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Hare, J Daniel
Morgan, David J. W.

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CHEMICAL CONSPICUOUSNESS OF AN HERBIVORE TO ITS NATURAL ENEMY: EFFECT OF FEEDING SITE SELECTION

J. DANIEL HARE[1] AND DAVID J. W. MORGAN

Department of Entomology, University of California, Riverside, California 92521 USA

Abstract. A physical refuge from the parasitoid *Aphytis melinus* is provided to the California red scale *Aonidiella aurantii* by the interior bark substrates of citrus trees, even though scales have lower fitness on bark in the absence of *A. melinus.* How bark-reared scales escape parasitism was unclear because *A. melinus* searches the interior of trees as effectively as the exterior. Host identification in *A. melinus* is mediated by a kairomone, *O*-caffeoyltyrosine, in scale covers. *O*-caffeoyltyrosine concentration varies with scale age and rearing conditions. We hypothesized that the reduced acceptance of bark-reared scale may be due, in part, to reduced quantities of *O*-caffeoyltyrosine in their covers. We reared scales on bark, leaves, and fruit of lemon and orange trees in the field at monthly intervals and then collected the scales and measured them. We bioassayed covers for their acceptability to *A. melinus* in the laboratory and then determined their *O*-caffeoyltyrosine content. Even after adjusting for the differences in scale body size, *O*-caffeoyltyrosine content in bark-reared scale covers was 45–85% less than that in covers of leaf- or fruit-reared scales, depending upon cultivar and rearing date. Covers of bark-reared scales were selected for probing only 40–45% of the time when compared to leaf-reared scales. Covers with the highest levels of *O*-caffeoyltyrosine were most likely to be selected for probing. We conclude that part of the mechanism by which California red scales on bark avoids discovery is through reduced *O*-caffeoyltyrosine content in their covers. This reduction is probably a consequence of the reduced nutritional quality of bark as a substrate for scale survival and growth.

Key words: Aonidiella aurantii; Aphytis melinus; *biological control; chemical ecology; host recognition; infochemical; kairomone;* O*-caffeoyltyrosine; refuge; tritrophic interactions.*

INTRODUCTION

Host selection by insect parasitoids is strongly influenced by ''infochemicals,'' or chemicals that convey information about the location, identity, and suitability of potential host species (Dicke and Sabelis 1988, Vet and Dicke 1992, Turlings et al. 1993, Vet et al. 1995). Kairomones are an important category of infochemicals that evoke a behavioral or physiological response that is adaptively favorable to the receiver but detrimental to the emitter (Dicke and Sabelis 1988, Whitman 1988). Kairomones are widely used by parasitic insects to locate and identify their hosts. The sources of such kairomones are diverse and include body odor, frass, webbing, salivary constituents, honeydew, body scales, egg chorions, and some host pheromones (reviewed by Vinson 1976, Weseloh 1981, Whitman 1988, Lewis and Martin 1990, Vet and Dicke 1992).

The fundamental criterion of a kairomone is that it reliably indicates the presence, identity, and suitability of a host (Vet et al. 1991). Thus, natural selection should favor parasitoids that utilize as kairomones only the chemicals that uniquely and reliably identify potential hosts. In contrast, in the absence of offsetting benefits or genetic fixation for kairomone production, natural selection should also eliminate the most ''conspicuous'' individuals from host populations. Because kairomones are probably advantageous to hosts in other contexts, selection for inconspicuousness is unlikely to eliminate the production of chemicals used as kairomones. Rather, selection may favor hosts that reduce the kairomone's concentration, increase its rate of elimination, or mask its production.

A parasitoid's ability to recognize a host is essential for effective biological control. Thus, host-induced variation in the parasitoid's ability to recognize hosts can contribute directly to the variation in the effectiveness of biological control programs. Both the conspicuousness and quality of phytophagous insects for discovery and use by parasitoids may vary depending upon which host plant species the host is reared (Price et al. 1980, Boethel and Eikenbary 1986, Duffey and Bloem 1986, Barbosa and Letourneau 1988, Hare 1992).

The role of the host plant on host quality is well illustrated by the system involving citrus cultivars, the California red scale *Aonidiella aurantii* (Maskell), and the introduced parasitoid *Aphytis melinus* DeBach. Probably the most important index of scale quality for utilization by *A. melinus* is scale size. Offspring size, sex, and initial fecundity are all strongly influenced by

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[1] E-mail: harejd@citrus.ucr.edu

the size of the scale host from which wasps emerge, and mid-third instars are most valuable (Luck and Podoler 1985, Opp and Luck 1986, Yu and Luck 1988, Hare and Luck 1991). The size to which scales grow, however, varies substantially among citrus cultivars and substrates within cultivars (Hare et al. 1990, Hare and Luck 1991, 1994). In general, scale are largest when reared on leaves and fruit compared to scales reared on bark, and when reared on lemon and grapefruit cultivars compared to orange or mandarin cultivars.

