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A REFUGE FOR RED SCALE UNDER CONTROL BY *APHYTIS*: STRUCTURAL ASPECTS¹

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Abstract. Red scale populations in eight grapefruit trees in a grove in southern California were sampled over 18 mo. We established that the interior of the trees was an area of partial refuge from parasitism by the major control agent, the parasitoid *Aphytis melinus*, and also by *Encarsia*, which was the second major parasitoid in the system. The refuge (interior) population contained >75% of the scale and >90% of the adult scale in the average tree. Parasitism by *Aphytis* in the exterior (twigs) was 27 times as high as in the refuge for second-instar scale, and 6 times as high for third instars. The differences in instantaneous parasitism rates were greater. Parasitism by *Encarsia* in the exterior was about twice that in the refuge. A field experiment showed that *Aphytis* could search in the interior and that it parasitized scales that had been placed there on lemons. Low parasitism rates in the interior may have been caused by the parasitoids' response to the bark substrate. The refuge population may account for the observed stability of the *Aphytis*-red scale interaction in some citrus groves.

Key words: *Aonidiella*; *Aphytis*; biological control; insect pest; parasitoids; predator-prey; refuge; stability.

INTRODUCTION

Biological control of many herbivorous arthropods, both pest and non-pest species, is viewed traditionally as being the outcome of a stable interaction between the prey (or host) and one or more of its natural enemies (Huffaker and Messenger 1964, Murdoch and Oaten 1975, Hassell 1978). Successful biological control projects thus provide systems in which this general idea can be tested. Of nine such projects, most provided moderate to good evidence for local instability; only one, the California red scale-*Aphytis melinus* system in southern California, appeared to be convincingly stable (Murdoch et al. 1985). In red scale, no experimental evidence exists for stability in the formal sense of a return towards equilibrium following a perturbation, but the populations fluctuated between narrow bounds over many generations, the mean did not appear to drift with time, and local extinction did not occur.

Population estimates of red scale (*Aonidiella aurantii* (Maskell): Homoptera, Diaspididae) and its parasitoid, *Aphytis melinus* DeBach (Hymenoptera: Aphelinidae), in a lemon grove in southern California over 2 yr provided further evidence for the stability of this system (Reeve and Murdoch 1985). However, usual explanations offered to account for stability (e.g., aggregation of one sort or another by the parasitoid, or density-dependent parasitism through time) did not seem to apply (Reeve and Murdoch 1985, 1986). Indeed, the parasitoid appeared to be a density-disturbing factor. Reeve and Murdoch (1986) suggested that, instead, a physical refuge might account for the observed stability.

Direct evidence for the existence of a refuge came from a set of haphazard samples from the interior of the lemon trees. These samples showed that the interior population achieved local densities three orders of magnitude greater than that in the exterior, had a much higher fraction of adults, and was parasitized by *Aphytis* at only 0.01 the rate in the exterior of the tree. Reeve and Murdoch hypothesized that the interior, refuge,

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population of the tree stabilizes the otherwise unstable parasitoid–host interaction by leaking newborn “crawlers” (the only motile stage other than adult males) to the exterior at a relatively steady rate.

The main purpose of the present paper is to determine whether a refuge indeed exists in this red scale population and, if so, to quantify it. We do not test the idea that this particular population is stable or, if so, that a refuge is the cause.

California red scale is a pest of citrus in the arid and semiarid regions of the world (Ebeling 1959). It is reported as infesting all areal portions of the tree (Nel 1933, Quayle 1938, Ebeling 1950, 1959, Bodenheimer 1951), yet traditionally the scale is sampled only from the green portion (stems, leaves, and fruit) (e.g., Ebeling 1950, Atkinson 1977, Carroll and Luck 1984, Samways 1985, Yu 1986). In many locations it is often under satisfactory control arising from a complex of natural enemies, the most important of which is one or other of the hymenopterous parasitoids *Aphytis melinus* or *A. lingnanensis* Compere (Rosen and DeBach 1978, 1979). Both species are facultatively gregarious ectoparasitoids. In southern California *A. melinus* controls the scale, and is the species in our study area.

