INDIRECT EFFECTS OF CITRUS CULTIVARS ON LIFE HISTORY PARAMETERS OF A PARASITIC WASP

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Abstract. We determined sex ratio, initial egg complement, and size of adult Aphytis melinus, an ectoparasitoid of California red scale, Aonidiella auranti. Host scales were reared on leaves of four citrus cultivars previously shown to differ in suitability for scale growth and survival. Wasps from scales reared on leaves of lemon (Citrus limon) produced nearly twice the proportion of female progeny as did wasps from scales reared on leaves of grapefruit (Citrus paradisi), orange (Citrus sinensis), or mandarin (Citrus unshiu). Moreover, female wasps from lemon-reared scales had highest initial egg complement, followed by wasps reared from grapefruit, mandarin, and orange. The quality of scales for the production of fecund, female wasp progeny also variedseasonally over all cultivars pooled. Scales reached largest size when reared in the cooler autumn temperatures and were more than twice as suitable for the production of fecund, female A. melinus as scales reared in early summer or midsummer. Results suggest that the mechanisms allowing persistence of the interaction between California red scale and A. melinus may vary among different citrus cultivars.

Key words: Aonidiella auranti; Aphytis melinus; citrus; prey-predator interactions; sex allocation; trophic interactions.

INTRODUCTION

Considerable attention has been given to multispecies interactions recently, and one of the more productive areas of study has been that involving trophic interactions comprising plants, their herbivorous arthropods, and the arthropods' natural enemies. Both the behavioral acceptability (“attractiveness”) and physiological quality of phytophagous insects for utilization by their natural enemies may vary depending upon the host plant species or genotype within species on which the phytophages were reared (for reviews, see Price et al. 1980, Boethel and Eikenberry 1986, Duffey and Bloem 1986, Barbosa and Letourneau 1988, Hare, in press). The consequences of host plant variation on the dynamics of herbivore and natural enemy interactions have not been examined explicitly. Thus, making predictions about the relative growth rates of herbivore and natural enemy populations on different host plant species or genotypes is fraught with difficulties. For example, a negative impact of resistant host plants on survivorship, growth, or fecundity of a particular natural enemy does not indicate that such resistance necessarily reduces the ability of the natural enemy to suppress the pest population. If the growth rate of the herbivore population is inhibited more than that of the natural enemy population, then host plant resistance would act synergistically with natural enemies to suppress the herbivore despite the reduction in certain life history parameters of the natural enemy (Starks et al. 1972, Kauffman and Flanders 1985, Gutierrez 1986, Hare, in press).

Ultimately, we seek to understand better the role of genetic and phenotypic variation in host plants upon the dynamics of prey and parasitoid populations. We have chosen for our model system the association among commercial citrus cultivars (Citrus spp.); the California red scale, Aonidiella auranti Maskell (Homoptera: Diaspididae), an introduced citrus pest; and Aphytis melinus DeBach (Hymenoptera: Aphelinidae), an ectoparasitoid introduced for the control of California red scale.

Previous research showed that several life history parameters of California red scale differed among four citrus cultivars, especially for scales reared on woody bark (Hare et al. 1990). Bark of “Satsuma” mandarin (Citrus unshiu Markovitch) was virtually unsuitable for scale survival. The few surviving females also were smallest on this cultivar. In contrast, “Lisbon” lemon (Citrus limon [L.] Burm.) and “Reed” grapefruit (Citrus paradisi Macf.) produced scales on their bark that survived and attained a size similar to that on their leaves; survival and scale size on the bark of “Navel” orange (Citrus sinensis [L.] Osbeck) was intermediate. Leaves of all four cultivars were both more suitable and more uniform for scale survival and growth than was bark.

The importance of such cultivar-based variation in scale size on the life history parameters of A. melinus is suggested by several previous studies (Luck and Poldor 1985, Opp and Luck 1986, Yu and Luck 1988). Wasp size, sex, and initial fecundity are all strongly influenced by the size of the scale host from which they emerge. Gravid or parturient California red scale are

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unsuitable as hosts for *A. melinus*, as are scales <0.15 mm² in size. Scales between 0.15 and 0.39 mm² are allotted mostly (90%) unfertilized (i.e., male) eggs by *A. melinus*, while those larger than 0.39 mm² are allotted fertilized (female) eggs (Luck and Podoler 1985, Opp and Luck 1986, Yu and Luck 1988).