Despite the lower quality of bark as a substrate, the bark substrate supports the majority of the scale population within a tree in many citrus cultivars (Carroll and Luck 1984*a*, Reeve and Murdoch 1986, Murdoch et al. 1989). This substrate provides the majority of scale crawlers settling on the more distal fruit and leaf substrates (Murdoch et al. 1996). In addition, the bark substrate provides a partial refuge from parasitization by *A. melinus* (Reeve and Murdoch 1986, Walde et al. 1989, Murdoch et al. 1995), even though *A. melinus* actively searches the interior of the trees (Murdoch et al. 1989). Murdoch and collaborators proposed two hypotheses for the low rate of parasitization of scale on the bark substrate. The first was that *A. melinus* either avoided searching, or was ineffective at finding scale on woody substrates. The second was that, although *A. melinus* finds scales on bark, it might reject a higher proportion of those on bark than on leaves and fruit. Initially, it was hypothesized that the rejection rate and reduced parasitization rates were caused by the reduced size of scale on the bark, but the reduction in size only accounted for about 1/10 of the reduction in parasitization rate (Walde et al. 1989). Thus, Walde et al. (1989) and Murdoch et al. (1989) suggested that there might be something in the nature of the bark, or of the scales on the bark, that made the bark substrate a refuge for scale from attack by *A. melinus.*

Aphytis melinus uses learned, volatile cues from host plants as long-range attractants to potential habitats of California red scale (Morgan and Hare 1998*a*). Once on the plant, then the wasp forages for hosts by walking. Recognition of California red scale by *A. melinus* is mediated by the presence and quantity of the nonvolatile compound, *O*-caffeoyltyrosine (hereafter OCT) in scale covers (Hare et al. 1993, Morgan and Hare 1997). OCT is probably the precursor of a component of the scale's cover and is incorporated into the cover matrix after secretion through polymerization; highest concentrations are found in covers of third-instar scales (Hare et al. 1993, Hare and Luck 1994). OCT is a contact kairomone to which wasps respond innately. After contacting a scale, wasps exhibit a complex, antenna-drumming behavior on the cover, and, if the cover contains a sufficient quantity of OCT, the wasp will begin probing the cover with her ovipositor (Hare et al. 1993, Morgan and Hare 1997). The threshold dose of OCT that stimulates ovipositor probing can be lowered by prior experience either with California red scale covers or with OCT (Hare 1996, Hare et al. 1997, Hare and Morgan 1997).

In field-reared scale, OCT concentrations were both lower and more variable than in laboratory-reared scale (Hare and Luck 1994). Generally, OCT concentrations tended to be higher in covers from scales reared on leaf and fruit substrates than on the bark of lemon and orange cultivars. There was, however, substantial overall seasonal variation in OCT concentrations as well, because scales reared on leaves during two midsummer rearings had lower OCT concentrations than scales reared during the early summer or fall (Hare and Luck 1994).

We suggest that the variation in OCT content in covers from scale reared on different cultivars, substrates, and times of the year may contribute to the observed variation in parasitization rates. Specifically, we test the hypothesis that scales reared on bark are less easily recognized by *A. melinus* than scales reared at the same time of year on leaves and fruit because they contain less OCT.

We conducted a number of experiments to determine how OCT may mediate host selection by *A. melinus* of California red scale reared on fruit, leaves, or bark of lemon (*Citrus limon* [L.] Burm.) and orange (*Citrus sinensis* [L.] Osbeck). We first verified that scale body size, cover size, and OCT content varied as a function of the cultivar, substrate, and time of year that the scale insect was reared. We then tested the preference of wasps for scale covers of insects reared on different substrates of both species. This was repeated four times throughout the summer at monthly intervals to determine if preferences varied seasonally. We measured the areas of the covers of test scales, the areas of the bodies from beneath those covers, and levels of OCT in each of the scale covers individually. We then determined if the preference for particular hosts was correlated with scale cover size, scale insect body size, or the amount of OCT on the covers.

Finally, we verified the implications from previous studies for wasps selecting scale insects from different substrates as hosts for their offspring. Developmental mortality and the size of emerging females from scale insects reared on fruit, leaves, and bark of lemon and orange were assessed during the growing season. We interpret our results within the context of possible trade-offs between the quality of substrates in their ability to support scale growth and the risk of discovery by natural enemies that those substrates confer to scale insects.

Methods

California red scale life history

Detailed descriptions of the biology of diaspidid scale insects can be found in Rosen (1990). Some salient points are as follows: All stages except the first

instar crawler and adult male are sessile and sightless (Ben-Dov 1990). All stages of the insect, except the crawler and the adult male, secrete a covering that lies over its dorsum for protection. This cover is external to the insect and is not composed of living tissue (Foldi 1990). Covers are composed of about equal portions of waxy filaments and polar, nonwaxy material that cements these filaments together, plus the cast skins of previous instars. The proportions of waxy and polar constituents vary among species, as does the color and thickness of covers (Foldi 1990). Scale covers are not attached to the scale during the scale's growing stages and can be removed easily. Scales whose covers are damaged or removed can repair or entirely replace their covers if scales do not desiccate first (Baker 1976). All diaspidids feed on individual cells of their host plants, not on phloem, and none produce honeydew (Ben-Dov 1990).

Bodenheimer (1951) provides a detailed life history of California red scale, and summaries appear in Hare et al. (1990) and Hare and Luck (1991). California red scale is multivoltine and develops all year. Two to three generations are produced annually, depending upon local temperatures. Females pass through three larval stadia before becoming adults, while males pass through two larval stadia, then prepupal and pupal stages before emerging as winged adults. Males and females are indistinguishable until the second stadium, when males become oblong while females remain round. California red scale has a worldwide distribution and has been reported from several perennial plant species. The most important hosts are *Citrus* spp., followed by *Rosa* spp. and a few ornamental species, e.g., *Euonymus* spp. (Bodenheimer 1951).

