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A REFUGE FOR RED SCALE: THE ROLE OF SIZE-SELECTIVITY BY A PARASITOID WASP¹

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Abstract. The presence of a physical refuge (an area where mortality due to parasitism is very low) has been demonstrated for California red scale, a pest of citrus. Density of red scale is very high, and parasitism by the principal parasitoid wasp, *Aphytis melinus* DeBach, is low on the trunk and woody branches of citrus trees as compared with the exterior twigs and leaves. One possible explanation for the low rate of parasitism is that scale in the refuge are less frequently parasitized due to their smaller size. Laboratory experiments show that *Aphytis* selects larger hosts, and the size distribution of parasitized scale in samples from a citrus grove shows a bias towards larger host individuals in the field. However, size-selectivity can account for only $\approx 10\%$ of the observed difference in parasitism rate and thus cannot be the primary explanation for the presence of the refuge.

Key words: *Aphytis melinus*; *Aonidiella aurantii*; biological control; host-feeding; red scale; refuge; size-selectivity; wasp.

INTRODUCTION

Physical refuges (areas where prey are protected from their natural enemies) can stabilize predator–prey (or parasitoid–host) models (Bailey et al. 1962, Maynard Smith 1974, Murdoch and Oaten 1975, Hassell 1978, but see also McNair 1986). A physical refuge has been shown to prevent extinction of prey in a few real systems. For example, Connell (1970) showed that the barnacle, *Balanus glandula*, can persist in the intertidal of the northwest United States only because there is a region (tidal height) where it is invulnerable to predatory snails. The presence of a refuge area (aquatic vegetation) also appears necessary for the coexistence of some corixid species with trout (Macan 1976).

A refuge might provide protection from natural enemies in a number of ways. The physical environment in the refuge may be such that it either excludes the natural enemy or interferes with detection or capture of prey. For example, the short period of time available for feeding prevents the predatory snail, *Thais*, from successfully attacking barnacles in the upper intertidal, and the complexity of the vegetation probably conceals corixids from trout. Alternatively, the physical environment may alter the characteristics of the prey so that it is no longer as desirable a prey item. This could arise, for example, from uptake of chemicals, differences in growth rate, size, or sex ratio.

Recent studies suggest that a physical refuge from parasitism may influence the population dynamics of California red scale, *Aonidiella aurantii* (Mask.), a homopteran pest of citrus (Reeve and Murdoch 1986, Murdoch et al., 1989). In contrast to several other biological control systems, populations of red scale appear to be quite stable; densities fluctuate little over time (Murdoch et al. 1984, Reeve and Murdoch 1986). This stability outside the refuge does not appear to be due to density-dependent parasitism, either in space or time (Reeve and Murdoch 1985, 1986), and may be due to the presence of a region where the scale are relatively invulnerable to their natural enemies. The refuge could contribute to stability by feeding a fairly constant supply of young (crawlers) to the population outside the refuge, thereby both preventing extinction of the scale population and moderating fluctuations in density.

In the inland coastal valleys of southern California, red scale is currently under satisfactory control arising from a complex of natural enemies, the most important of which appears to be the parasitoid wasp, *Aphytis melinus* (Hymenoptera: Aphelinidae; DeBach 1974, Clausen 1978).

Red scale infests every part of citrus trees, the exterior (fruit, leaves, young green stems), and interior (the woody bark of the structural branches) (Ebeling 1959). Research to date has focused on the subpopulations located on the exterior portion of the tree. The subpopulation in the interior appears very different from that in the exterior: in both a lemon grove and a

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grapefruit grove the density of scale on wood was much higher, adult scale relatively more common, and parasitism rate much lower than in the exterior (Reeve and Murdoch 1986, Murdoch et al. 1989). The woody branches thus seem to constitute, for scale, a spatial refuge from *Aphytis*.

Several hypotheses could explain the very low parasitism rates observed in the interior: (1) *Aphytis* may avoid flying near the interior of the tree. (2) *Aphytis* may avoid searching, or be ineffective at finding scale on woody substrates. (3) Although *Aphytis* can find scale on the bark, it may reject a higher proportion of these scale than of those encountered in the exterior.

The first hypothesis probably is false. Gregory (1985) showed that *Aphytis* was captured on pheromone-baited traps at least as frequently in the interior as in the exterior. Murdoch et al. (1989) showed that scale outplanted on lemons were parasitized at least as heavily in the interior as in the exterior. What remains is to determine if the frequency of visits by *Aphytis* to the interior vs. the exterior remains similar in the absence of attractors such as fruit or artificial pheromone sources.

