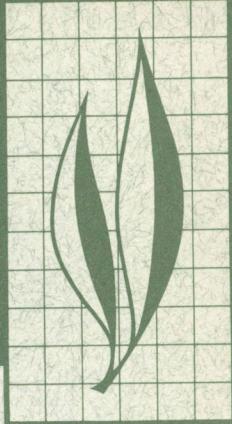


HILGARDIA

A JOURNAL OF AGRICULTURAL SCIENCE PUBLISHED BY
THE CALIFORNIA AGRICULTURAL EXPERIMENT STATION

Volume 46, Number 7 • October, 1978



Biological Control of the San Jose Scale *Quadraspidiotus perniciosus* (Comstock) (Homoptera: Diaspididae) in Southern California

Biological Studies on *Aphytis aonidiae* (Mercet) (Hymenoptera: Aphelinidae), an Important Parasite of the San Jose Scale

Hanif Gulmahamad and Paul DeBach



Biological Control of the San Jose Scale (*Quadrapsidiotus perniciosus* (Comstock) (Homoptera: Diaspididae) in Southern California

San Jose scale is well distributed throughout southern California on a variety of host plants but is quite rare in general. Only occasional plants, and usually only a portion of each, have any appreciable numbers of scales. Examples of these plants in several climatic zones were studied. Historical evidence, wide geographical distribution, and deductive and inductive reasoning essentially ruled out the weather as having any appreciable regulatory effect on scale populations.

Out of some six species of natural enemies that attack the San Jose scale in southern California, only three were found to be of any consequence—the hymenopterous parasites, *Aphytis aonidiae* (Mercet) (see Note, page 205) and *Prospaltella perniciosi* Tower, and the parasitic mite, *Hemisarcopeltis malus* Shimer. *Aphytis aonidiae* is the most common and widespread, constituting nearly 80 percent of the specimens reared or counted. It was virtually the only species present in two of the five districts studied and was dominant in all. *Prospaltella perniciosi* and *H. malus* appeared limited to areas having coastal climatic influences; *A. diaspidis* was rare and inconsequential.

Winter climate affected the age distribution of scale stages; and at the coldest location, host-parasite synchrony was interrupted during the winter. This was partially alleviated by overwintering diapause of *A. aonidiae*. The four milder locations had scale stages suitable for parasite development all year. Total percentage parasitization was never impressively high, yet it was always associated with much higher proportions of scales dead from cryptic causes. The majority of such deaths was ascribed to host-feeding by adult female *A. aonidiae*. *Hemisarcopeltis malus* developed only on mature third-stage female scales, *A. aonidiae* only on second-instar and third stages, and *P. perniciosi* on second-instar, second molt, and third stages. Thus, these three can coexist and complement one another. These life-table studies may indicate, but do not in themselves prove, that parasites were regulatory at the densities observed in the field.

Paired-cage comparisons between scale trends on plots having parasites *vs.* those with parasites excluded proved that the parasites

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Biological Studies on *Aphytis aonidiae* . . .

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Biological Studies on *Aphytis aonidiae* (Mercet) (Hymenoptera: Aphelinidae), an Important Parasite of the San Jose Scale¹

INTRODUCTION

THE SAN JOSE SCALE, *Quadraspidiotus perniciosus* (Comstock), has long been a very destructive pest of deciduous fruit trees and various ornamentals (Hoyt and Burts, 1974; Madsen and Morgan, 1970; Popova, 1961; Marlatt, 1953; 1906; Quaintance, 1915). This diaspine scale has been accidentally introduced into many countries and is now considered a major pest in most regions of the world where deciduous fruits are grown (Anonymous, 1968; Madsen and Morgan, 1970).

Numerous attempts at biological control of the San Jose scale have been made in many areas of the world (Rosen and DeBach, 1976; Mathys, 1966; Bohm, 1963; Mathys and Guignard, 1962; Neuffer, 1962; Rehman, Ghani, and Kazimi, 1961; Benassy and Bianchi, 1960; Rao and Rao, 1960; Huba, 1958). Nearly all of these involved the introduction of the endoparasitic aphelinid, *Prospaltella perniciosa* Tower and often its mass production and periodic colonization. These attempts at biological control have met with various degrees of success (Rosen and DeBach, 1976).