The most successful of some 52 natural enemies introduced to control California red scale in California is *A. melinus,* which was introduced in 1957. *A. melinus* quickly became established in southern California and has provided economic biological control of California red scale ever since. In contrast, *A. melinus* can provide economically acceptable suppression of California red scale in the San Joaquin Valley only through an annual series of approximately 13 biweekly augmentative releases of 19 000 wasps per hectare per release (Luck et al. 1996).

Laboratory cultures

Laboratory cultures of California red scale were reared on 'Eureka' lemon fruit (26°C, 40–60% RH, L16:D8 photoperiod) in the University of California Insectary at Riverside as previously described (Tashiro 1966). *Aphytis melinus* were reared on oleander scale, themselves reared on lemon fruit (26°C, 40–60% RH, L16:D8 photoperiod) as previously described (Opp and Luck 1986). Fresh lemons with scales were placed in a cage with *A. melinus* adults twice a week to maintain the colonies.

Field rearings

We established field populations of California red scale on experimental trees by infesting trees with crawlers from the laboratory scale colony following procedures outlined in Hare and Luck (1991). Two lemons with mature, crawler-producing female scales were hung in each of eight previously cleaned branches 2–5 cm diameter in each of four trees of 'Eureka' lemon, and 'Valencia' orange. The trees were growing in a mixed planting of 18 cultivars at Agricultural Operations, University of California at Riverside.

We placed a sleeve cage (1 m long by 0.32 m diameter) around each branch to protect the scales from resident *A. melinus* and other natural enemies. The lemons with mature California red scale were removed after one week, resulting in populations of California red scale varying 7 d in age on leaves, fruit, and bark of each branch. Four inoculations were carried out and were initiated on 31 March, 5 May, 2 June, and 1 July 1997.

Scale development was monitored visually and with a day-degree model using temperatures recorded hourly with a 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 branches were collected for laboratory studies.

Whole branches with experimentally infested scales, cages, and labels, were cut from the tree and brought into the laboratory. Scales used for measurement of field levels of OCT were removed immediately for analysis. The remaining material was stored in a cold room (4°C) for behavioral assays. Branches were harvested on 19 May, 9 June, 7 July, and 4 August for the four inoculations, respectively.

OCT analysis

After removing and measuring the area of the scale cover, we placed each scale cover in a microcentrifuge tube. An extraction solvent was made up from 75% methanol and 25% of a solution of 0.075% trifluoroacetic acid (TFA) in water. The internal standard, ferulic acid, the 3-methoxy analogue of caffeic acid, was added to the solution at a concentration of 0.1 μg/mL. The extraction solvent (0.2 mL) was added to the microcentrifuge tube containing the scale cover, then the tube was closed and placed in a sonicating bath for 12 h. The extraction solvent was filtered through an Acrodisc 13 CR PTFE syringe filter (Gelman Scientific, Ann Arbor Michigan, USA). The solution was evaporated to dryness in a microcentrifuge freeze dryer (Savant Industries, Holbrook, New York, USA), then 20 μL of 1:1 acetonitrile : 0.075% TFA in water was placed in the tube. The solution was mixed thoroughly.

We injected five μL of the solution into a Hewlett

Packard model 1050 high performance liquid chromatograph with a diode array detector (Hewlett Packard Chemical Analysis Group, Wilmington, Delaware, USA). The chromatograph was fitted with a microbore C18 column (Phenomenex Ultramex 3 C18, 100 × 1.0 mm diameter, Phenomenex, Incorporated, Torrance, California, USA), through which 18% acetonitrile in 0.075% aqueous TFA was passed at 0.125 mL/min. Elution was monitored by UV absorbance at 325 nm, and the concentration of the extracted kairomone was calculated relative to the internal standard.

Scale body size, cover size, and OCT content under field conditions

Within one day of harvesting branches from the field, we collected 30 scale insects from each of the six substrate–cultivar combinations for each of the four rearing dates with the following exception. Not enough scales were available from the bark substrates during the third rearing to be used in bioassays and these additional measurements, thus the bark substrates were not included in samples from the third rearing period. A total of 660 scales were collected and measured.

The area of scale insect bodies was measured by placing them on hemocytometer and measuring the longest and shortest radii. The area of the bodies was calculated using the equation for an ellipse ($\pi r_1 r_2$, where r_1 and r_2 are the radii). The covers were measured, as described above, and immediately immersed in 0.2-mL extraction solvent with internal standard for OCT analysis. We repeated the scale collection for each of the four inoculations.

We addressed three questions relevant to our specific hypothesis with these data: (1) Do scale bodies, covers, and OCT content vary with cultivar, substrate, and time of year that scales are reared? (2) Do covers that vary in size according to growing conditions (cultivar, substrate, and rearing date) conceal bodies of the same size? (3) Does the OCT content of covers from bodies of the same size differ according to substrate and growing conditions? These questions were answered first by analysis of variance (ANOVA) on scale body size, cover size, and OCT content, then using analysis of covariance (ANCOVA) with either cover size or OCT as the response variable and body size as a covariate. All analyses were performed using PROC GLM of SAS (SAS Institute 1988). All data also were transformed using the $\log_{10}(X + 1.0)$ transformation for OCT concentrations and $1/\sqrt{(\text{area})}$ for cover and body areas to ensure normality and independence of treatment mean and variances.

