intervals (95% QI) of the mean differences for each damage category. Quantile intervals are an effect size estimated based on each model's posterior parameter distributions. Quantile intervals of the mean differences that exclude 0 suggest a difference between treatments.

Treatment impacts on the total proportion of initial fruit surface area damaged (across all damage types) was modeled with generalized linear mixed models (GLMM) using template model builder (*glmmTMB*; package *glmmTMB*; Brooks et al. 2017) for each above 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. Cultivar was included as a fixed effect in the analysis for treatment differences in clementines. The significance of model effects was determined using analysis of deviance Type II Wald χ^2 tests (*Anova*; package *car*; Fox and Weisberg 2019) for both the continuous and zero-inflated model components.

To test whether the amount of fruit removal impacted fruit abscission for each 2019 experiment we only analyzed trees in which undamaged fruit were removed and we used mixed effects Cox models (*coxme*; package *coxme*; Therneau 2020) with the proportion of fruit removed from the terminal as a fixed effect and tree and cage as random effects. Cox mixed effect models explicitly consider the time of abscission. To test whether damage extent and insect-exposure impacted fruit abscission for the 2019 experiments, we only analyzed trees without fruit removal and again used mixed effects Cox models with initial fruit surface area damaged per fruit and treatment as fixed effects and tree and cage as random effects. Again, cultivar was included as a fixed effect in the analysis for the experiment in clementines. Since treatment and damage extent are correlated, we calculated the Generalized Variance Inflation Factors (GVIFs) using *vif* (package *car*; Fox and Weisberg 2019, Fox and Monette 1992). Only low collinearity was detected ($\text{GVIF}^{\frac{1}{2-df}} < 3.3$), thus we could interpret all factors together in the model (Kock and Lynn 2012). We again used Type II Wald χ^2 tests (*Anova*; package *car*; Fox and Weisberg, 2019) to assess the significance of model effects.

The impact of treatment (fixed effect) on the proportion of fruit surface area scarred at harvest for each 2019 experiment was analyzed using Wilcoxon rank sum nonparametric tests (*wilcox.test*; package *stats*; R Core Team 2020), because the distributions of scar size were nonnormal.

Results

2018 Experiments

Experiment in Navel Oranges

Earwigs generated considerable amounts of serious damage to young navel orange fruit, producing surface chewing damage and deep holes in many fruit after 7 d of exposure (Figs. 1A, B and 2A). Averaging branches exposed to earwig nymphs and adults, ~19% of fruit were damaged. The few fruit that were damaged in the control

treatment (3.3%) likely reflected branch rubbing and rare events of background herbivory. The basic ordinal model (category-specific effects and without unequal variance) 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 chewing and deep hole damage, respectively) than the control treatment (Fig. 2A). The earwig adult treatment produced intermediate levels of damage compared to the control and nymphal earwig treatments but did not statistically differ from either (95% QIs overlapped 0).

Earwig exposure also increased the proportion of the fruit surface area that was damaged (Figs. 2 and 3). 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%). The proportion of fruit surface area damaged differed significantly between treatments: whether fruit were fed on or not differed across treatment. The zero-inflated component was marginally significant ($X^2 = 5.83$, $df = 1$, $P = 0.05$; Figs. 2A and 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 ($\beta = 2.4$, $df = 83$, $t = 2.19$, $P = 0.08$). Most earwigs survived when enclosed on branch terminals (Supp Table 1 [online only]).

Experiment in True Mandarins

On true mandarins, earwigs rarely generated serious damage to developing fruit (Fig. 2B); 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 category-specific model exhibited the best fit. Fruit from the earwig nymph treatment had more serious damage than fruit exposed to earwig adults and fruit in the control treatment. Compared to the no earwig 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), slightly larger proportions of

fruit with small cuts (95% QI: 0–0.13), and slightly larger proportions of fruit with surface chewing damage (95% QI: 0–0.07).