Sex allocation of solitary parasitic Hymenoptera based upon host size or other aspect of “quality” is commonly observed (e.g., Clausen 1939, Charnov et al. 1981, Charnov 1982), although its significance on the dynamics of parasitoid populations is relatively unexplored (Comins and Wellings 1985, Waage 1986), especially when variation in host quality is independent of host density. Clearly, the growth rate of the parasitoid population would be more strongly determined by the number of female than male progeny.

One previous study suggesting the importance of differential sex allocation on parasitoid population dynamics is based upon the competitive exclusion of *Aphitoid lingnanensis* Compere by *A. melinus* (Luck and Podoler 1985). *A. melinus* does not require as large a host to produce daughters as *A. lingnanensis*; therefore *A. melinus* produces more female progeny from the available host population. Eventually *A. melinus* eliminated *A. lingnanensis* from all but a fraction of its initial range in California (Luck and Podoler 1985).

We undertook the present study to determine if scales reared on lemon, grapefruit, orange, and mandarin differed in their suitability as hosts for *A. melinus*. Our initial hypotheses were: (1) that sex ratios of progeny are more female-biased on those citrus cultivars most suitable for California red scale because such cultivars produce the largest scales, (2) that size and fecundity of female parasitoid progeny would also vary directly with the suitability of citrus cultivars for California red scale, and (3) that cultivar-induced variation in life history parameters of *A. melinus* is more pronounced on scales reared on bark than on those reared on leaves because of the more pronounced differences in scale size among cultivars when reared upon bark than upon leaves.

**Materials and Methods**

**Host and parasitoid life histories**

The biologies of California red scale and *A. melinus* are relatively well known. That of the scale was described by Quayle (1938) and Bodenheimer (1951). That of *A. melinus* was described by Rosen and Debach (1979) and Luck and Podoler (1985). Briefly, California red scale utilizes all aboveground tissues of citrus trees, although substrates in exterior portions of the canopy (fruit, leaves, green twigs) are more suitable for scale survival and growth (Walde et al. 1989, Hare et al. 1990). Mature females produce mobile first instars (“crawlers”) that walk to suitable feeding sites and settle within 2–6 h after emergence. Female and male scales remain at the site of settling for the duration of their development; males emerge as winged adults. California red scale develops all year in California and 2–3 generations are produced annually.

*Aphitoid lingnanensis* lays one (rarely two) eggs beneath the scale’s cover on the outside of the scale’s body. The scale is paralyzed when the egg is laid; thus scale growth stops after parasitization. All the food available to a wasp’s offspring for development is contained in the scale at the moment of attack. Normally, male and female second instars, and virgin third-instar females are attacked, but virgin third-instar females are the preferred host (e.g., Yu 1986, Walde et al. 1989). In addition to affecting sex allocation, scale size also affects wasp size, which in turn affects lifetime fecundity of female progeny. As with many parasitic Hymenoptera (Charnov et al. 1981, Charnov 1982), larger *A. melinus* females are more fecund (Opp and Luck 1986, Yu 1986).

**Scale-rearing procedures**

Scale populations of uniform age distribution were established on experimental trees by infesting trees with crawlers from a laboratory scale colony maintained on lemon fruit (Tashiro 1966). Two lemons with mature, crawler-producing female scales were hung in each of four previously cleaned branches 2–5 cm in diameter in each of five trees per cultivar. The trees were growing in a mixed planting of 11 cultivars at Agricultural Operations, University of California, Riverside. The history of the scale colony and its maintenance, tree growing conditions, site preparation, and crawler inoculation procedures were similar to those described in Hare et al. (1990). Our procedures differed from those previously described in that bark sites were washed with a spray of water to remove resident scale and accumulated dirt, and crawlers were allowed to wander naturally from their mothers to sites of their own choosing on the tree branch.

A sleeve cage (1 m long by 0.32 m in diameter) enclosed each branch to protect the scales from resident *A. melinus* and other natural enemies. Lemons with fresh scales replaced the older ones after 7 d, and this second group of lemons was removed after an additional 7 d. These procedures resulted in relatively light populations of California red scale (≈5 individuals/1000 mm² of substrate surface) on leaves and bark of each branch, with an age range of 14 d. Three experimental trials were carried out and were begun with inoculations on 30 May 1989 for the first trial, 17 July 1989 for the second, and 8 September 1989 for the third trial (Fig. 1). Different trees were used for each trial to avoid introducing any effect of “wounding” on subsequent host plant suitability associated with branch removal at the end of each trial.