Response of A. melinus *to field-reared scale covers*

Wasps were prepared for bioassay by removing them during their pupal stage from the host and host plant material and placing them in a container until adult emergence (Hare et al. 1997). This prevented wasps from receiving early adult experience with the lemon fruit on which they were cultured. We placed newly emerged wasps (<2 h post eclosion) in a container with a squash (*Cucurbita maxima* Dutch.) infested with California red scale. This was to provide wasps with experience with their hosts without experience with citrus. We then removed the wasps and placed them in an empty container for 1 d to allow maturation of eggs (Rosenheim and Rosen 1991). We placed a smear of honey in the containers throughout the wasps' adult life for nutrition (Collier 1995). On the day of bioassay, we isolated female wasps and held them individually in vials with a drop of honey.

TABLE 1. Summary of behavioral choice experiments when *A. melinus* females were offered pairs of covers from scales reared on different citrus cultivars and substrates.

Leaf vs. fruit	Leaf vs. bark	Lemon vs. orange
1) Lemon	3) Lemon	5) Fruit
2) Orange	4) Orange	6) Leaf
		7) Bark

Notes: Experiment 1, covers from leaf-reared scales vs. covers from fruit-reared scales from lemon; experiment 2, covers from leaf-reared scales vs. covers from fruit-reared scales from orange; experiment 3, covers from leaf-reared scales vs. covers from bark-reared scales from lemon; experiment 4, covers from leaf-reared scales vs. covers from bark-reared scales from orange; experiment 5, covers from fruit-reared scales of lemon vs. covers of fruit-reared scales of orange; experiment 6, covers of leaf-reared scales of lemon vs. covers of leaf-reared scales of orange; experiment 7, covers of bark-reared scales of lemon vs. covers of bark-reared scales of orange.

To test for the effect of cultivar, substrate, and time of year on scale cover preference by *A. melinus,* we used scale insects from branches stored in a cold room (4°C) for no more than 5 d. We assayed scale cover preference by offering a wasp a choice of four scale covers, two from one substrate, and two from another (Table 1). Four scale insects, matched for cover size to within 0.02 mm, were removed from their respective substrates. We measured cover size and body size as described above. The covers, after removal from the scale bodies, were then placed in a square (2 mm separation) on a microscope slide. We placed a Plexiglas barrier around the scale covers, and then we placed a second microscope slide on the barrier to form an observation chamber (Luck et al. 1982).

For the bioassay, a female wasp was introduced into the chamber. The first scale it investigated with its antennae (drumming), and the first scale it attempted to probe with its ovipositor (probing) was recorded. The wasp was then removed. Ten wasps were offered each scale set, then the scale covers were removed and immersed individually in 0.2-mL extraction solvent for OCT analysis. Thus, 10 probes were recorded for each group of four scale covers. The proportion of times that each scale cover was probed was then calculated. For each of the seven substrate/cultivar comparisons, four scale sets were tested, each with 10 fresh wasps. We repeated the bioassays four times over the year, once

for each scale cohort, to assess seasonal variation in preference for scale grown on different citrus cultivars and substrates. A total of 448 scale covers were bioassayed and analyzed (seven comparisons × four replicate sets of four covers repeated over four rearing dates) with 10 wasps each (total of 4480 wasps), and then analyzed for OCT content.

Data were grouped into three sets for analysis of variance, two substrate comparison sets, and one cultivar comparison set (as in Table 1). For all sets, the proportion of scales selected for probing was analyzed by two-way ANOVA. The effects in the ANOVA model were cultivar, substrate, the cultivar by substrate interaction, cohort, and replicate group of scale covers within cohort.

Because of the (expectedly) high variation in OCT content among scale covers from scales reared at different times of the year and on different cultivars and substrates, we asked if wasps could respond to relative differences in OCT content among the four scale covers in each group. Therefore, we ranked scale covers according to their OCT content within each group (1 to 4, with 1 being the highest rank). Scale cover and body size were ranked in a similar fashion as well as the rank order in which each of the covers was selected for probing. Then the association between OCT rank and probing rank, cover size rank and probing rank, or body size rank and probing rank was analyzed by a *G* goodness-of-fit test. The null hypothesis was no association among ranks, i.e., wasps select scale covers at random with regard to OCT content, cover size, or body size.

Quality of red scale as a host for A. melinus

To confirm previous studies (Hare and Luck 1991) on the effect of variation among rearing times on the quality of California red scale for utilization by *A. melinus,* we collected additional experimentally reared scale on lemon and orange fruit from the field on each of the four dates above. The infested lemon and orange fruit were placed in a sting chamber (Hare et al. 1997) with approximately 50 female *A. melinus* adults. After one day, the wasps were removed, and the fruit with parasitized scale were incubated for 10 d under the conditions described above. By the end of this period, wasps had reached pupation.

A random sample ($n = 100$) of scale insects was inspected under a binocular microscope. We counted the number of parasitized scale insects with dead parasitoids and the number of parasitized scale insects with parasitoids that had successfully reached pupation. Unparasitized scale mortality was not measured because no method could be found to remove all dead scale insects prior to testing without also removing the covers of living scale; therefore mortality in the field could not be differentiated from mortality over the test period. Wasps do not oviposit on dead scales (D. J. W. Morgan, *personal observation*), so we could be sure that all parasitized scales were living at the time of parasitism.

Thirty parasitized scale insects (covers and wasp pupae) from each cultivar/cohort combination were collected and placed in vials. The size of the cover of each scale insect was measured using a binocular microscope with an ocular micrometer. The clutch size, sex, and hind tibia length (HTL) of wasps emerging from each scale insect were measured under a compound microscope with an ocular micrometer. HTL is a good index of wasp size and fecundity (Opp and Luck 1986, Yu and Luck 1988). To assess the quality of wasps under different growing conditions, we used an ANOVA to test for differences in male and female HTL among cohorts, clutch sizes, and cultivars.