Earwigs also generated only minor increases in the proportion of fruit surface area damaged (Figs. 2 and 3). Fruit with small cuts had an average of 1.5% damage (range 1–5%), and fruit with surface chewing had an average of ~7.7% damage (range 3–10%). Only one fruit, which was in the control treatment, had a deep hole with 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 ($X^2 = 6.17$, $df = 2$, $P = 0.05$; Figs. 2B and 3B) and the conditional component ($X^2 = 19.79$, $df = 2$, $P < 0.001$; Fig. 3B). While there were no significant pairwise differences for whether or not feeding occurred (zero-inflated component), the control had more damaged area than the earwig nymph ($\beta = 1.51$, $df = 230$, $t = 4.08$, $P = 0.0002$) and earwig adult treatment ($\beta = 1.95$, $df = 230$, $t = 3.15$, $P = 0.005$); this was due to two fruit with high levels of background damage. Most earwigs survived when enclosed on branch terminals (Supp Table 1 [online only]).

2019 Experiments

Experiment in Navel Oranges

Earwigs produced serious damage on many developing navel orange fruit after 6 d of exposure (Figs. 1A, B, and 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 chewing (95% QI: 0.08–0.28), and deep holes (95% QI: 0.19–0.56).

Earwigs also increased the proportion of fruit surface area damaged (Figs. 4A and 5). Fruit with small cuts averaged ~1% damage (range: 1–5%), fruit with surface chewing averaged ~9% damage (range: 2–40%), and fruit with deep holes averaged ~16% damage (range: 2–55%). Fruit in the earwig treatment were both more frequently damaged and had higher proportions of the 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. 5A) and the zero-inflated component ($X^2 = 66.92$, $df = 1$, $P < 0.001$; Fig. 4A).

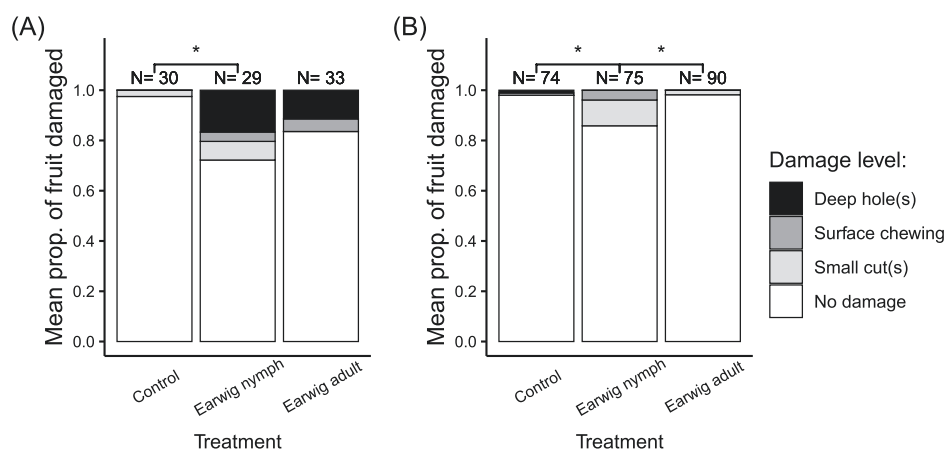


Fig. 2. 2018: Mean proportion of fruit at each damage level (none, small cut(s), surface chewing, and deep hole(s)) across insect treatments (Control: no earwig; Earwig nymph: one earwig nymph; Earwig adult: one earwig adult) in A) navel oranges (*Citrus sinensis*) and B) true mandarins (*Citrus reticulata*). Means were calculated by averaging first by cage and then by treatment. Treatment sample sizes are given above each bar. Asterisks indicate that quantile intervals of mean differences in damage proportion in at least one damage level between treatments exclude 0, suggesting differences in damage levels across treatments.