Our companion paper (see pages 205 to 238) has revealed that *Aphytis aonidiae* (Mercet) is the dominant and most

widely distributed parasite of the San Jose scale in southern California, where the scale is under good biological control.

The present laboratory study was conducted to gather biological data which might help explain the effectiveness of the uniparental California San Jose scale form of *A. aonidiae* in the control of the San Jose scale, and possibly reveal characteristics of biosystematic significance. It is emphasized that there are various widely distributed forms, or sibling species, or both, included under the names *A. aonidiae* and its very close relative, *A. mytilaspidis* (Le-Baron). Certain of these have been pointed out and studied by DeBach (1964) and Rössler and DeBach (1972a,b). The latter workers studied a uniparental form of *A. mytilaspidis* from Crete, which is very likely the true *A. mytilaspidis*. However, the exact taxonomic status of various forms referred to in the literature as *A. mytilaspidis* or *A. aonidiae* is uncertain. But if they have an unpigmented thoracic sternum, and thus differ from what we now consider to be true *A. mytilaspidis*, which has a pigmented sternum, they are very likely *A. aonidiae*.²

¹ See footnote 1 (page 205) in preceding article.

² See NOTE (page 205) in preceding article.

MATERIALS AND METHODS

Maintenance of San Jose scale cultures

The San Jose scale was reared in the insectary in a constant temperature room maintained at $26.7 \pm 1.1^\circ\text{C}$ and 50 ± 5 percent relative humidity. The bulk of the scale culture was maintained on citron melon, *Citrullus* sp. To infest new host material, melons bearing crawler-producing scales were arranged in the insectary rearing room, with the long axis at a right angle to a window which allowed daylight to enter the room from one side only. San Jose scale crawlers are positively phototropic and gather on the illuminated ends of the melons. New melons to be infested were thoroughly washed and dried. Crawlers which had accumulated on the illuminated end of the producing melons were then very gently brushed off onto a sheet of white paper. The paper was gently tapped above the surface of the new host melon, scattering the crawlers as evenly as possible. Infested melons were stored in a dark corner of the room. The crawlers settle quickly and at random in the dark; thus an even distribution and stage of scale development was obtained.

Wild gourds (primarily *Cucurbita foetidissima*) were occasionally used to maintain San Jose scale cultures in the

insectary. The gourds were gathered in the wild in southern California in summer and fall. They were thoroughly washed and dried before they were infested with scale crawlers.

A small culture of San Jose scale was also kept on russet potatoes. The potatoes were scrubbed to reduce the thickness of the skin, and then were washed and dried. Eight to 10 of these were placed in a small wire tray, and scale crawlers were scattered on them as described previously.

Parasite-handling procedure

The knowledge that *Aphytis* spp. are generally positively phototactic has been utilized in designing a unit to collect parasites reared from field material for biological studies (Fig. 1).

Host material containing parasites

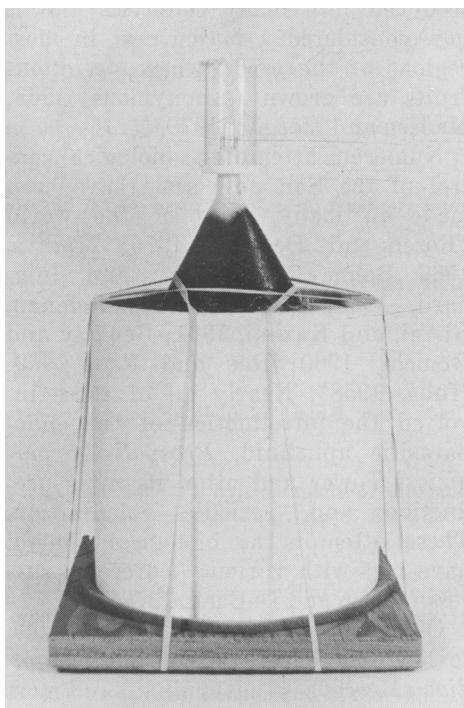
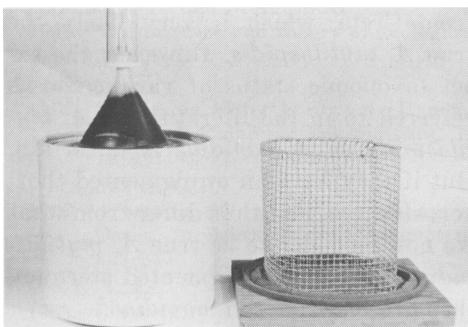