This methodology could not be repeated on leaves and bark because California red scale died due to substrate desiccation once this plant material had been removed from the tree. Because of the higher overall quality of fruit for utilization by California red scale compared to leaves and bark (Hare and Luck 1991, and references therein), this may be a conservative test for variation in scale quality for *A. melinus* as a function of rearing date.

To confirm the expected variation among substrates on scale quality for *A. melinus,* two lemon and two orange branches from the last cohort were left on the trees. Fifty wasps were introduced into each bagged branch and the branch was left on the tree until wasps pupated. The branches were then removed and wasp mortality and host quality measurements were carried out as above. Mortality data were analyzed by a three-way contingency table using log-linear models (Sokal and Rohlf 1989). For the data collected from fruit, the factors were cultivar, cohort, and mortality. For the data collected from the different substrates, the factors were cultivar, substrate, and mortality.

Results

Scale body size, cover size, and OCT content under field conditions

Scale body size, cover size, and OCT content all varied depending upon when and where California red scale were reared. Such variation in scale body and cover size is not unprecedented (Hare and Luck 1991, 1994) and illustrates the problem that *A. melinus* faces in initially assessing host quality on the basis of the host's cover size. After adjusting for variation in body size, scale cover size differed significantly due to rearing date ($F_{3, 637} = 8.73$, $P < 0.001$), substrate ($F_{2, 637} = 4.52$, $P < 0.05$), the rearing date by substrate interaction, ($F_{5, 637} = 9.63$, $P < 0.001$), the cultivar by substrate interaction ($F_{2, 637} = 8.00$, $P < 0.001$), and the three-way interaction ($F_{5, 637} = 6.87$, $P < 0.001$, Fig. 1). The linear effect of scale body size on scale cover size also was highly significant ($F_{1, 637} = 2217.61$, $P < 0.001$, $r^2 = 0.58$). Thus, although scale cover size is

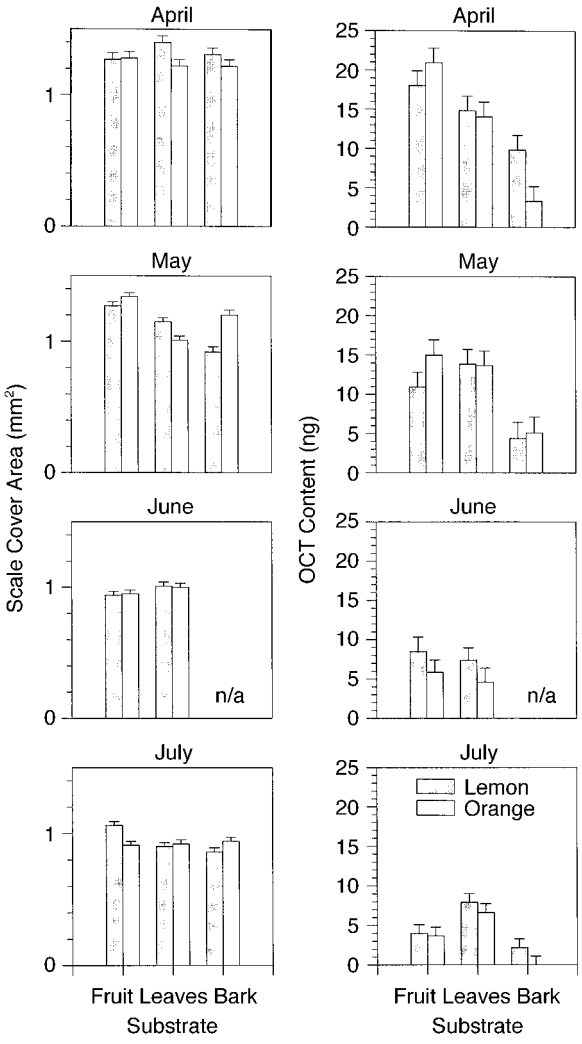

FIG. 1. Scale cover area (mean + 1 SE; mm²) and OCT content (mean ± 1 SE; ng/cover) adjusted for scale body area (mm²) from ANCOVA for scales reared on fruit, leaves, or bark of lemon or orange at monthly intervals during 1998. Too few scales survived on bark of either cultivar for measurement during the third (June) rearing.

generally correlated with scale body size, scales of similar body sizes can have variable cover sizes depending upon when and where scales were reared. Scale cover size is not a precise indicator of scale body size, and it is not surprising that whatever preference *A. melinus* has for cover size is learned and not innate (Morgan and Hare 1998*b*).

After adjusting for variation in scale body size, scale cover OCT content also continued to differ significantly due to rearing date ($F_{3, 637} = 30.45$, $P < 0.001$), substrate ($F_{2, 637} = 62.86$, $P < 0.001$), the rearing date by substrate interaction ($F_{5, 637} = 2.38$, $P < 0.05$), and the cultivar by substrate interaction ($F_{2, 637} = 6.35$, $P < 0.01$, Fig. 1). Overall, the linear effect of scale body size on OCT content also was highly significant statistically ($F_{1, 637} = 26.29$, $P < 0.001$) but not very predictive ($r^2 = 0.03$). These results suggest that one consequence of scale crawlers settling on the bark of lemon or orange trees is to minimize their chemical conspicuousness to *A. melinus.* The degree to which conspicuousness is minimized may vary with seasonal temperatures and is minimized overall when scales are reared under the highest summer temperatures (see also Hare and Luck 1994).