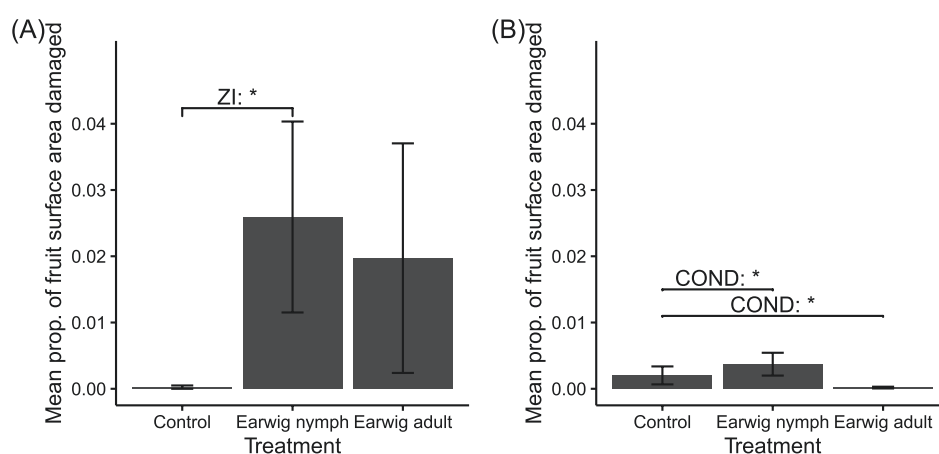


Fig. 3. 2018: Mean \pm standard error of the proportion of total fruit surface area damaged across three treatments: Control, no earwig; Earwig nymph, one earwig nymph; and Earwig adult, one earwig adult at initial fruit evaluation in A) navel oranges (*Citrus sinensis*) and B) true mandarins (*Citrus reticulata*). Means were calculated by averaging first by cage, and then by treatment (fruit with no damage, zeros, included in mean calculations). Asterisks indicate significant pairwise comparisons ($P < 0.05$) between treatments from either the zero-inflated (ZI) or conditional (COND) component of the zero-inflated beta models.

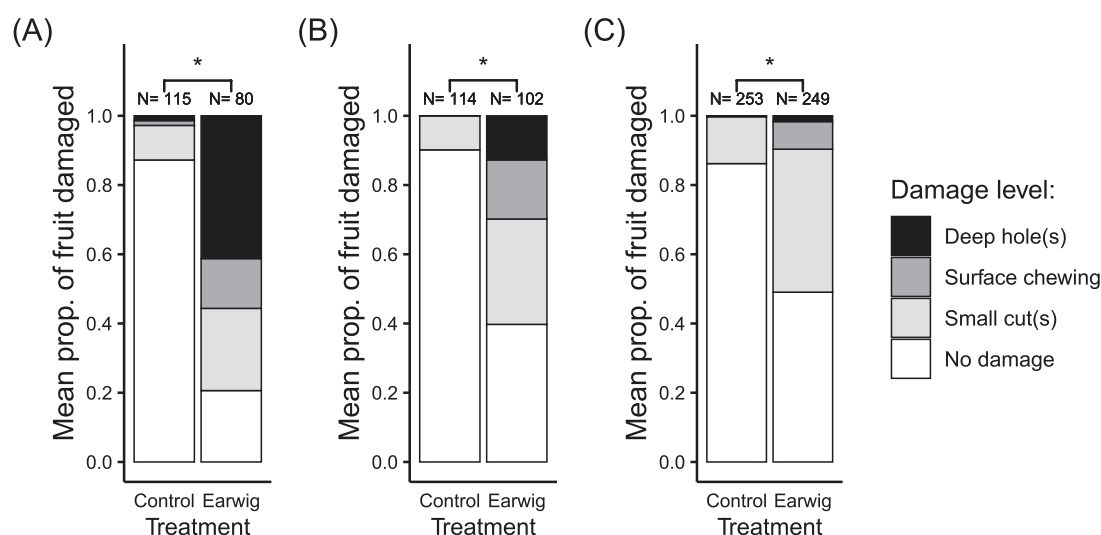


Fig. 4. 2019: Mean proportion of fruit at each damage level (none, small cut(s), surface chewing, and deep hole(s)) across insect treatments (Control: no earwig; Earwig: two earwig nymphs) in A) navel oranges (*Citrus sinensis*), B) clementines (*Citrus clementina*), and C) true mandarins (*Citrus reticulata*). 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. Asterisks indicate that quantile intervals of mean differences in damage proportion in at least one damage level between treatments exclude 0, suggesting differences in damage levels between compared treatments.