This paper is the first in a series that seeks to test the refuge hypothesis. We address the following questions: (1) Is there a dense interior population in grapefruit trees and, if so, how large is it relative to that in the outside of the tree? (2) Is there a preponderance of adults in the interior population which would have an increased potential to influence total dynamics via crawler production? (3) Does the interior population experience lower parasitism by both *Aphytis* and *Encarsia perniciosi* Tower (Hymenoptera: Aphelinidae)? (*Encarsia* is a solitary thelytokous endoparasitoid of red scale.) (4) If parasitism is lower in the interior, what is the cause?

LIFE HISTORIES

The life history of red scale, an introduced pest, has been described by several authors (Nel 1933, Quayle 1938, Ebeling 1950, 1959, Bodenheimer 1951). Briefly, females are viviparous and release crawlers that disperse over the plant for a short period. When they find a suitable site they settle and insert their stylets (mouth parts), molt, and secrete a waxy scale cover over their bodies. Female scales remain at this spot for the rest of their lives; males, upon molting to an adult, are winged. They seek out mates via a pheromone (Roelofs et al. 1978). At each molt (a nongrowing interlude), the exuviae are incorporated into the cover and the stylets are removed and reinserted, a process that can lead to death. During the growing stages, or instars, the scale body is detached from the cover and the cover is enlarged by adding to its margin. Females are fertilized during the third instar, some time after the second molt, an act that is followed by a number of morphological changes including reattachment of the body to

the cover and the production of a waxy sheath beneath the body. The scale's life cycle is completed in 36 d at 28°C, and about 3.5 generations occur per year in our study area. Reproduction and growth are continuous but they are greatly reduced or cease during winter.

The biology, systematics, and ecology of *A. melinus* are described by Rosen and DeBach (1979). It was introduced into California in 1956–1957. The egg, larval, and pupal stages develop on the scale body, but beneath the scale cover. The scale is paralyzed when the egg is laid. About 15% of the scales receive more than one egg (Luck et al. 1982), but rarely do more than one *A. melinus* oviposit on a given host (Luck and Podoler 1985). About three *Aphytis* generations occur for every one of the scale. *Aphytis* also kills some scales it does not parasitize, by probing the body with the ovipositor; such probing sometimes is followed by feeding on the body fluids. Both adult male and female wasps are capable of flight. The wasp parasitizes primarily stages that are not attached to the cover and that are large enough (second and third [virgin] female instars, and male second instars). However, all stages except second molt and gravid adults are vulnerable to host feeding (Abdelrahman 1974, Yu 1986).

Encarsia perniciosi was introduced into California in 1947 (Rosen and DeBach 1978). In the laboratory the wasps will successfully oviposit in all scale stages but, if the scale was younger than the third instar when parasitized, it looks like a second molt when wasp emergence occurs. In the field the wasp also emerges mainly from male and female scales that resemble the second molt, and from adult female scale. Its eggs are laid within the scale body and its development is mediated by the scale's development; the younger the scale stage the longer the wasp's development (D. F. Yu and R. F. Luck, unpublished manuscript).

METHODS

We report here on the results obtained from a set of unmanipulated grapefruit trees in a grove near Fillmore, California.

Structure of grapefruit trees

Usually the distal twigs of a grapefruit tree elongate twice (occasionally three times) a year, once in spring and again in the autumn. Not all twigs participate in such a flush of growth, nor does a given twig participate in all flushes. A circular bud scar or node is formed when growth stops, and provides evidence of a previous flush. The section of twig between two such bud scars (or between the tip and a bud scar) is designated the flush. The bud scars indicating the flush are easily distinguished on younger stems, but are obscured by the bark on the older twigs and branches.