Response of A. melinus *to field-reared scale covers*

Wasps offered a choice between scale covers grown on leaves and bark preferentially selected covers from scales reared on leaves for probing ($F_{1, 125} = 6.53$, $P < 0.05$, Fig. 2). When offered a choice of covers grown on fruit or leaves, wasps showed no preference, however ($F_{1,93} = 1.17$, NS). These patterns did not vary over the season (cohort effects: $F_{3, 125} = 0.02$, NS for Leaf vs. Bark comparison and $F_{3,93} = 2.02$, NS for Fruit vs. Leaf comparison). Wasps also showed no overall preference for scales reared on either lemon or orange over all substrates pooled ($F_{1, 171} = 0.45$, NS), nor was there a significant cultivar by substrate interaction effect on scale cover selection for probing ($F_{2, 171} = 0.03$, NS, Fig. 2). After all trials were pooled, wasps showed a preference for probing scale covers with the highest

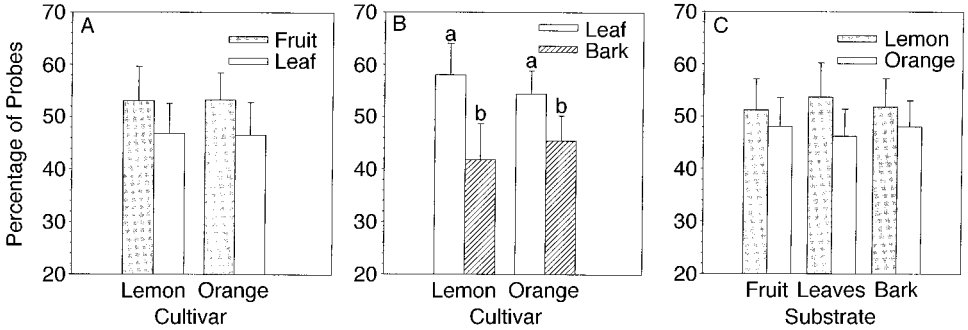

FIG. 2. Scale cover selection by *A. melinus* in behavioral bioassays. Histograms show mean (+1 SE) percentage of scale covers selected for probing when reared on different combinations of citrus cultivars and substrates within cultivars. (A) Fruit-reared vs. leaf-reared covers (experiments 1 and 2; Table 1); (B) leaf-reared vs. bark-reared covers (experiments 3 and 4; Table 1); (C) lemon-reared vs. orange-reared covers from fruit, leaves, or bark (experiments 5–7; Table 1).

TABLE 2. Correspondence of scale covers ranked by *O*-caffeoyltyrosine (OCT) content, cover area, or body area vs. rank of covers selected for probing after pooling all choice data.

	Probing rank			
Rank	1 (highest)	2	3	4 (lowest)
OCT content				
1 (highest)	45	24	18	19
2	25	31	30	45
3	22	41	46	36
4 (lowest)	14	20	29	29
Cover size				
1 (largest)	18	29	36	28
2	22	31	31	30
3	35	25	24	27
4 (smallest)	31	30	33	18
Body size				
1 (largest)	16	29	38	27
2	27	26	26	35
3	35	29	28	20
4 (smallest)	28	30	32	22

Note: The expected cell value is 28 under the null hypothesis of no association.

OCT content of those available ($G_9 = 34.28$, $P < 0.001$, Table 2). Wasps did not preferentially select covers on the basis of cover size ($G_9 = 13.78$, $P = 0.13$) or on the basis of the size of the bodies that the covers once protected ($G_9 = 15.19$, $P = 0.09$).

Quality of California red scale as a host for A. melinus

Hind tibia length (HTL) of female wasps emerging from field-reared scale on fruit differed only among rearing dates ($F_{3, 237} = 176.65$, $P < 0.001$, Table 3) but not due to cultivar, clutch size, or the cultivar × cohort interaction (all $P > 0.14$). Clutch sizes were either 1 (264 wasps) or 2 (154 wasps). Hind tibia lengths of male wasps also differed significantly among rearing dates ($F_{3, 163} = 173.78$, $P < 0.001$). In contrast to females, male HTL differed due to clutch size ($F_{1, 163} = 7.33$, $P < 0.01$). For both sexes, wasps were smaller in cohorts 3 and 4, when they were reared during the warmer summer temperatures of June, July, and August, than when reared during April and May. Male wasps were slightly smaller when reared with a sibling than when reared alone.

During the July and August rearing period, female HTL length differed significantly only due to substrates ($F_{2,72} = 3.93$, $P < 0.05$, Table 4). Wasps from fruit- and leaf-reared scales were of similar size, but larger than those reared on bark; these differences were independent of cultivar ($F_{1,72} = 0.51$, $P = 0.48$) and clutch size ($F_{1,72} = 0.01$, $P = 0.91$). Male HTL also differed significantly due to substrates ($F_{1,37} = 11.26$, $P < 0.01$, Table 4) and were larger when reared on scale on fruit than scale on leaves. Because of the high wasp mortality (see below), no male wasps were recovered from bark-reared scale. Male HTL also differed significantly between cultivars ($F_{1,37} = 5.21$, $P < 0.05$) and between clutch sizes ($F_{1,37} = 4.93$, $P < 0.05$). Male wasps were larger when reared from scale on orange fruit than lemon fruit and when reared alone than when reared with a sibling.