Abscission of fruit was high with 82.2% of navel orange fruit abscising overall between the removal of mesh bags and harvest. No predictor (treatment, proportion of initial total fruit surface damaged, proportion of fruit removed, and cultivar for the clementine models) was significant for the proportion of fruit removed from branch terminals. Without any fruit removal (under natural abscission), abscission of fruit with deep holes was actually lower than abscission of undamaged fruit for navel oranges (deep holes: ~71% vs. undamaged: 89%). Most earwigs survived when enclosed on branch terminals. (Supp Table 2 [online only]).

When the 2019 experiment was harvested in February 2020, more than half of the remaining navel orange fruit from the earwig treatment initially had deep holes, whereas the remaining fruit from the control initially had small cuts or no damage (Fig. 6A). Navel orange fruit that initially had small cuts had hardly noticeable

scarring at harvest (Fig. 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 navel orange fruit that initially had deep holes developed large scars at harvest that were often rectangular and sometimes had branching edges (Fig. 7D). There was a marginal difference in the total proportion of fruit surface scarred at harvest between the earwig and control treatments ($W = 88.5$, $P = 0.07$; Fig. 8A).

Experiment in Clementines

Earwigs also generated serious damage to the developing fruit of clementines (Figs. 1C, D, and 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

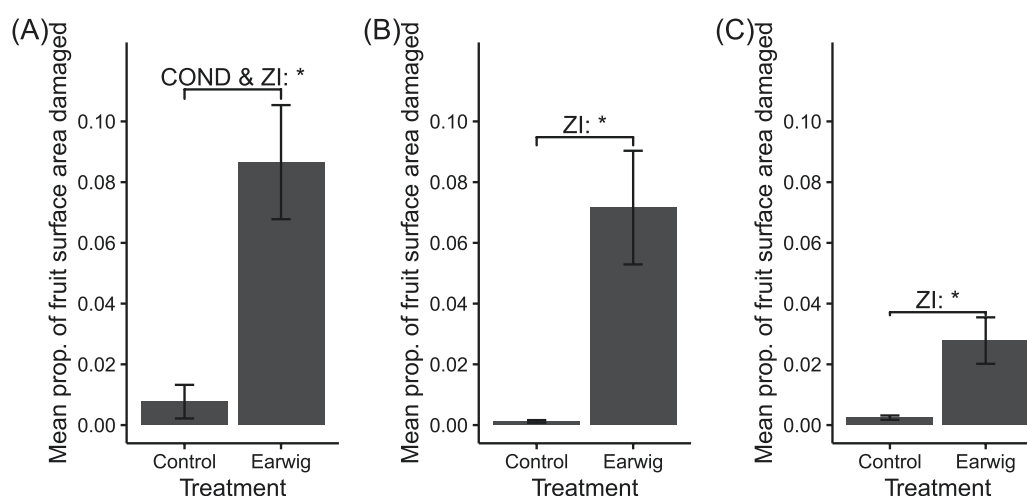


Fig. 5. 2019: Mean ± 1 standard error of proportion of total fruit surface damaged across treatments (Control, no earwig; Earwig, two earwig nymphs) at initial fruit evaluation in A) navel oranges (*Citrus sinensis*), B) clementine (*Citrus clementina*), and C) true mandarins (*Citrus reticulata*). Means 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). Asterisks indicate significant pairwise comparisons ($P < 0.05$) between treatments from either the zero-inflated (ZI) or conditional (COND) component of the zero-inflated beta models.