This paper investigates one aspect of the third hypothesis: that *Aphytis* does not use scale on wood because, for a given instar, the scale found there tend to be smaller than those in the exterior. Two lines of evidence suggest this hypothesis is plausible. First, field samples indicate that parasitized scale are not a random subset of the available scale on twigs; parasitism is skewed toward larger size classes (Yu 1986). Secondly, if *Aphytis* is either egg or time limited, selection of larger scale for oviposition may be advantageous as compared with wasting eggs or time on small scale. It is known that eggs deposited on larger scale develop into larger *Aphytis* (Yu 1986, Reeve 1987), and that fecundity is correlated with female size (Opp and Luck 1986). There also appears to be a minimum acceptable host size (0.39 mm²) for production of female *Aphytis* (Luck and Podoler 1985, Opp and Luck 1986). The potential therefore exists for a gain in fitness through use of larger hosts. *Aphytis* carries only a small complement of mature eggs at any point (a maximum of about six, Opp and Luck 1986), so egg limitation, and hence advantage in placing these few eggs in prime locations are distinct possibilities.

This study tests the hypothesis that the difference in parasitism rate between the populations inside and outside the refuge can be explained by the difference in size of the hosts on the substrate types. We (1) determined in the laboratory whether *Aphytis* actually selects hosts based on size, when confounding factors such as age and substrate are kept constant, (2) determined the observed distribution of parasitism among size classes of scale in the field in both the interior and exterior, and (3) compared observed and expected variation in parasitism rates across substrates, given the distribution of sizes on each substrate.

METHODS

Biology of red scale and Aphytis melinus

Details of the biology of California red scale and *Aphytis melinus* are given in Murdoch et al. (1989). Female scale produce crawlers that move to a feeding site and then remain there the rest of their lives. Females pass through three instars and two molts (interinstar stages) prior to maturation. Males pass through two instars prior to pupation and emerge as winged adults.

Aphytis is an external, facultatively gregarious parasitoid, laying 1–3 eggs per host. It drills a hole in the scale cover, paralyzes the scale, and lays eggs either beneath or above the scale body. The parasitoid eggs hatch, the larvae feed on the host body, pupate, and the adults crawl out from under or chew a hole through the scale cover. Development time is temperature dependent, averaging 2 wk at 26°C (Yu and Luck 1988). *Aphytis* will parasitize female second- and third-instar and male second-instar scale, but virgin female third instars have been shown to be the preferred host in the laboratory (Abdelrahman 1974, Rosen and DeBach 1979, Reeve 1987). *Aphytis* causes additional mortality by mutilation (probing with the ovipositor) and by host-feeding.

Red scale are found on all aboveground parts of citrus trees. We have defined four substrate types within trees: fruit, leaves, stems (first-to-fourth growth flushes) and wood (branches older than the fourth flush).

Parasitoid selectivity based on size

The objective of the first set of experiments was to determine to what extent *Aphytis* is selective when offered a range of sizes of third-instar hosts of the same age on the same substrate. Since, in field populations, body size is correlated with age of the scale and with substrate type, a laboratory study was necessary to isolate the effects of host size.

A size distribution of same-aged third instars that encompassed most of the range of sizes seen across all substrates was obtained by allowing crawlers to settle on lemon fruit over a 24-h period, and then rearing the scale at 33° through to about the 3rd d of the third instar. Average size at 3 d into the third instar was 0.354 mm² (range 0.18–0.64 mm²). Seventy per cent of the scale were <0.39 mm², the minimum size required to produce female *Aphytis* (Luck and Podoler 1985). Since *Aphytis* avoids mated third-instar scale, insemination was prevented by removing male second-instar scale as soon as they were distinguishable.