TABLE 3. Hind tibia lengths (HTL; mean ± standard errors; mm) of *A. melinus* males and females reared on lemon or orange fruit at monthly intervals from April through July 1997.

Cohort and cultivar	Male HTL	Female HTL
April		
Lemon	0.218 ± 0.006 (4)	0.284 ± 0.007 (17)
Orange	0.215 ± 0.006 (4)	0.282 ± 0.005 (14)
May		
Lemon	0.278 ± 0.007 (10)	0.310 ± 0.007 (11)
Orange	0.265 ± 0.005 (22)	0.306 ± 0.005 (24)
June		
Lemon	0.177 ± 0.003 (43)	0.218 ± 0.004 (48)
Orange	0.170 ± 0.003 (25)	0.214 ± 0.003 (65)
July		
Lemon	0.183 ± 0.004 (35)	0.215 ± 0.004 (32)
Orange	0.177 ± 0.004 (29)	0.220 ± 0.003 (35)

Note: Sample sizes are in parentheses.

Wasp mortality was significantly associated with substrate ($G_6 = 141.747$, $P < 0.001$) and was higher on bark than on leaves or fruit (Fig. 3). Mortality was independent of cultivar, however ($G_5 = 3.849$, $P > 0.05$, Fig. 3). For scales reared on fruit at monthly intervals, wasp mortality was independent of cultivar ($G_7 = 5.083$, NS) and rearing date ($G_9 = 7.485$, NS, Fig. 3).

DISCUSSION

Substrate selection by individual crawlers of California red scale has substantial lifelong consequences upon that individual's probability of survival and re-

TABLE 4. Hind tibia lengths (HTL; mean ± standard errors; mm) of *A. melinus* males and females reared on lemon or orange fruit, leaves, or bark during July 1997.

Substrate and cultivar	Male HTL	Female HTL
Fruit		
Lemon	0.178 ± 0.004 (16)	0.215 ± 0.006 (26)
Orange	0.195 ± 0.003 (10)	0.205 ± 0.004 (15)
Leaves		
Lemon	0.162 ± 0.006 (6)	0.198 ± 0.005 (6)
Orange	0.179 ± 0.005 (13)	0.204 ± 0.003 (30)
Bark		
Lemon	NA†	0.190 (1)
Orange	NA	0.163 ± 0.008 (4)

Notes: No male wasps were recovered from bark-reared scale, and only one female wasp was recovered from bark-reared scale on lemon. Sample sizes are in parentheses. NA = not available.

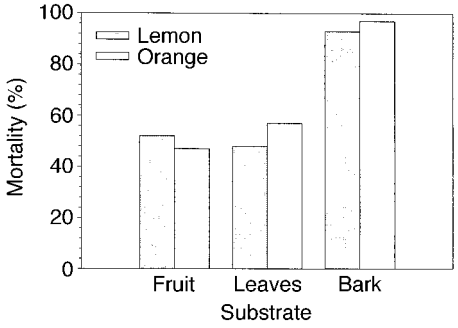

FIG. 3. Wasp mortality (%) when reared on scales, that were reared on lemon or orange fruit, leaves, or bark during the fourth rearing period of 1997.

production. The bark substrate is inferior to leaves and fruit for scale survival and growth. One potential advantage of settling on bark substrates is that surviving crawlers avoid all mortality from substrate abscission. Another advantage to choosing the bark substrate is that surviving scale individuals are less likely to be selected for attack by *A. melinus.*

Here, we show that it is the scales themselves that are less attractive to *A. melinus,* and the reduced attractiveness of bark-reared scales is not entirely due to substrate characteristics (e.g., Murdoch et al. 1989). Such a reduction in attractiveness of scales reared on bark due to reduced OCT is not complete, however, because ~40%–45% of covers from bark-reared scales, depending upon cultivar, were still the first covers selected for probing compared to covers from leaf-reared scales. Unfortunately, too few scale covers from bark-reared scales were available to be tested directly against covers from fruit-reared scale. Based on the similar to slightly higher size and OCT content of covers from fruit compared to leaves, we would expect that the preference for scale reared on bark to be no greater than 40% when compared to covers from scales when reared on fruit, and probably less. These results do not negate the role of other hypothesized factors, extrinsic to the scale and its cover, such as dirt, or the color and texture of bark that also may reduce the attractiveness of bark-reared scale (e.g., Walde et al. 1989). Such other factors would act in addition to the reduced intrinsic chemical conspicuousness of California red scale covers, and we would expect the relative importance of all of these factors to vary among citrus groves as a function of cultivar, plant age, climate, growing conditions, and other factors.

The probability that an individual California red scale will be attacked by *A. melinus* declines with decreasing OCT content in that scale's cover. In several previous laboratory studies, we showed that *A. melinus* could respond quantitatively to variation in OCT levels (Hare et al. 1993, Millar and Hare 1993, Morgan and Hare 1997, 1998*b,* Hare and Morgan 1997). Here, we extend those results to include covers from field-reared scales as well. The fact that *A. melinus* preferentially selects scales whose covers have relatively high OCT content suggests that *A. melinus* could be a strong agent of natural selection favoring California red scales that minimize the OCT content of their covers as much as possible. This could be achieved in two general ways. The first is through minimizing its rate of production, and the second is through maximizing its rate of incorporation.