In our study we distinguished two main regions of a tree: (1) the interior, consisting of the trunk and structural branches extending out to the base of the fourth

most recent flush; (2) the exterior, beginning where the interior region ends. The fourth flush is typically the oldest substrate whose bark has visible chlorophyll, and usually marks the transition from soft green stem to the woody part of the branch. The density of chlorophyll increases outwards from the fourth to the first flush (Schneider 1968). The exterior portion of the branch containing the four most recent flushes is made up of stem, leaves, and fruit. The sample trees contained between 400 and 700 such fourth flushes (i.e., twigs) and, in this low-yield year, had an average of just over 100 fruit.

Most leaves arise from the two most recent flushes. The fourth oldest flush has no leaves; leaves are never older than 2 yr, and probably average $\approx 1-1.5$ yr (Schneider 1968). Fruits take ≈ 16 mo to grow and mature (Schneider 1968), and were sampled on only 24 of 31 sampling dates.

We calculated the area of each substrate (i.e., wood, stem, leaves and fruits) on each tree, and used this in estimating the total scale population. The area of each branch (A) was determined from measurements of its length (l) and its basal (b) and distal (d) circumferences [$A = l(b + d)/2$]. The total area of wood was then obtained by summing across branches.

The total surface area in square centimetres (A) of leaves on a twig was calculated from its empirically derived relationship with the length (L) and width (W) of the largest leaf and the total number of leaves (N) on the twig (based on measurements of 66 twigs):

$$A = 90.0 + 0.00258(LWN); \quad r^2 = 0.85.$$

Each stem was assumed to approximate a cone, so its surface area is length \times basal circumference/2. The surface area of a twig is the area of the stem plus leaves. The number of twigs per branch, as a function of the basal circumference of the branch, was counted for the branches subtended by two major branches (about half the twigs in a tree) in each of five trees (a total of 93 branches). The resulting regression, where b is basal circumference,

$$\ln(\text{no. twigs}) = -2.7 + 2.3 \ln(b); \quad r^2 = 0.77,$$

was used to estimate the number of twigs on each branch of the sampled trees, and hence the total surface area of twigs.

Total fruit area was recorded separately. We assumed a fruit approximated a sphere and calculated its area accordingly. Fruit were absent on some dates.

The average tree had just over 134 m² total surface area, with leaves making up 85%, stems 10%, wood 4%, and fruits 1%.

Sampling procedures

The grove was divided into eight blocks and the central tree in each block was sampled on 31 dates from June 1984 until December 1985. Samples were

taken every 2 wk from June to October 1984 and from May to October 1985, and once a month at all other times.

To sample the interior of the tree, all branches including the trunk were mapped, tagged, and measured (length and basal and distal circumference). The information was stored in a microcomputer. Branches were sampled from June 1984 until April 1985 by selecting branches and distances from their bases at random. These interior samples were highly variable, so to reduce sampling error we classified branches as either high- or low-density on the basis of visual estimates of scale density, and thereafter took two random samples from each class in each tree. Each sample was a 1.1 cm diameter disk of bark (1 cm²), removed using a cork-borer, taken from the upper surface of the branch, where density of scale is highest.

To translate the number of scales per disk into the number on an entire ring of bark around the branch, and hence in the tree's interior, we counted the number of scales on 20 randomly selected complete rings of bark, and on a standard disk sample taken from each ring. The density of scale in a standard core (D_c) is a good predictor of the density on a complete ring (D_r) ($D_r = D_c^{0.56}$, $P < .001$, $n = 20$, $r^2 = 0.85$).

The exterior of each tree was sampled by taking four (later two) twigs at random heights and compass directions. On 11 dates, we recorded the exterior scale densities by flush age; on the remaining dates these data were lumped for all four flushes. Five fruit were chosen haphazardly from each tree on 24 sampling dates.

The average scale density on each substrate over the entire sampling period was calculated as follows, using twigs as an example. The total number of scale found on all four samples from tree i on date j was divided by the total area (in units of 100 cm²) of the twigs sampled, to give the density in that tree on that date, $D_{ij} = \text{number}/100 \text{ cm}^2$. The average number per 100 cm² over the entire sampling period for tree i is then the sum across all dates, divided by the number of sampling dates, i.e., $d_i = (\sum D_{ij})/24$. The overall mean for the grove was then obtained by averaging across the eight trees; $d = (\sum d_i)/8$. Thus each date and tree contributed equal weight to the overall mean density. Each tree contributed a single datum, and differences among trees provide the measure of sampling error.