Aphytis were provided with honey, and allowed to mate for 48 h prior to the experiment. (*Aphytis melinus* requires 24 h in the presence of a food source such as honey to mature eggs [Opp and Luck 1986].) Ten 2-d-old female *Aphytis* were enclosed in a chamber (0.6 × 0.4 × 0.2 m) for 24 h with ≈100 third-instar scale, distributed on seven lemons. Honey was not provided

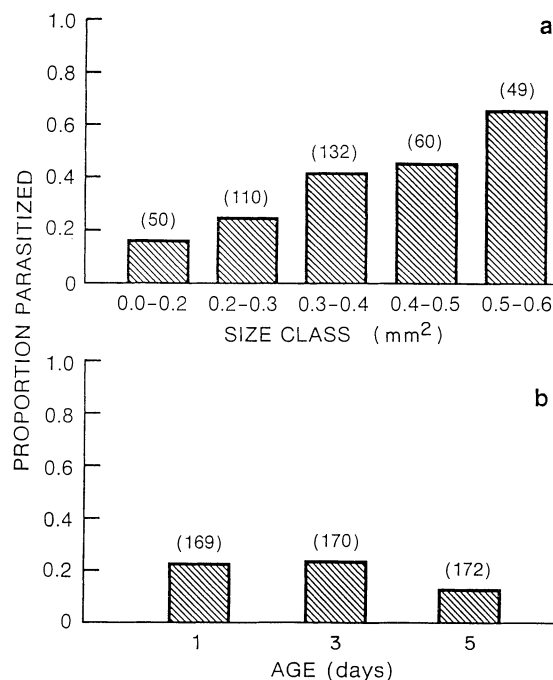


FIG. 1. Distribution of parasitism by *Aphytis* with respect to (a) size and (b) age of red scale in laboratory choice experiments. Replicate trials have been combined. Number in parentheses is total number of available scale in each class.

during the experimental runs. Four identical replicate trials were conducted. Hosts were measured and scored for parasitism and host-feeding. Parasitism was indicated by the presence of an egg on the body surface, and host-feeding by the removal of body fluids (shrunken body, with massive discoloration).

Data were analyzed using a log-linear model, and best-fit models were selected by the procedure suggested by Feinberg (1970). For analysis, scale were divided into size classes of 0.1-mm² intervals. Variables were size class, replicate, and parasitism or host-feeding. Inclusion of an interaction term between parasit-

ism and size class (or host-feeding and size class) in the best-fit model indicated a statistically significant effect of size on the probability of being parasitized (or host-fed).

Parasitoid selectivity based on age

On any given substrate in field populations, larger scale tend also to be older. To determine whether *Aphytis* prefer to parasitize older scale, females were exposed to three different age classes of third-instar larvae, 1 d, 3 d, and 5 d after the molt stage. Size ranges of the age classes were: 1 d: 0.13–0.50 mm², 3 d: 0.17–0.61 mm², 5 d: 0.17–0.64 mm². Average sizes were 0.31, 0.34, and 0.42 mm², respectively. Twenty 2-d-old *Aphytis* were presented with 180 scale, 60 in each age class, distributed on six lemons, for 24 h. Three replicate trials were conducted. Data were analyzed as above, testing for an interaction between age class and parasitism or host-feeding. To remove the confounding of size and age, the analysis was repeated on a restricted size range of scale (0.30–0.45 mm²). All three age categories had similar size distributions within this range, and average sizes were 0.37, 0.38, and 0.39 mm² for 1-, 3- and 5-d-old scales, respectively.

Several precautions were taken to minimize aberrant behavior on the part of the parasitoid. The large arena allowed parasitoid flight, and the number of hosts per lemon approximated densities seen in the field. The design of the experiment was expected to maximize the probability of observing selectivity. Hosts were overabundant, thus parasitoids should not have been forced on to less preferred hosts. Physical heterogeneity was low (no leaves or twigs) so that hosts were easily located; encounter rate and perceived density of hosts should have been high. Finally, hosts were on a preferred substrate so that visitation rate should have been high. Size-selectivity under these conditions indicates only that the parasitoid is capable of responding to host size; field encounter rates will likely influence

TABLE 1. Scale size affected parasitism (par) and host-feeding (hf) rates by *Aphytis* given a range of scale sizes in the laboratory. Host age did not affect either rate. Log-likelihood ratios (LR) are presented for the best-fitting log-linear models.

Variable	Best-fit model	LR	df	P*
Host size				
Parasitism	par × size†	32.9	30	0.33
Host-feeding	(hf × size) + (size × rep‡)	22.3	15	0.13
Host age				
1) Full range of scale sizes				
Parasitism	par × rep	15.3	12	0.23
Host-feeding	hf + rep	20.8	14	0.11
2) Restricted range of scale sizes				
Parasitism	(par × rep) + (age × rep)	3.1	6	0.80
Host-feeding	no satisfactory fit§

* P is the probability that the model is NOT a good fit; acceptable models must have $P > .05$.