Scale development was monitored visually and with a day-degree model (Allen 1976), using temperatures recorded hourly by a thermocouple and temperature recorder placed within the canopy of one of the experimental trees. Female scales reach the third instar
after accumulating 350 degree-days (Yu and Luck 1988). Therefore, after at least 350 degree-days had accumulated from the midpoint of the inoculation period the experimental scales were exposed to *A. melinus*.

*A. melinus* parasitization and development

Several thousand 24-h-old, honey-fed and mated *A. melinus* were obtained from a commercial insectary. Upon receipt, these were divided into groups of \( \approx \)500 wasps to facilitate handling. Each group was anesthetized with CO\(_2\), and the individuals were sexed and placed in snap-cap vials (25 females and 5 males per vial). The next morning, one vial with wasps was placed within each branch cage and opened. Two days (48 h) later, the cages were opened and branches were vigorously shaken to dislodge and disperse any surviving *A. melinus*, after which the cages were re-sealed.

A degree-day model using a sine wave interpolation between daily high and low temperatures (Allen 1976) was developed for *A. melinus* using the threshold of 6.8°C and 273 degree-days for full development (Kfir and Luck 1984). This model was used to calculate the expected emergence dates for the wasp progeny. Prior to wasp emergence, whole branches, with their cages and labels (cultivar, tree, and replicate branch) were cut from the tree. The cut ends were sealed with paraffin to prevent desiccation and the branches were stored in a cold room (4°C) until processed.

Scale size and parasitization rates

Branches were brought to the laboratory where scales were examined with a dissecting microscope (10× or 12×) after lifting the covers from the scale bodies. For parasitized scales, the length of pupae and the length and width of scale covers were measured with an ocular micrometer and recorded. We used the area of the scale cover as an index of the scale’s body size at the time of parasitization. After measurement, each pupa was placed in a labeled glass vial (9 × 30 mm) and stoppered with a cotton plug. Vials with pupae were then placed in sealed plastic boxes lined with moistened paper towels to maintain high humidity. The vials were maintained at room temperature until the adult wasps emerged.

Pupae were collected either until all the scales on leaves or bark of a branch had been dissected, or until 10 pupae had been obtained from each substrate. A total of 414 pupae was recovered from leaves and 19 from bark in the first trial; 218 and 128 pupae were recovered from leaves and bark in the second trial, and 232 and 113 pupae were recovered in the third trial. Most of the pupae recovered from bark were from lemon-reared scales.

*A. melinus* pupal mortality

The proportion of all pupae that died prior to emergence was calculated for each branch and was transformed (arcsin √<i>x</i>) prior to analysis. For each trial and cultivar, the lengths of all pupae that died were cast into frequency distributions, and the relationships between cultivar, pupal length, and the proportion of dead pupae in each size class were subjected to an analysis of covariance (ANCOVA). In this analysis, a significant effect of common slope would indicate an effect of pupal length on mortality across cultivars, a significant difference in adjusted treatment means would
indicate an effect of cultivar on pupal mortality after adjusting for length, while a significant heterogeneity among slopes would indicate that the linear relationship between pupal length and mortality varied among cultivars.

**A. melinus** size, sex ratio, and fecundity

Upon wasp emergence, a drop of honey was placed in each vial as a food source (Opp and Luck 1986). Twenty-four hours later, all adult wasps were killed by freezing and mounted on microscope slides using procedures described in Opp and Luck (1986). The hind tibia lengths of all wasps were measured with an ocular micrometer (100 x) as an index of wasp size. Wasps were sexed and ova of all females were counted. The \( \sqrt{(x + 0.5)} \) transformation also was applied to the number of ova per female prior to analysis.

The sex ratio (proportion female) of survivors was calculated for each branch and was transformed (arcsin \( \sqrt{x} \)) prior to analysis. Frequency distributions of pupal size and sex ratio were also constructed for each trial x cultivar combination and also analyzed by ANCOVA. A significant effect of common slope would indicate a relationship between pupal length and its sex across cultivars, a significant difference in adjusted treatment means would indicate an effect of cultivar on sex allocation after adjusting for pupal size, while significant heterogeneity among slopes would indicate that the linear relationship between pupal length and sex varied among cultivars.