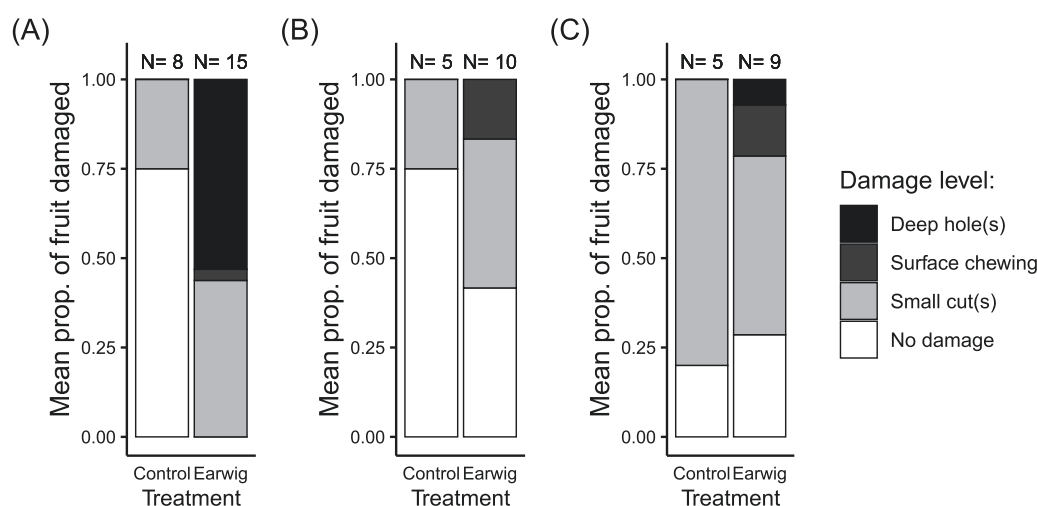


Fig. 6. Mean proportion of fruit remaining to harvest of each initial damage level category (none, small cut(s), surface chewing, and deep hole(s)) across treatment (Earwig: two earwig nymphs; Control: no earwig) for A) navel orange (*Citrus sinensis*), B) clementines (*Citrus clementina*), and C) true mandarins (*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.

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 chewing (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).

Earwigs also increased the proportion of clementine fruit surface area damaged (Figs. 4B and 5B). Fruit with small cuts had an average of ~2% damage (range: 1–10%), fruit with surface chewing 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 the surface area damaged compared to the control; there was a significant difference in the zero-inflated component ($X^2 = 50.5$, $df = 1$, $P < 0.001$;

Fig. 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 components ($X^2 = 0.68$, $df = 1$, $P = 0.68$). Most earwigs survived when enclosed on branch terminals (Supp Table 2 [online only]).

More clementine fruit abscised than navel orange fruit; 88.9% of fruit abscised overall between the removal of cages and harvest. All fruit with deep holes abscised, compared to 88% abscission of fruit without damage, but there were only three clementine fruit with deep holes. The earwig treatment but not the control retained fruit that initially had surface chewing damage (Fig. 7B). Similar to what was found for navel oranges, clementine fruit that initially had small cuts only had small scars that were hardly noticeable at harvest (Fig. 7B)