In the absence of other factors, California red scale should produce covers that closely fit their bodies, and as rapidly as possible. It therefore may not be obvious why scales that settle on fruit produce relatively large covers. One potential advantage to larger covers may be through enhanced survival of progeny. Mature female scales are viviparous and produce 2–3 crawlers per day, totaling 100–150 over the female's lifetime. The newly hatched crawler remains under its mother's cover for a few hours before emerging and seeking its feeding site, usually within another 2–6 h. Perhaps larger covers permit a greater number of progeny to complete post-hatching development (e.g., hardening of the exoskeleton before seeking feeding sites). Alternatively, excessively large cover formation simply may be a serendipitous consequence of improvements in the nutritional quality of these commercial cultivars for scale growth through domestication and artificial selection for improved agronomic characteristics. Neither of these hypotheses has been tested to date, however.

The rate at which OCT is incorporated into scale covers appears to be driven by external environmental conditions. In the laboratory, these rates were greater at high temperatures, and also at low humidity (Hare and Luck 1994). The lower levels of OCT in covers from field-reared scales during June, July, and August compared to levels in covers when reared in April and May are consistent with this hypothesis. Indeed, given the wide variation in OCT levels, it appears that California red scale is quite effective in minimizing the OCT content in its covers during the hotter summer months (see also Hare and Luck 1994).

Bark-reared scales were of reduced quality for utilization by *A. melinus* compared to fruit- or leaf-reared scales, because wasp mortality was higher, and the size of surviving wasps was smaller when reared from bark-reared scales. Wasps from bark-reared scale are also probably less fecund (Luck and Podoler 1985, Opp and Luck 1986, Yu and Luck 1988, Hare and Luck 1991). Because of the reduced fitness of progeny from small scales, *A. melinus* probably is also under strong selection to quickly recognize and reject inferior hosts (McNamara and Houston 1986, Morgan and Hare 1998*b*). The evidence presented here and in our previous laboratory studies strongly suggests that this rapid evaluation and rejection is mediated by the low OCT content in covers of bark-reared scale.

The role that natural enemies, such as *A. melinus,*

may play in the evolution of substrate selection behavior by California red scale crawlers is unclear, however. Assuming the existence of additive genetic variation in substrate selection behavior, then a case could be made that substrate-selective mortality due to *A. melinus* could confer a selective advantage to crawlers that preferentially select bark substrates where mortality from *A. melinus* would be minimized. However, the existence of other natural enemies in the system adds complications. Another introduced parasitoid, *Encarsia perniciosi* (Tower) coexists with *A. melinus* in southern California coastal citrus, but is a relatively more effective parasitoid of smaller California red scale, and scales on twigs and bark than is *A. melinus* (Yu et al. 1990). Thus, to an extent, the mortality from *A. melinus* that California red scale crawlers might avoid by settling on bark could be replaced by mortality from *E. perniciosi.* A third introduced parasitoid, *Comperiella bifasciata* Howard, also parasitizes California red scale on fruit to a greater extent than scale on wood (Carroll and Luck 1984*b*), but host selection by *C. bifasciata* is mediated by a chemical compound far larger and more unstable than OCT (R. F. Luck, *unpublished data*). Thus, the bark substrate may not provide California red scale the same level of protection from different natural enemies, nor might the same mechanism of minimizing scale conspicuousness be effective against all natural enemies.

At present, there also are no studies addressing the existence of any genetic variation in the behavior of feeding-site selection by first-instar crawlers, and such variation may be difficult to measure for the following reasons. First, the first-instar crawlers can only make one choice because they lose their legs after settling. Moreover, although wandering time may be somewhat longer on the fruit and leaves of less suitable citrus species, and in the presence of high densities of settled scale, the majority of settling still occurs within 2–6 h (Willard 1972, Hare et al. 1990). This rapid response time might suggest that the need to find quickly even a marginal feeding site may override the need to spend additional time searching for a feeding site where the discovery by natural enemies might be minimized. Indeed, in our previous field experiments, most settling occurred within a few centimeters of the site of crawler production (Hare et al. 1990, Hare and Luck 1991). Further research would be required to ascertain if *A. melinus* and other parasitoids might be imposing natural selection upon scale crawlers to settle on marginally inferior substrates in order to minimize their risk of discovery (i.e., to seek out enemy-free space [Berdegue et al. 1996]). Such research also would be most relevant if carried out in habitats less removed from the system's evolutionary context than the California citrus agroecosystem.

Our study is among the first to address the ecological significance of quantitative variation in kairomone content among host individuals on host selection by parasitoids. Most previous research has focused simply upon the qualitative responses of parasitoids to kairomones (i.e., acceptance or rejection of a host based upon the presence or absence of a kairomone) without addressing the significance of quantitative variation. The absence of other such quantitative studies is probably because the chemical identities of many kairomones are still unknown, and no precise methods of chemical measurement for such compounds have yet been developed. Quantitative studies similar to ours on the chemical mediation of other host–parasitoid associations in the field may be delayed until appropriate quantitative chemical methods are developed, in many cases.

In summary, feeding site selection by California red scale crawlers probably is constrained by limited mobility of first-instar crawlers, and some crawlers may be forced to select nutritionally inferior sites before they die. *A. melinus,* however, is under strong selection pressure to identify and quickly reject unsuitable or inferior hosts. This is mediated by a quantitative response of female wasps to variation in the amount of free OCT in scale covers. The reduction in the quantities of free OCT in covers of bark-reared scales is most likely an indirect result of the crawlers having selected a nutritionally inferior substrate.

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