**Overall scale quality for A. melinus reproduction**

An index of the overall quality of California red scale for *A. melinus* population growth was calculated as the product of the mean proportion of female progeny produced times their mean initial fecundity. This product is equivalent to the net number of ova per adult and combines the effects of differential sex allocation with differences in the initial egg production by *A. melinus*. Values were calculated on a per-tree basis and subjected to the logarithm(x + 1.0) transformation so that the data would meet the assumptions of normality, homoscedasticity, and independence for analysis of variance (ANOVA).

**Data analysis**

Data were analyzed by ANOVA when all assumptions for ANOVA were met. Nested ANOVAs were used for single trials; variation among cultivars was tested over the variation among trees within cultivars, and variation among trees within cultivars was tested over variation among branches within trees. In analyses of all trials pooled, the effects of variation among cultivars, among trials, and the (trial × cultivar) interaction were tested over the variation among trees within (trial × cultivar) cells. All analyses were conducted using the PROC GLM procedure of SAS (1985) using the Type III sums of squares when unequal sample sizes occurred.

**RESULTS**

Too few *Aphytis melinus* pupae were recovered from scales reared on bark of most cultivars to warrant analysis. Thus, we present the results for *A. melinus* from leaf-reared scales only.

**Scale cover size**

Because the distributions of scale cover areas were skewed within cultivars (e.g., Fig. 2), scale cover areas were analyzed among cultivars within trials using the Kruskal-Wallis test. These differed among cultivars in all three trials \( (H_3 = 29.193, P < .0001; H_3 = 12.164, P = .007; \) and \( H_3 = 19.289, P = .0002 \) for Trials 1–3, respectively). Their pattern of variation differed among trials, however; that for Trial 2 differed substantially from that for either Trial 1 or 3 (Table 1).

The cover areas of scales reared on lemon leaves ranked first in size in Trials 1 and 3 but fourth in size in the second (Table 1). In contrast, cover areas of scales reared on mandarin ranked fourth in size in Trials 1 and 3 but first in Trial 2. The areas of those reared on grapefruit and navel were always intermediate. We cannot explain the apparent interaction between trial and cultivar on scale cover size. Overall, scale covers were the largest in the third (autumn) trial (Table 1).

**A. melinus pupal lengths**

The distributions of *A. melinus* pupal lengths also were skewed among cultivars within trials (e.g., Fig. 3) and also were analyzed using the Kruskal-Wallis test. These lengths differed among cultivars in the first and third trials \( (H_3 = 15.572, P = .0014, \) and \( H_3 = 21.548, P < .0001, \) respectively) but not the second \( (H_3 = 5.915, P = .116) \).
Table 1. Median (± 1 se) scale cover areas of California red scale reared on four citrus cultivars and parasitized by Aphytis melinus, and lengths of A. melinus pupae from those scales in each of three trials.

<table>
<thead>
<tr>
<th>Trial 1</th>
<th>Scale cover area (mm²)</th>
<th>Pupal length (mm)</th>
<th>Sample size</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mandarin</td>
<td>0.533 ± 0.013</td>
<td>0.630 ± 0.012</td>
<td>54</td>
</tr>
<tr>
<td>Orange</td>
<td>0.557 ± 0.022</td>
<td>0.620 ± 0.011</td>
<td>108</td>
</tr>
<tr>
<td>Grapefruit</td>
<td>0.592 ± 0.044</td>
<td>0.620 ± 0.011</td>
<td>117</td>
</tr>
<tr>
<td>Lemon</td>
<td>0.621 ± 0.071</td>
<td>0.661 ± 0.014</td>
<td>135</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Trial 2</th>
<th>Scale cover area (mm²)</th>
<th>Pupal length (mm)</th>
<th>Sample size</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mandarin</td>
<td>0.693 ± 0.111</td>
<td>0.656 ± 0.027</td>
<td>35</td>
</tr>
<tr>
<td>Orange</td>
<td>0.625 ± 0.086</td>
<td>0.615 ± 0.032</td>
<td>54</td>
</tr>
<tr>
<td>Grapefruit</td>
<td>0.597 ± 0.112</td>
<td>0.615 ± 0.023</td>
<td>35</td>
</tr>
<tr>
<td>Lemon</td>
<td>0.584 ± 0.049</td>
<td>0.639 ± 0.013</td>
<td>94</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Trial 3</th>
<th>Scale cover area (mm²)</th>
<th>Pupal length (mm)</th>
<th>Sample size</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mandarin</td>
<td>0.570 ± 0.055</td>
<td>0.697 ± 0.043</td>
<td>13</td>
</tr>
<tr>
<td>Orange</td>
<td>0.604 ± 0.059</td>
<td>0.663 ± 0.016</td>
<td>70</td>
</tr>
<tr>
<td>Grapefruit</td>
<td>0.636 ± 0.082</td>
<td>0.700 ± 0.018</td>
<td>48</td>
</tr>
<tr>
<td>Lemon</td>
<td>0.722 ± 0.079</td>
<td>0.720 ± 0.016</td>
<td>101</td>
</tr>
</tbody>
</table>