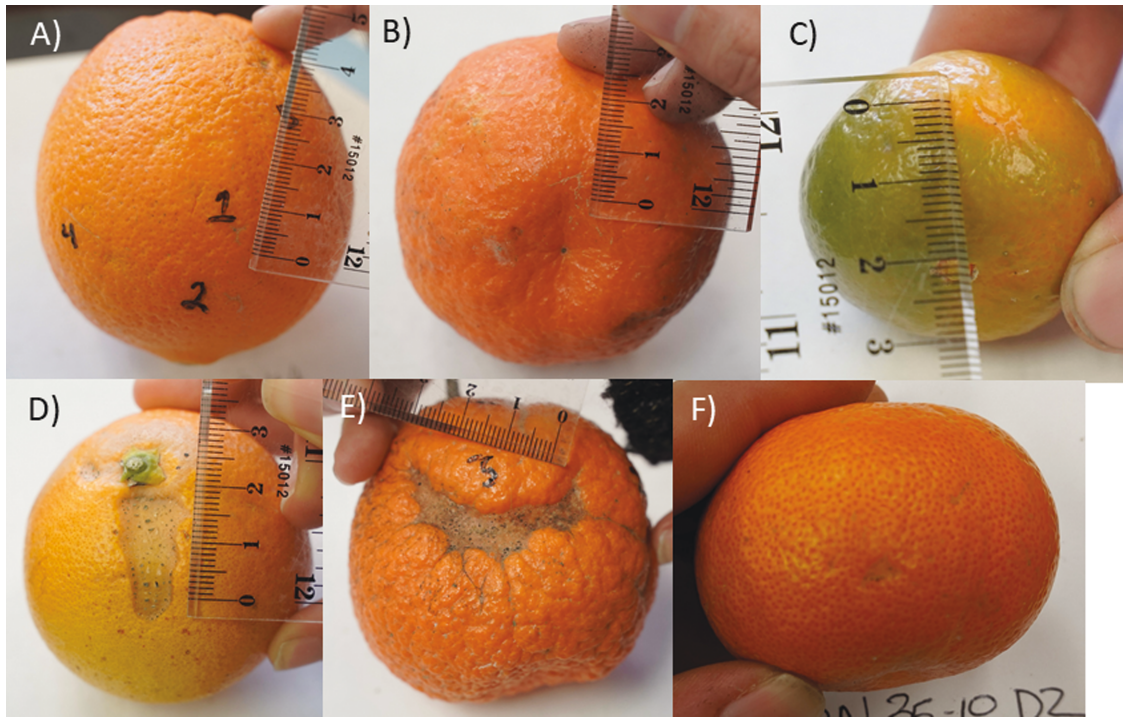


Fig. 7. Examples of the appearance of damaged fruit at harvest. A–C represent fruit that originally had only small cuts. D–F represent fruit that initially had serious damage (surface chewing or deep holes). A) Navel orange (*Citrus sinensis*) fruit that initially had 1% small cut damage. B) Clementine (*Citrus clementina*) fruit that initially had 2% small cuts. C) True mandarin (*Citrus reticulata*) fruit that initially had 5% small cut damage. D) Navel orange fruit that initially had 2% surface chewing and 2% deep hole damage. This fruit is the same fruit displayed in Fig. 1A, matured. E) Clementine fruit that initially had 10% small cuts and 20% surface chewing damage. F) True mandarin fruit that initially had 5% small cuts and 2% deep hole damage.

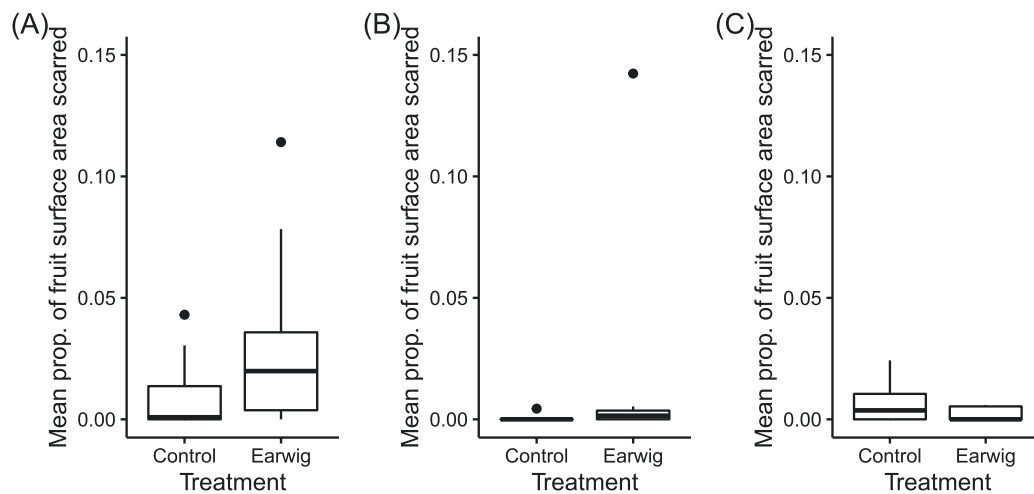


Fig. 8. Boxplot showing median and interquartile range of proportion of fruit surface area scarred at harvest across treatment (Control, no earwig; Earwig, two earwig nymphs) for A) navel oranges (*Citrus sinensis*), B) clementines (*Citrus clementina*), and C) true mandarins (*Citrus reticulata*).

or no noticeable scarring (for two out of the five fruit). One of the three clementine fruit that initially had surface chewing damage had no scarring present at harvest, and two out of three with surface chewing developed scars. One of them developed a large, crescent-shaped, and branching scar (Fig. 7E). The other only had small scars at harvest. There was no significant difference in the proportion of fruit surface area scarred at harvest between the earwig and control treatments ($W = 36$, $P = 0.18$; Fig. 8B).