The time-averaged fraction of the population falling into a particular age class (e.g., adult) was obtained by dividing the total number of individuals in the age class on a given tree, over the entire sampling period, by the total number of scale found on that tree over the whole period. The overall average was then obtained by averaging the contributions from the eight different trees. The contribution of a sampling date to the overall mean was thus weighted by the abundance of scale on that date. (In winter when density was low the fractions were poorly estimated.) Each tree again was given equal

weight and the differences among trees provided the measure of sampling error.

The fraction parasitized was estimated on all sampling dates. All live and parasitized red scales were recorded by instar or molt stage and, if the scale was a late second instar or older, it was recorded by gender. If a twig supported a dense scale population, each flush was subdivided into equal areas, and scales were counted in the subsamples from each flush until the total number counted exceeded 30 live individuals. This count was then adjusted to give the total number on the entire twig. The scale body (not the cover) of second-instar scales and older were measured (length \times width) using an ocular micrometer. Second molts and virgin and gravid female scales were isolated in a rearing unit to identify the endoparasitoid if present. All *Aphytis* larvae or pupae were transferred for rearing to an oleander scale, *Aspidiotus nerii* Bouche, using the technique of Luck and Podoler (1985) as modified by Yu (1986). Scales containing eggs, larvae, or pupae of *Aphytis* were recorded by instar and those containing eggs or young larvae were measured. Because *Encarsia* emerges from an apparent second molt, the fraction of scales parasitized by this wasp was estimated from (the number of parasitized second molts)/(the number parasitized + the number of second molts). These data were recorded by branch number, position within the crown, and tree number. The mean fraction parasitized over the entire sampling period was calculated in the same way as the fraction in a particular age class.

To determine the relationship between scale density and position within an interior branch, one entire branch was sampled from each of eight non-sampled trees in late summer 1987. Standard core bark samples were taken at 20-cm intervals along the branch.

Outplanted scale

In light of differences discovered in the fraction parasitized on different substrates, an experiment was carried out in August 1985 to test the hypothesis that *Aphytis* would parasitize scale in the interior at a high rate if the scale were on a more attractive substrate than bark. Each tree received two lemons, each with 40 virgin female scale, one hung in the exterior close to leaves and one hung in the interior, in contact with bark. Each lemon was placed in a large-mesh nylon bag. After 10 d the lemons were returned to the laboratory for the scoring of parasitized scale.

Refuge removal experiment

To test the hypothesis that the higher scale density in the interior reflected merely the greater length of time available for scale to accumulate there, the interior population of scale was almost completely removed in one set of trees and not in control trees, and recolonization was measured. We chose six trees in a row in an area of the grove that was not in the main experiment and assigned them randomly to treatment

and control. In April 1985 in the interior region of the three treatment trees we removed the scale population using plastic pot scrubbers. The three control trees were left untreated. Four random disc samples were taken from the interior of each tree in May, to test the effect of the treatment. This sampling procedure was repeated in November, when four standard exterior samples were also taken from each tree.

RESULTS

In the first three sections of the Results we describe how various characteristics of the scale population varied among different parts of the tree. In each case we were concerned with the mean value for the entire sampling period. Trees were replicates ($n = 8$; see Methods: Sampling Procedures) and data are given as means ± 1 SE.

Abundance and age distribution of scale on different substrates

To determine the fraction of the total scale population contributed by the interior (i.e., wood), we first determined for each substrate the scale density averaged over the entire sampling period. The average density of live scales was lowest on leaves and highest on wood (Table 1), and the differences among substrates were highly significant (the data were log-transformed to equalize the variances). The average density in the exterior was obtained by weighting the means on leaves and stems by the fraction each of these substrates contributed to the total surface area in the exterior, and was only $\approx 1\%$ of the density in the interior (Table 1).