† Inclusion of an interaction term between size (or age) and parasitism (or host-feeding) indicates that size or age affected these rates.

‡ Effect of differences among replicate experiments.

§ No model provided a satisfactory fit; host-feeding appeared to be random with respect to age and replicate.

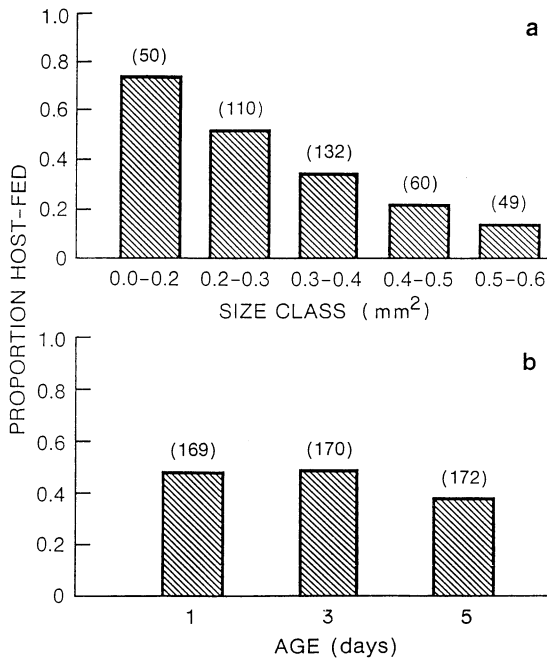


FIG. 2. Distribution of host-feeding by *Aphytis* with respect to (a) size and (b) age of red scale in laboratory choice experiments. Replicate trials have been combined. Number in parentheses is total number of available scale in each class.

whether such behavior is realized outside the laboratory.

Parasitoid selectivity in the field

Data from a field population of scale were analyzed to determine whether parasitized scale were a random subset of available size classes of third-instar hosts. Samples of fruit, leaves, stems, and wood were taken from eight trees in a grapefruit grove located in the inland coastal valley region of southern California (Murdoch et al. 1989). Scale were identified, measured, and scored for parasitism on 31 dates over an 18-mo period.

For each substrate type, the distribution of third-instar parasitized hosts was compared with the distribution of unparasitized third-instar hosts. Parasitized scale were restricted to those with egg(s) of *Aphytis* since the *Aphytis* larva feeds on the scale body, and thus the size of hosts containing *Aphytis* larvae at the time of sampling was not a correct measure of host size at time of attack. Size distributions of parasitized and unparasitized scale were compared using the *G* test (Zar 1974).

RESULTS

Parasitoid selectivity in the laboratory

Effect of scale size. — *Aphytis* preferred to deposit eggs on larger third-instar scale when given a range of sizes (Fig. 1a). Parasitism averaged only 16% for the smallest scale and 65% for the largest size class. The significant effect of size on probability of parasitization was in-

dicated by the inclusion of an interaction term between parasitism and host size in the best-fit model (Table 1).

Aphytis also showed a strong preference among sizes of scale when host-feeding, but here the selection was reversed, and was towards smaller scale (Fig. 2a). The percent of scale host-fed varied from 73% of the smallest size class to 14% of the largest class, averaged over the four replicate experiments. Again, the statistical significance of the effect is shown by the inclusion of an interaction term between scale size and host-feeding in the log-linear model (Table 1).

Effect of scale age. — Age of scale did not affect the probability of parasitism or of host-feeding (Figs. 1b and 2b, Table 1). (Note that in Table 1, the best model does not include scale age.)

The same conclusion was obtained when age and size were uncoupled by considering only a restricted size range of host scale. Neither parasitism nor host-feeding was a function of host age (Table 1).

Parasitoid selectivity in the field

Third-instar scale tended to be smallest on wood, followed by those on stem, leaves, and fruit (Fig. 3). The percentage of third-instar scale >0.39 mm², the apparent threshold size for production of female parasitoids (Luck and Podoler 1985), was 49% on wood, 56% on stems, 66% on leaves, and 76% on fruit (averaged over the entire sampling period).

Parasitism by *Aphytis* was significantly skewed toward the larger size classes on all substrates (again, data combined across the 18-mo period; Fig. 4). On each substrate, distributions of parasitized vs. unparasitized scale were compared using a *G* test, fruit: *G* = 201.5, *df* = 8, *P* < .001, leaves: *G* = 14.3, *df* = 5, *P* = .014, stems: *G* = 75.5, *df* = 0, *P* < .001, wood: *G* = 13.0, *df* = 3, *P* = .005.