Pupae from scales reared on lemon ranked either first or second in length, while those reared on scales from orange ranked either third or fourth in length (Table 1). The lengths of pupae from scales reared on mandarin and grapefruit were of intermediate rank, but the lengths of those from scales reared on mandarin leaves were greater than those from scales reared on grapefruit leaves in two of the three trials (Table 1). Overall, the largest pupae were collected from scales reared in the autumn (Trial 3), whereas the smallest pupae were collected from scales reared in midsummer (Trial 2).

A. melinus pupal mortality

The proportion of pupa that died after collection differed only among trials (Table 2). The least mortality occurred in Trial 3 (13.9%), whereas the highest occurred in Trial 1 (64.7%). Although part of the variation in pupal mortality might have been caused by our increasing adeptness over the course of the experiment in collecting pupae without injury, reduced pupal mortality in the autumn trial is also probably related to their larger size.

Pupal mortality declined with increasing length (Fig. 4A). After adjusting for the differences in pupal length, pupal mortality still did not differ significantly among cultivars ($F_{3,61} = 1.11$, $P = .35$), nor did the relationship between pupal length and mortality differ among cultivars ($F_{3,58} = 0.28$, $P = .84$).

A. melinus sex ratio

Sex ratio (proportion females) differed significantly only among cultivars (Table 2). Scales reared on lemon leaves produced nearly twice the percentage of female $A$. melinus (37.1%) as did those reared on leaves of the three other cultivars (18.8, 17.9, and 17.2% for grapefruit-, mandarin-, and orange-reared scales, respectively, Fig. 5A). The wide confidence interval for mandarin in Trial 3 was the result of low parasitization rates of scales on mandarin foliage and relatively low survival of $A$. melinus to adulthood. All scales from two trees were allocated all male eggs (all of four surviving wasps from scales from both trees combined were males) and scales from one tree produced all female wasps (total of four). Scales from the other two trees did not produce any surviving $A$. melinus. These anomalies with mandarin did not affect the overall results because sex ratio still differed significantly only among cultivars when mandarin was deleted from the analysis ($F_{2,39} = 3.49$, $P = .04$).

Sex ratio increased with increasing pupal length (Fig. 4B). After adjusting for differences in pupal length among cultivars, sex ratio did not differ significantly among cultivars ($F_{3,39} = 2.62$, $P = .06$), nor did the relationship of pupal length to sex ratio differ among cultivars ($F_{3,58} = 0.45$, $P = .72$).

A. melinus adult size

Neither male nor female wasps differed in hind tibia length when reared on scales from different cultivars when the data from all trials were pooled (Tables 2 and 3). Hind tibia lengths of males differed significantly only among trials (Table 2) and were slightly longer in the third (autumn) trial (Table 3). Female hind tibia lengths were more uniform among trials, however.

Initial egg complement

The total number of ova (after the females fed 24 h following emergence) differed significantly only among cultivars (Table 2, Fig. 5B). Wasp from lemon-reared scales had highest initial egg complement (5.60 ova per female), followed closely by wasps from grapefruit-reared scales (5.40 ova per female). Wasp from orange-reared scales had lowest initial fecundity (2.49 ova per female), with wasps from mandarin-reared
scales intermediate (3.40 ova per female). Initial egg complement was significantly and positively correlated with hind tibia length \((r = 0.57, n = 137, P < .0001)\), a result consistent with previous studies on this and other species showing that larger wasps are more fecund (Charnov et al. 1981, Charnov 1982, Opp and Luck 1986). Again, the pattern of results was not altered when data from mandarin were deleted from the analysis. Initial egg complement still differed significantly only among cultivars \((F_{2,28} = 4.06, P < .03)\).