Experiment in True Mandarins

Earwigs generated serious damage (surface chewing or deep holes) on only a small proportion (~9%) of developing fruit of true mandarins (Fig. 4C), and the deep holes observed on true mandarin fruit were relatively small (Fig. 1E and F). Instead, earwigs mostly generated small cuts on the true mandarin fruit. In the control treatment ~12% of true mandarin fruit were damaged, whereas ~46% of fruit in the earwig treatment had some damage (Fig. 4C). 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 chewing (95% QI: 0.02–0.09) and deep holes (95% QI: 0–0.03).

Earwigs produced relatively small increases in the proportion of the true mandarin fruit surface that was damaged (Figs. 4 and 5). Fruit with small cuts had the least damage with an average of ~2% damage (range: 1–25%), fruit with surface chewing had an average of ~15% damage (range: 2–70%), and fruit with deep holes had an average of ~12% damage (range: 7–20%). Fruit in the earwig treatment were both more frequently damaged and had slightly higher proportions of fruit 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 a marginally significant difference for the conditional component ($X^2 = 2.92$, $df = 1$, $P = 0.09$; Fig. 5C). Most earwigs survived when enclosed on branch terminals. (Supp Table 2 [online only]).

True mandarin fruit abscised at a higher rate than navel oranges and clementines, with 95.3% of true mandarin fruit abscising overall between the removal of cages and harvest. The proportion of fruit removed from branch terminals for true mandarins was a significant predictor of abscission rate ($X^2 = 4.91$, $df = 1$, $P = 0.03$). High fruit removal (defined here as removal of $\geq 50\%$ of fruit) reduced the risk of abscission in comparison to low (0–20%) or moderate (20–50%) fruit removal (Supp Fig. 1 [online only]).

Only one true mandarin fruit that initially had deep holes and one that had surface chewing were retained to harvest from the earwig treatment (Fig. 6C). All true mandarin fruit, no matter the initial damage on fruit, had only small scars (Fig. 7C and 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. 8C).

Discussion

In this study, we found differences across citrus species in vulnerability to fruit damage from earwig feeding. Earwigs fed extensively on young navel orange fruit, producing damage in the form of fruit surface chewing and deep holes. Earwig-damaged navel orange fruit developed scars and several remained at harvest. In contrast, few true mandarin fruit were seriously damaged by earwigs, leading to minimal fruit scarring at harvest. On clementines, earwigs caused intermediate damage. There was only one clementine 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 plantings, these across-species comparisons should be interpreted with caution. However, findings from this study are generally supported by other research (Cass et al. 2019b, Mueller et al. 2019, Cass et al. 2021 unpubl. ms.).

Our current findings reinforce previous work that also concluded that earwigs can severely damage navel orange 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 navel orange fruit. However, we also suggest that herbivory by earwigs varies considerably across citrus species. True mandarin fruit had generally minimal damage at harvest. Previously, it was found that fork-tailed bush katydids chew into and heavily damage navel orange fruit but left mostly only small bite marks on true mandarin

fruit (Cass et al. 2019b). These studies suggest that herbivores are tasting, but then rejecting true mandarin fruit, leading to only minimal damage. Fewer true mandarin fruit were scarred by thrips compared to navel orange fruit as well (Mueller et al. 2019).