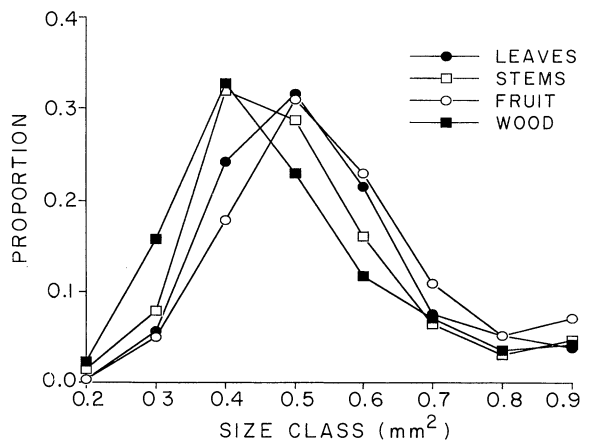


FIG. 3. Size-distributions of third-instar scale on four substrate types: wood, stem, leaf, and fruit. Data from 18 mo are combined. Distributions are significantly different (log-likelihood ratio test), LR = 247.5, *df* = 27, *P* < .001.

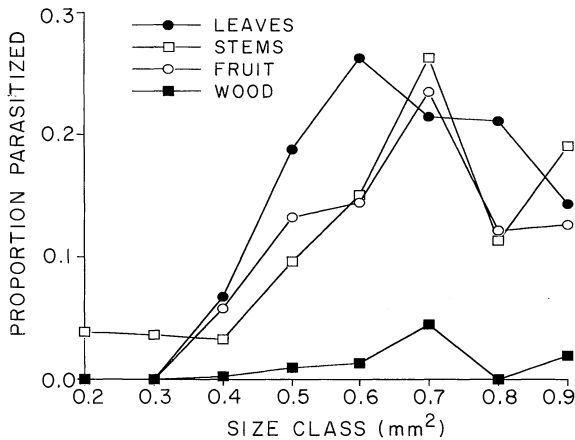


FIG. 4. Distribution of parasitism with respect to size of third-instar red scale from field samples on four substrate types: wood, stem, leaf, and fruit.

Observed vs. expected parasitism rate in refuge

Actual parasitism rates (*Aphytis* eggs on third-instar scale) averaged over 18 mo were 0.9% in the refuge compared to 12.9% in the exterior. We can test the hypothesis that the lower parasitism rate seen in the refuge can be attributed to size-selectivity by *Aphytis* by calculating the expected parasitism rate on wood, given the size-specific rates in the exterior. The expected number of parasitized scale in the refuge in a particular size class i (E_i), was simply the sum over all size classes of the number available in each size class in the refuge (N_i) times the size-specific parasitism rates observed in the exterior (P_i), i.e., $E_i = N_i P_i$ (Table 2).

After this correction for differences in size between refuge and exterior, the expected parasitism rate in the refuge, averaged over the entire sampling period, was 11.4%. This is slightly lower than that seen in the exterior (12.9%), but much greater than that observed (0.9%). Clearly, the smaller size of third-instar scale in the refuge can account for only a very small portion of the observed difference in parasitism rates between the populations inside and outside the refuge: parasitism of scale in the refuge is still only $\approx 1/10$ of the rate expected on a size-corrected basis. Seasonal patterns are similar to that seen over the total period (Table 2).

Expected encounter rate

The size-distribution data were used to compare the refuge and exterior with respect to the densities of third instars larger than the minimum size required to produce a female parasitoid (0.39 mm²). This provides an estimate of relative encounter rates if parasitoids were to search an equivalent area on each substrate. From Table 3, it can be seen that there are 3–18 times as many large third instars per unit area on wood than on stems, and >200 times as many per unit area on wood as on leaves. Thus, on average, *Aphytis* must search 12 cm² of wood, 80 cm² of stem, 700 cm² of

TABLE 2. Observed (exterior and refuge) and expected (refuge) per cent of third-instar scale parasitized by *Aphytis*. N = the number of third-instar scale in the sample.