**Table 2.** *F* statistics from ANOVAs on measured parameters. Degrees of freedom in parentheses.

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>Pupal mortality</th>
<th>Hind tibia length</th>
<th>Sex ratio</th>
<th>Ova per female</th>
<th>Ova per adult</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Male</td>
<td>Female</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cultivar</td>
<td>1.64 (3.44)</td>
<td>0.99 (3.40)</td>
<td>1.86 (3.34)</td>
<td>3.30* (3.42)</td>
<td>2.96* (3.32)</td>
</tr>
<tr>
<td>Trial</td>
<td>15.33*** (2.44)</td>
<td>5.28** (2.40)</td>
<td>0.36 (2.34)</td>
<td>2.74 (2.42)</td>
<td>2.63 (3.32)</td>
</tr>
<tr>
<td>Interaction</td>
<td>1.01 (6.44)</td>
<td>1.35 (6.40)</td>
<td>0.97 (6.34)</td>
<td>0.32 (6.42)</td>
<td>1.49 (6.32)</td>
</tr>
</tbody>
</table>

* * .05 > P ≥ .01, ** .01 > P ≥ .001, *** P < .001. Denominator degrees of freedom varied with the number of trees providing useful data for each analysis. For example, some trees had no scale that produced adult female wasps; thus these trees were not included in analyses of female hind tibia length or ova per female.
and 2, respectively). Lemon leaves produced consistently the highest quality scales for *A. melinus* in all three trials, and, over all trials pooled, lemon-reared scales were nearly three times the quality of orange- or mandarin-reared scales (1.53 net ova per adult on lemon-reared scales vs. 0.55 and 0.49 net ova per adult on orange- and mandarin-reared scales, respectively). Grapefruit-reared scales were slightly more than half the quality of lemon-reared scales (0.81 net ova per adult). This pattern also was unchanged by deleting mandarin from the analysis. Overall scale quality still differed significantly among trials ($F_{2,33} = 4.00, P < .03$) among the remaining cultivars ($F_{2,35} = 4.37, P < .03$), but not due to the trial × cultivar interaction ($F_{2,35} = 0.75, P = .56$).

**discussion**

Substantial heterogeneity existed in the suitability of leaf-reared California red scale for the production of female *A. melinus*. Scale suitability differed both seasonally and with cultivar, but the two sources of variation did not interact. Scales reared on lemon leaves were more likely to be allocated a fertilized (female) egg by *A. melinus* than scales reared on the leaves of grapefruit, orange, or mandarin. Moreover, the resulting daughter was likely to have a higher initial egg complement than those emerging from scales reared on the leaves of the other cultivars. Simultaneously, California red scales reared under the warmest summer temperatures were less likely to be allocated fertilized eggs by *A. melinus*, and the resulting female progeny from those scales were likely to have lower initial egg complements than those emerging from scales reared under the cooler autumn temperatures.

The effect of season on California red scale quality is most likely the result of high summer temperatures reducing California red scale body size (Yu and Luck 1988, Hare et al. 1990) to below that required for successful survival of female progeny (Luck and Podoler 1985, Opp and Luck 1986, Yu and Luck 1988). The cultivar effect is also probably manifested through scale size by the influence of the host plant on scale growth. However, the differences in scale quality among these four cultivars are probably not due to simple differences in the nutritional quality of foliage among cultivars, because variation in scale survival, growth, and fecundity were all independent of the considerable variation in soluble protein and free amino acid concentrations among cultivars (Hare et al. 1990).