Multiplying these densities by the area contributed by each substrate, we estimate that, averaged over the entire sampling period, the average tree supported $> 110\,000 \pm 13\,500$ scale. The interior had 77% of the total, stems 15%, leaves 7%, and fruits only 1%. Thus scale in the interior dominated the total population.

The potential for the interior to dominate the population dynamics is even more marked when age distribution is considered. The adult fraction of the scale population was three times as high in the interior as on any of the other substrates (Table 1). The interior region thus harbored on average $92 \pm 1\%$ of all adults in the tree. The increase in the fraction adult from fruit to wood was associated with a declining fraction of first instars (Table 1).

Scale density and age distribution may change with the age of the substrate (Table 1), since average substrate age increased from leaves through stems to wood (see Methods: Structure of Grapefruit Trees). There is also some evidence for this relationship within a substrate. In the samples taken from eight complete branches, density did increase with age of the substrate, i.e., inwards from the fourth flush towards the trunk (Fig. 1). However, the relationship ($y = 0.19 - 0.09x$, where y is the relative abundance of the branch and x is the distance from the trunk), although highly signif-

TABLE 1. Distribution by substrate of density, percentage adult, and percentage first instar (firsts) of live scale. Differences among fruit, leaves, stems, and wood (interior) were tested by ANOVA; the eight trees were replicates. Data are means \pm 1 SE.

	Exterior			Interior wood	Twigs§
	Fruit	Leaves	Stems		
Density* (no./100 cm ²)	2.95 \pm 0.86	0.80 \pm 0.15	15.0 \pm 2.89	189.0 \pm 19.2	2.37 \pm 0.44
Percent† adults	3 \pm 1	4 \pm 1	7 \pm 1	20 \pm 1	7 \pm 1
Percent‡ firsts	60 \pm 2	50 \pm 3	44 \pm 2	37 \pm 1	45 \pm 2

* $F_{3,28} = 60.53, P < .001$.

† $F_{3,28} = 49.81, P < .001$.

‡ $F_{3,28} = 18.14, P < .001$.

§ Leaves and stems combined.

icant ($P < .001$), explained only 26% of the variance. Marked patchiness within branches characterized scale density, rather than a monotonic increase in density towards the trunk. Within stems there appeared to be a tendency for scale density to increase from first to fourth flush, but the trend was not significant (Table 2).

The adult fraction increased significantly with age of substrate within stems, albeit over a small range of absolute values (Table 2). On branches, however, the fraction adult was not correlated with substrate age (i.e., distance from the trunk). Nor was total scale density related to fraction adult in the standard disc samples from the interior branches. Samples from high-density branches had on average about three times as many scales as those from low-density branches, but there was no difference between the fraction adult on high-density (fraction adult = 0.17 ± 0.01) and low-density (fraction adult = 0.14 ± 0.02) branches (t test: $t = 1.5, n = 8, P = .16$).

Distribution of parasitism

We examine the fraction parasitized on the different substrates, again averaged over the period of observation. The main patterns in parasitism by *Aphytis* coincided with that seen above for scale density and age distribution: the fraction parasitized was markedly and significantly greater on the exterior substrates than on wood (Table 3a). This pattern was consistent in all three vulnerable stages of scale (second-instar females, virgin third-instar females, and second-instar males). The parasitism rate in the exterior (twigs) exceeded that in the interior by 6-fold (in virgin female third instars) to 27-fold (in the less heavily parasitized second-instar scale). Parasitism, however, was not consistently highest on fruit.

These data should actually underestimate the difference between the interior and the exterior in the rates at which scale are parasitized per unit time (henceforth "instantaneous parasitism rate"), since scale develop more slowly in the interior (W. W. Murdoch et al., *personal observation*) and they are therefore vulnerable over longer periods. We can test this by looking at the fraction parasitized by *Aphytis* eggs only, since the egg stage lasts only a few days and therefore gives a measure

of close to instantaneous parasitism rate. The instantaneous parasitism rate by *Aphytis* on third instars on twigs was 15 (rather than 6) times that in the interior (wood) (Table 3b). When only parasitism as eggs was measured, the difference between interior and exterior was also higher in the two other vulnerable stages (Table 3b).