Season	Exterior (observed)		Refuge (expected)*		Refuge (observed)	
	%	(N)	%	%	(N)	
Summer	22.6	(698)	20.9	0.8	(500)	
Fall	10.7	(931)	8.1	1.0	(705)	
Winter	10.8	(571)	12.0	0.0	(90)	
Total	12.9	(2200)	11.4	0.9	(1295)	

* Expected rate in the refuge is based on observed parasitism of similar-sized scale in the exterior.

fruit, or 2700 cm² of leaves to find one host suitable for the production of one female offspring.

DISCUSSION

Our laboratory and field results show that, although *Aphytis* prefers larger scale, and scale in the refuge are smaller, the low rate of parasitism in the refuge cannot be explained by the small size of scale there. When the difference in size distribution on the two substrates was taken into account, parasitism rate on wood was expected to be 89% of that in the exterior. In fact, parasitism on wood was <10% of the rate on twigs. Thus, even if the skewed distribution of size of parasitized scale on twigs reflects size-selectivity on the part of the parasitoid, differences in size distribution can play only a very minor role in explaining differences in parasitism rate between substrates.

No attempt was made to distinguish sex of the parasitoid offspring in this study. However, it is obvious from the results that differences in size distribution among the substrate types cannot explain the difference in parasitism rate, even if we restrict our calculations to scale larger than the threshold size used for female offspring (Table 3). The differences in size distribution among substrates are not large enough to change the fact that third instars (the preferred prey of *Aphytis*) are far more dense in the refuge. Thus, while both the laboratory and field results indicate *Aphytis* does select hosts based on size, size-selectivity alone cannot explain the large difference in parasitism by *Aphytis* between the interior and exterior of a citrus tree.

Few studies have attempted to separate the effects of size and age on host selection by any parasitoid (Vinson 1976). This distinction is probably not a significant one for analyzing within-substrate patterns of parasitism for red scale, since size will be closely correlated with age. It is critical, however, if the objective is to explain differences among substrates in parasitism rate; while third instars on fruit and leaves tend to be larger than those on wood, they are not necessarily older. The laboratory experiments show that *Aphytis* does preferentially parasitize larger third-instar hosts when they are the same age and on the same substrate. Since there was no evidence that *Aphytis* tends to par-

TABLE 3. Density (number per square metre) of large (>0.39 mm² body size) third-instar scale on the four substrate types. Data are counts from eight trees averaged over an 18-mo sampling period.

	Wood		Stem		Leaves		Fruit	
	\bar{X}	(SE)	\bar{X}	(SE)	\bar{X}	(SE)	\bar{X}	(SE)
Summer	1026	(163)	57	(11)	3.4	(1.0)	4.8	(1.9)
Fall	587	(67)	196	(36)	4.7	(1.5)	8.8	(5.5)
Winter	1260	(180)	185	(51)	3.8	(1.1)	17.9	(6.1)
Average	863	(102)	122	(22)	3.7	(1.0)	13.8	(4.0)

asitize older scale, the skewed distribution of parasitism observed in field samples can be attributed to size rather than age selection.

This study examined selectivity within third-instar scale, the preferred stage. Other laboratory studies have shown that *Aphytis* selects female third instars over male or female second instars (Abdelrahman 1974, Reeve 1987). It has been conjectured that this selectivity is based on size differences, but the possibility that chemical differences (pheromones, etc.) are responsible has not been eliminated.

Our results also show that *Aphytis* in the laboratory select smaller scale for host-feeding. This behavior may influence the distribution of mortality among substrates. Host-feeding appears to be a substantial source of mortality. In the laboratory, mortality due to host-feeding is comparable to that due to parasitism (this study, Reeve 1987), and field measurements also indicate that *Aphytis* kills a large number of hosts by mutilation and/or host-feeding (Reeve 1985). Certainly, parasitism rates obtained from field samples must greatly underestimate the mortality imposed by *Aphytis*. If *Aphytis* selectively host-feeds on smaller individuals among third-instar scale in the field as well as in the laboratory, the mortality from host-feeding could be greater in the refuge than on the exterior substrates. The amount by which total mortality due to *Aphytis* in the exterior exceeds that in the refuge could then be less than indicated by parasitism rates alone.

Among alternative hypotheses for the existence of the refuge, we presently favor the idea that the wood is an unattractive substrate for *Aphytis*, either due to color preferences of the parasitoid (Gregory 1985), or due to the complexity (roughness and dirt) of the substrate. Testing this hypothesis will require additional information on the behavior of *Aphytis* on the various substrate types.

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