The results of the second trial may present some interesting exceptions to the generalization that scale quality for *A. melinus* is a direct function of scale size. Although lemon-reared scales in the second trial produced the smallest covers, they were still allocated the largest proportion of female progeny. A previous laboratory study showed that scale cover area and scale body area were highly correlated during the second-instar and third-instar growing stages when scales were

**Overall scale quality for A. melinus reproduction**

Net ova per adult differed significantly due to the main effects of cultivars and trials. The trial × cultivar interaction was not statistically significant (Table 2, Fig. 5C). Scales reared in the autumn were more than twice as suitable for *A. melinus* population growth (1.39 net ova per adult) than scales reared in early or mid-summer (0.70 and 0.55 net ova per adult in Trials 1

[Fig. 5. *Aphytis melinus* sex ratio at adult emergence (A), mean no. ova per female 24 h after emergence (B), and the product of the mean proportion of adult female progeny and their initial fecundity (C) from California red scales reared on leaves of four citrus cultivars. Values are backtransformed grand means and upper 95% confidence intervals from analyses performed on transformed data (Sokal and Rohlf 1981). Values are based upon five trees per cultivar and four branches per tree within each trial.]
TABLE 3. Pupal mortality and hind tibia lengths of surviving adult female and male *Aphytis melinus* from California red scale reared on four citrus cultivars in each of three trials. Data are cultivar means ± 1 se calculated from means of all trees within each (trial × cultivar).

<table>
<thead>
<tr>
<th>Trial 1</th>
<th>Pupal mortality (%)</th>
<th>Hind tibia length (mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Female</td>
<td>Male</td>
</tr>
<tr>
<td>Mandarin</td>
<td>76.3 ± 10.5</td>
<td>0.190 ± 0.005</td>
</tr>
<tr>
<td>Orange</td>
<td>41.9 ± 9.8</td>
<td>0.190 ± 0.007</td>
</tr>
<tr>
<td>Grapefruit</td>
<td>62.0 ± 8.9</td>
<td>0.209 ± 0.004</td>
</tr>
<tr>
<td>Lemon</td>
<td>66.1 ± 8.3</td>
<td>0.224 ± 0.007</td>
</tr>
<tr>
<td>Trial 2</td>
<td>Female</td>
<td>Male</td>
</tr>
<tr>
<td>Mandarin</td>
<td>41.1 ± 13.3</td>
<td>0.209 ± 0.015</td>
</tr>
<tr>
<td>Orange</td>
<td>43.1 ± 5.8</td>
<td>0.196 ± 0.021</td>
</tr>
<tr>
<td>Grapefruit</td>
<td>66.5 ± 9.3</td>
<td>0.191 ± 0.017</td>
</tr>
<tr>
<td>Lemon</td>
<td>48.1 ± 7.5</td>
<td>0.201 ± 0.004</td>
</tr>
<tr>
<td>Trial 3</td>
<td>Female</td>
<td>Male</td>
</tr>
<tr>
<td>Mandarin</td>
<td>31.0 ± 15.6</td>
<td>0.198*</td>
</tr>
<tr>
<td>Orange</td>
<td>18.1 ± 5.4</td>
<td>0.203 ± 0.011</td>
</tr>
<tr>
<td>Grapefruit</td>
<td>16.4 ± 8.8</td>
<td>0.207 ± 0.002</td>
</tr>
<tr>
<td>Lemon</td>
<td>21.3 ± 6.2</td>
<td>0.211 ± 0.008</td>
</tr>
</tbody>
</table>

* Only one tree produced any adult females.

reared on lemon fruit (*r* = 0.918 and 0.904 for second- and third-instar females and *r* = 0.725 for males, *n* ≥ 700, Yu 1986). Such strong correlations were not found when scale cover areas and body sizes of mature adults were compared when reared on different cultivar × substrate combinations (Hare et al. 1990); scale cover areas were reduced to a greater extent than scale body sizes on poor-quality substrates. If such variation holds true for the growing stages, then scale cover areas may not reliably indicate scale body size for comparisons across cultivars and substrates.

Similarly, purely on the basis of scale cover size, we would have expected mandarin-reared scales to have been allocated the largest proportion of female *A. melinus* in the second trial. We found, however, that three of the five scales with covers >1.6 mm$^2$ in area were each allocated two sons. (Of the two remaining scales in this size class, one was allocated one son, and the other was allocated one daughter.) Because both the numbers of scales available and the numbers of *A. melinus* pupae collected were consistently the lowest from mandarin, and because this pattern did not occur in the other trials or cultivars we are unable to account fully for this observation. The potential for superparasitism resulting from confining wasps in cages with the relatively small numbers of hosts available on mandarin cannot be ignored, however.