The present study found moderate levels of damage caused by earwigs on clementine fruit. Thrips scarring was also found to be intermediate on clementines in comparison to navel oranges and true mandarins (Mueller et al. 2019). Katydid, in contrast, were found to cause high levels of serious damage to clementine fruit (Cass et al. 2021). In the current study, fruit damage by earwigs did not differ across the two clementine cultivars. A previous study found that fruit damage by katydids also did not differ across clementine cultivar (Cass et al. 2021). Because clementines only had a moderate proportion of earwig-damaged fruit initially and abscission of clementine fruit was high, only one fruit with a large, prominent scar was retained to harvest. Thus, more research is needed to better characterize the morphology of earwig-generated scars on clementine fruit.

Feeding deterrence 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 true mandarins and clementines) 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, using cultivars of tangerines and navel oranges, has shown significant differences in rind morphology and oil gland eruption in mature fruit across citrus species and cultivar (Montero et al. 2012). Oil gland eruption occurs in response to herbivores and may deter herbivory. Although these studies on the chemistry and morphology of citrus fruit rind were done on mature fruit, these differences may also be present in developing true mandarin, clementine, and navel orange fruit. Further research on the rind chemistry and morphology of developing fruit is needed.

Differences in earwig fruit feeding across citrus species observed across our experiments could also be due to differences in availability of alternative food sources across the different experimental citrus plantings. As omnivores, earwigs could consume less fruit tissue if also offered insect prey. Thus, differences in densities of aphids or scale insects across different citrus blocks could have contributed to the observed differences. Alternatively, the quality of foliage could also affect the likelihood of fruit consumption. Earwigs have been thought to prefer fresh leaf flush over hardened leaves (Romeu-Dalmau et al. 2012, Grafton-Cardwell et al. 2020). More research is needed to assess which factors might modulate feeding by earwigs on fruit. Future research should examine earwig fruit feeding with and without insect prey. Differences in earwig feeding observed across the different citrus species could also have been due to differences in tree ages across the experimental plantings. The experimental true mandarin trees at LREC are younger than the navel orange trees. However, leaf tissue of older plants is frequently found to be more resistant to herbivory than the tissue of younger plants (Coley 1980). Additionally, earwigs are frequently observed consuming foliage on young trees (Grafton-Cardwell et al. 2020). Thus, it seems unlikely that the younger age of the true mandarin trees would contribute to the reduced herbivory by earwigs.

There was no evidence for preferential abscission of earwig-damaged fruit. This is consistent with a previous study that showed that abscission was not increased for navel orange 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 true mandarins. In contrast to the present study, the proportion of fruit removed

was shown to have a strong effect on navel orange fruit retention (Kahl et al. 2021). The variable effects of fruit removal on abscission of navel orange fruit seen between studies could possibly be explained by differences in statistical power (the previous study had a higher sample size). The damage caused by earwigs may not be extreme enough (in size or depth) to trigger fruit abscission. Katyids that caused more extreme damage were included in Kahl et al. 2021. Nonetheless, both studies suggest that earwigs chew deep holes into navel orange fruit that can cause economically significant damage. Clementine fruit with deep holes chewed by earwigs may preferentially abscise, as all clementine fruit with deep holes abscised, but more research is needed because there were only three clementine fruit with deep holes. Tolerance to earwig damage through selective fruit abscission is not 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. Previously, it was suspected that earwigs damage young, developing fruit, but the outcome of that damage on mature fruit was unknown (Grafton-Cardwell et al. 2003, 2020; Orpet et al. 2019). If navel orange and clementine fruit are exposed to earwig herbivory early in the growing season, because selective abscission and healing likely do not occur, the generated damage will lead to downgrading of fruit at the packinghouse.

Damage caused by earwigs differed across citrus species. Earwigs appear to be important herbivores on navel orange fruit. Earwigs caused moderate damage on clementine fruit as well, suggesting that earwigs are likely pests of clementine fruit. However, very few clementine fruit remained to harvest and more research is needed on the impacts of earwigs on clementine fruit. In contrast, earwigs mostly only generated small scars on true mandarin fruit, making earwigs nonpests on true mandarins. This work advances knowledge of differential susceptibility to herbivores across citrus species and complements previous research that found that true mandarins can resist herbivory by katyids (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 seem to generally not be needed for earwigs on true mandarins.

Supplementary Data

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

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