Fig. 1. Parasite phototactic collection unit. Left, with the two parts separated to show the mesh cylinder used for holding the host material. Right, assembled for use.

ready to emerge was placed into the wire mesh cylinder, and the container with the funnel and vial was placed over it. Honey stripes to provide necessary food for adult parasites were placed inside the vial, which was then illuminated 24 hours per day from above.

The parasites made their way into the vial collection chamber soon after emergence from the pupal stage, so they were mostly less than 24 hours old. Fresh vials were inserted every 24 hours. When enough parasites had accumulated in the vial, it was removed,

and the thumb was quickly used to close the hole in the vial cap. The cap was later removed, and the vial was placed with the open end downward on a clean sheet of white paper. When several parasites had crawled down onto the paper, the vial was quickly lifted and moved to another area on the paper. Then $\frac{1}{4}$ -dram vials streaked with honey were carefully inverted over each parasite. This process was repeated until the number desired for tests was collected. Unless otherwise stated, all parasites used in the following experiments were collected and handled in this way.

RESULTS

Thelytoky

Males are not necessary for reproduction in the form of *A. aonidiae* that attacks San Jose scale in southern California. Females produce female progeny generation after generation. Under natural conditions in the field, occasional rare males do occur, but generally amount to less than 2 percent. Of 796 specimens checked after being reared from field material in Riverside, only 13 or 1.6 percent, were males. Similarly, males are rare in the laboratory. Whether they are functional, or ever fertilize females, we did not test. However, Rössler and DeBach (1972a) found that the rare males of a thelyto-

kous form of *A. mytilaspidis* (Le-Baron) were functional, and could impregnate and fertilize females.

Adult longevity

The following experiment was set up in order to gather some data on adult longevity. Inasmuch as the form used is thelytokous, all data in this study refer only to females.

Twenty-two clean $\frac{1}{4}$ -dram glass vials each received a thin honey stripe. An adult female parasite was placed in each vial, using the technique described previously. The vials were plugged with a loose wad of cotton, and then were placed upright in a holding board. The

TABLE 1
LONGEVITY OF *APHYTIS AONIDIAE* FEMALES FED HONEY AND KEPT AT
 $25.6 \pm 1.1^\circ \text{ C}$ AND 50 PERCENT RELATIVE HUMIDITY

Cage number*	Survival	Cage number*	Survival
	days		days
1	11	12	36
2	29	13	36
3	31	14	37
4	32	15	38
5	33	16	38
6	34	17	38
7	34	18	40
8	34	19	40
9	35	20	42
10	35	21	42
11	36	22	48

* Tabulated in order of increasing survival. One parasite per cage.

holding board with the vials was placed in a temperature cabinet held at $25.6 \pm 1.1^\circ\text{C}$ and 50 ± 5 percent relative humidity (R.H.). Every day at ca. 4:00 p.m., the vials were rapidly examined under a dissecting microscope, and then were replaced in the temperature cabinet until the next day. Observations were made daily until all the parasites had died. The number of days each parasite remained alive was recorded, and the results obtained are presented in Table 1. The range of longevity for *A. aonidiae* was 11 to 48 days, and the average was 35.4 ± 6.9 days.

Fecundity and adult progeny

Experiments were designed to obtain data on fecundity and progeny production (F_1 adults) under laboratory conditions.