The interior is also a partial refuge from *Encarsia* parasitism, although the difference is less marked in this species; parasitism by *Encarsia* on second-instar scales in the exterior was just twice that in the interior (Table 3c). In this case the pattern across the exterior substrates was different, with scale on fruit being the least heavily parasitized.

There was no consistent trend in parasitism with substrate age (flush) within twigs (Table 2). We also analyzed parasitism on the eight complete-branch samples and found no correlation between parasitism and either age within the branch (distance from trunk) or the probable age of the branch (basal circumference). Parasitism also does not seem to explain the differences in scale density among branches within the interior: parasitism rates by *Aphytis* were the same in high-density (10 of 223 scales parasitized) and low-density (3 of 100 scales parasitized) wood samples ($\chi^2 = 0.38, P > .50$). The same pattern was found in parasitism

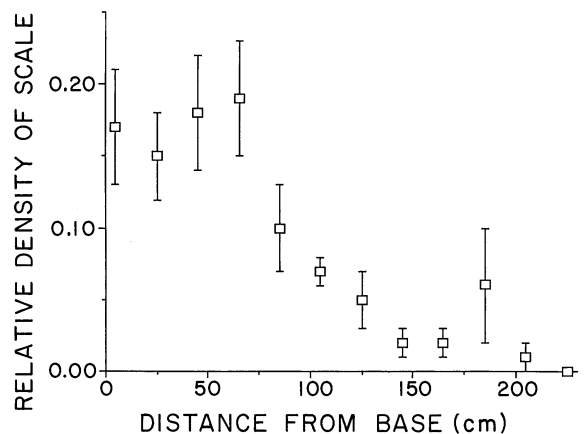


FIG. 1. Effect of distance from base of branch on relative density of scale. Means (\pm 1 SE) are based on counts from eight randomly selected branches. $r^2 = 0.262, P < .001$.

TABLE 2. Differences among tree growth flushes in density of live scale, percentage adult, and percent parasitism of third-instar scale by *Aphytis*. Replicates were eight trees; data are means \pm 1 SE.

	Flushes of tree growth*			
	First	Second	Third	Fourth
Density† (no./100 cm ²)	9.59 \pm 2.61	11.82 \pm 3.00	14.04 \pm 4.69	13.03 \pm 3.77
Percent adult‡	1 \pm 0.4	3 \pm 1	5 \pm 1	6 \pm 2
Parasitism§	48	31	14	34

* A flush is the section of twig between two adjacent bud scars. The fourth flush is the oldest.

† $F_{3,28} = 0.64$, $P = .430$ (ANOVA).

‡ $F_{3,28} = 10.00$, $P = .004$ (ANOVA on arcsine-transformed data).

§ $G = 18.93$, $P < .001$ (comparison of numbers parasitized vs. not parasitized).

by *Encarsia*: 2 of 175 parasitized in high-density patches and 2 of 52 parasitized in low-density patches ($\chi^2 = 1.67$, $P > .10$). These results also suggest that local egg-limitation is not important in the parasitoids, since if it were we would expect the rate to be lower in the high-density patches; i.e., the functional response appears to be linear rather than type 2 over this density range.

Scale density and age of substrate

Scales were more abundant in the interior (Table 1). The interior substrate was at least several years older than the exterior substrate, and on average was at least 20 yr older. The refuge removal experiment (Methods), however, showed that the greater scale density in the interior cannot be explained by the longer period during which scale there can accumulate.