We originally hypothesized that any effect of cultivar on *A. melinus* life history parameters would be more evident on bark-reared than on leaf-reared scales due to the relatively smaller (but statistically significant) differences in body size of scales reared on leaves of different cultivars compared to those reared on bark (Hare et al. 1990). We were unable to test this hypothesis because of the small numbers of scales surviving on bark of orange and mandarin. Nevertheless, even the slight differences in scales when reared on leaves of different citrus cultivars apparently are sufficient to affect life history parameters, especially sex allocation, of *A. melinus*.

Charnov et al. (1981, Charnov 1982) predicted that if the incremental gain in fitness with increasing size was greater for females than males, sex ratio should vary as a function of host size, with sons being allocated to small hosts and daughters to large hosts. Moreover, host size should be perceived on a relative basis, i.e., a host is large or small relative to the distribution of host sizes available. In contrast to theory, sex allocation on the basis of absolute host size has been found about as frequently as it has on the basis of relative host size (Jones 1982, King 1987, 1989, Hails 1989, Heinz and Parrella 1989). If *A. melinus* were allocating sex on the basis of relative differences in host size, then we might not expect any variation in sex ratio among cultivars or trials, even though the size distribution of potential hosts differed substantially. Assessments of relative host size imply that female wasps determine the size distribution of all available hosts, yet our experimental *A. melinus* had access only to the scales within their respective cages. If sex allocation were being made on a relative basis, then we would have expected to see relatively uniform sex ratios per branch with relatively little overall sex ratio variation among cultivars or among trials. *A. melinus* apparently allocates sex primarily on the basis of absolute size (Luck and Podoler 1985, Opp and Luck 1986, Yu and Luck 1988). Therefore, we predict that any factors (or their combinations) that inhibit growth of scales, such as differences in host suitability among cultivars, climatic differences, and differences in cultural practices, will secondarily reduce
the proportion of scales suitable for allocation of female eggs by *A. melinus*.

We also suggest that the host–parasitoid interaction between California red scale and *A. melinus* may function differently on the different citrus cultivars. Lemon is simultaneously the most suitable cultivar for the production of *A. melinus* and one of the two most suitable for survival and reproduction of California red scale on bark, a substrate that *A. melinus* exploits less (Gregory 1985, Walde et al. 1989, Yu et al. 1990). Scales reared on mandarin leaves are the least suitable cultivar for the production of *A. melinus*, but mandarin is also the least suitable cultivar for the survival of California red scale on bark. Orange appears to be more suitable for California red scale survival, growth, and reproduction than mandarin, but the scales reared on orange leaves are also more suitable for utilization by *A. melinus*.

Results of these experiments, which focus only on the variation in quality of scales of similar age distributions, pose several interesting questions. First, to what extent does the reduction in the quality of leaf-reared scales for *A. melinus* reproduction offset the need for a bark "refuge" for California red scale in order to permit both host and parasitoid populations to persist (see Murdoch et al. 1989 and references therein)? Second, is the reduced suitability of orange and mandarin for scale population growth balanced by an *equal* reduction in the suitability of the scales on these cultivars for *A. melinus*? If the suitability of scales for *A. melinus* was reduced more than was the growth rate of California red scale populations on orange and mandarin, then the net growth rate for California red scale would be greater on these cultivars than it would be on lemon and grapefruit. Although the latter are more suitable for the growth of California red scale populations, they may be even more suitable for *A. melinus*.

It is difficult at present to predict the effect of variation among citrus cultivars on the interactions of scale and parasitoid populations. A reduced sex ratio and mean fecundity of *A. melinus* seen when reared from scales inhabiting a particular cultivar is not, by itself, sufficient to conclude that *A. melinus* is less effective in controlling California red scale on that cultivar. The direct effects of host plant variation on the growth rates of the California red scale populations also must be considered. Only with such detailed studies at the population level can the role of the host plant in the interaction between California red scale and *A. melinus* be ascertained.

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**Literature Cited**


———. 1989. Host-size-dependent sex ratios among para-


Yu, D. S. 1986. The interactions between California red scale, **Aonidiella aurantii** (Maskell), and its parasitoids in citrus groves of inland southern California. Dissertation. University of California at Riverside, Riverside, California, USA.