First, bark samples taken in May, 1 mo after scale had been scrubbed from the interior of three treatment trees, showed that interior scale density had been greatly reduced by scrubbing: the mean in these trees was 48.7 ± 23.6 scales/100 cm² compared with 338.8 ± 50.2 scales/100 cm² in the control trees (t test, $P < .01$). Second, within 6 mo, i.e., by November, the density in the interior of the treated trees (265.0 ± 26.3 scales/100 cm²) had increased to 75% of that in the control trees (352.0 ± 82.7 scales/100 cm²), the dif-

ference was not statistically significant (t test, $P = .46$), and the density in the interior of the treated trees was >20 times that in the exterior in the control trees (10.7 ± 0.9 scales/100 cm²).

The eight trees in our standard sampling study were all at least 20 yr old. Thus the roughly 100-fold difference in scale density between interior and exterior in these trees (Table 1) cannot be explained by the different lengths of time the two parts of the tree have had to accumulate scale.

Evidence for search by *Aphytis* in the interior

Aphytis parasitizes scale in the interior at a low rate (Table 3). A variety of possible mechanisms could explain this result. One is that *Aphytis* cannot or does not search much in the interior because of its location, rather than because of the quality of the substrate there. An alternative is that the bark substrate is unattractive.

To distinguish between these explanations we hung lemons, each containing 40 scale, in both the interior and exterior of all eight trees (see Methods). The fraction of scales parasitized on lemons in the interior (0.229 ± 0.031) was not significantly different from that in the exterior (0.144 ± 0.051), $t_{14} = 1.29$, $P > .20$. This result suggests it is the nature of the bark environment, or of the scales, in the interior that makes this area a refuge, rather than its position in the interior.

TABLE 3. Distribution of percent parasitism of scales by substrate. Differences among substrates tested by ANOVA followed by Duncan's multiple range test (eight trees as replicates). Different superscript letters indicate significantly different parasitism rates ($P < .05$). Data were arcsine square-root transformed prior to analysis, and are presented as untransformed means \pm 1 SE.

	Exterior			Interior wood	Twigs*	ANOVA results		
	Fruit	Leaves	Stems			F	df	P
a) Total parasitism by <i>Aphytis</i>								
Second-instar females	22.2 \pm 1.9 ^d	14.3 \pm 3.0 ^a	9.7 \pm 1.1 ^a	0.4 \pm .3 ^b	10.8 \pm 1.5	29.24	3, 28	<.001
Virgin third-instar females	34.5 \pm 3.2 ^a	27.8 \pm 5.6 ^a	21.4 \pm 1.0 ^a	3.9 \pm .9 ^b	22.5 \pm 0.9	13.84	3, 28	<.001
Second-instar males	29.2 \pm 2.8 ^b	46.6 \pm 5.5 ^a	24.6 \pm 4.3 ^b	3.8 \pm 2.1 ^c	37.6 \pm 5.2	24.47	3, 28	<.001
b) Parasitism by <i>Aphytis</i> eggs only								
Second-instar females	2.4 \pm 0.4 ^a	2.3 \pm 0.7 ^a	2.3 \pm 0.4 ^a	0.1 \pm 0.1 ^b	2.4 \pm 0.4	8.55	3, 28	<.001
Virgin third-instar females	11.3 \pm 3.2 ^a	13.6 \pm 3.3 ^a	9.2 \pm 0.4 ^a	0.7 \pm 0.4 ^b	10.7 \pm 0.7	7.40	3, 28	.001
Second-instar males	4.5 \pm 2.5	16.0 \pm 3.8	7.8 \pm 1.9	0.7 \pm 0.7	14.5 \pm 3.4	5.28	3, 28	.005
c) Parasitism by <i>Encarsia</i>								
Second-instar molts	7.2 \pm 1.9 ^b	16.7 \pm 4.5 ^a	25.3 \pm 2.7 ^a	11.2 \pm 2.4 ^b	22.3 \pm 4.5	4.73	3, 28	.009

* Leaves and stems combined.

DISCUSSION

This study confirms the suggestion of Reeve and Murdoch (1986) that the interior region of some citrus trees, especially lemon and grapefruit, constitutes a refuge for scale from attacks by the parasitoid, *Aphytis melinus*. The tree's interior is also a refuge from parasitism by the other major parasitoid in the system, *Encarsia perniciosi*, although to a lesser extent. In both cases, however, the refuge is partial and not absolute.

Although parasitism is much lower in the interior than in the exterior (consisting of the twigs, i.e., stems, leaves, and fruit), and scale density is ≈ 100 times higher in the interior, we have not demonstrated that the difference in parasitism alone explains the difference in scale density. Scale grow, mature, and reproduce faster in the exterior than in the interior (R. F. Luck, D. S. Yu, and J. D. Hare, *personal observation*), so the difference in density does not appear to be related to spatial variation in plant nutrients. We also showed experimentally that the interior population can develop to almost its prevailing density (and to 20 times the density in the exterior) within 6 mo, so the higher scale density in the interior is not the result of population growth over more years than in the exterior. This conclusion is further supported by the fact that the average density in the study trees in both the interior and exterior did not increase over the 18 mo of the study (W. W. Murdoch, *unpublished manuscript*), and by the fact that in general young trees tend to have the highest scale densities (Bodenheimer 1951, R. F. Luck, *personal observation*).

Low parasitism in the interior appears to result from the unattractiveness of bark to searching *Aphytis*. Gregory (1985) hung yellow or transparent sticky traps at various distances from the trunk out to the exterior in orange trees. The traps were baited with red scale sex pheromone, to which *Aphytis* is attracted. *Aphytis* were trapped about as frequently in the interior as in the exterior. Gregory also hung out different colored cards and found that green and yellow were highly attractive, whereas light brown cards, whose spectral reflectance properties are similar to those of the bark in the interior of lemon trees, were least attractive and caught only about half as many female *Aphytis* as did yellow cards. This difference alone does not seem large enough to explain the low rate of parasitism in the refuge, but it does support the notion that the bark's low attractiveness accounts for the refuge. Our experimental demonstration that parasitism of scale on lemons hung in the interior of grapefruit trees is as great as that on lemons hung in the exterior provides further strong support for the hypothesis that it is the nature of the bark substrate that suppresses parasitism in the interior. Walde et al. (1989) test and reject the hypothesis that lower parasitism in the interior is caused by the scale there being smaller (and therefore less attractive) than in the exterior.

The refuge might be expected to be dynamically important to the overall population. It contained three-quarters of the total scale population in the average tree and $>90\%$ of the adults. The fraction parasitized by *Aphytis* in the interior was about an order of magnitude lower than that in the exterior.

Our present hypothesis to account for the stability of the *Aphytis*-red scale interaction (Murdoch et al. 1985, Reeve and Murdoch 1986) is that the refuge population "leaks" newborn crawlers (the only motile stage other than adult males) out into the exterior of the tree at a relatively steady rate and in sufficient numbers to overcome any tendency of the interaction there towards local extinction or large fluctuations. The very high number of adults in the refuge does suggest that they probably produce most of the crawlers in the tree. However, information on scale fecundity on different substrates is needed to confirm this hypothesis. Questions of amount and direction of crawler movement and the constancy of crawler production also remain. It is also possible, of course, that the refuge could stabilize the interaction simply by producing scales out of phase with those produced in the exterior.

Physical refuges have been discovered in other ecological systems, for example on the seashore where they appear to be important in maintaining some prey populations in the face of annihilating predation outside the refuge (e.g., Connell 1961), and in an insect-fish interaction in freshwater (Macan 1976). Surprisingly, though, demonstrations of physical refuges in terrestrial systems and in biological control seem to be rare. Huffaker (1957) suggested that the weed St. John's-wort frequently escapes attack in shady areas by the controlling chrysomelid beetle, although the phenomenon has not been studied in detail.

Future papers in this series will examine the hypothesis that the refuge population helps stabilize the exterior interaction between *Aphytis* and scale. The mere presence of a refuge, of course, does not guarantee that it tends to stabilize. Indeed, while simple theory (e.g., Murdoch and Oaten 1975, Hassell 1978) suggests that refuges typically are stabilizing, McNair (1986) has shown that in theory they can also destabilize predator-prey interactions.

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