Fecundity tests used third-instar and noncrawler-producing adult female scales. Thirty-day-old scales grown on citron melon at 26.7°C and 50 percent R.H. were used. Parasites less than 24 hours old were introduced into circular 60×15 -mm plastic-cloth-covered cells affixed tightly to the melon, and enclosing about 300 scales. Three female parasites were placed in each cell with honey for food, and left for five days. They were then removed and transferred to new cells at 5-day intervals until all three original parasites had died. Four replicates were run for a total of 12 females tested. From pilot tests, the number of hosts used was known to be a distinct surplus. The test conditions were $24.2 \pm 1^\circ\text{C}$ and 60 ± 5 percent R.H., with a light-dark photoperiod of 10:14. After each 5-day ovipositional interval, the covers of the scales in each cell were removed, and the number of eggs deposited was recorded. The mean number of eggs laid during each 5-day period, as well as the total per female lifetime, was calculated.

Mean total fecundity per female was

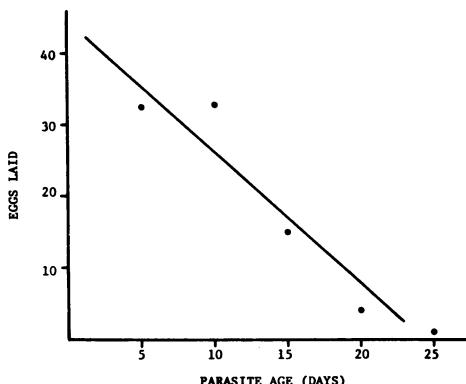


Fig. 2. Relation between age (days) and mean number of eggs laid by a single female *Aphytis aonidiae* in 5-day intervals during her lifetime on third-stage scales.

85.1 eggs, with a minimum of 35 and a maximum of 102. When the mean number laid per female during each subsequent 5-day interval of her lifetime is graphed, it is evident that, as the parasites became older than 10 days, egg deposition declined sharply (Fig. 2). The data also reveal that about 75 percent of the eggs were laid during the first 10 days of adult life. The postovipositional period for *A. aonidiae* ranged from two to four days before death occurred.

From a study of the structure of the reproductive system, Sorokina (1971) estimated that the potential fecundity of *A. mytilaspidis* was 40 to 45 eggs. Unfortunately, the host from which this parasite was reared was not given. This value is much less than that of our form of *A. aonidiae*. Popova (1962) recorded a potential fecundity of 100 for *A. mytilaspidis* which was found to attack San Jose scale in Russia. The data we obtained (Fig. 2) agree rather well with Popova's figure. The fecundity figure obtained by Rössler and DeBach (1972a) for the Greek uniparental *A. mytilaspidis* was less than about 39 progeny per female.

Two tests for progeny production by *A. aonidiae* were conducted, one with 30-day-old San Jose scale on russet po-

tatoes, the other with San Jose scale on wild gourds. Test conditions were modified to fit the experiment but were similar to those described previously for fecundity tests. However, in these tests, deposited eggs were allowed to continue development until the adult progeny emerged. There were 20 replicates of individual females per test.

Average progeny production by *A. aonidiae* reared on San Jose scale growing on russet potatoes was 11.5 ± 8.8 . The range of progeny produced was 2 to 31. Average progeny production by San Jose scale on wild gourds was 14.1 ± 13.8 , and the range of progeny produced was 1 to 51. Because of the large variation, these data do not show a significant advantage for either host plant. The values obtained in these tests for progeny production by *A. aonidiae* are lower than those reported by Khasimuddin and DeBach (1976) and Rössler and DeBach (1972a) for members of the *A. mytilaspidis* complex.

There is a large discrepancy between a mean fecundity of 85.1 and a mean progeny production of 11.5 on potatoes and 14.1 on gourds. The question naturally arises as to the reason for this discrepancy, even though in the first experiment we were dealing with total fecundity, and in the latter experiments with adult progeny (i.e., daughters produced). Generally with *Aphytis* spp. tested under ideal conditions, and with a surplus of hosts, the number of eggs laid closely approximates the number of adults that develop from those eggs. However, we observed that *A. aonidiae* sometimes superparasitized San Jose scale in the laboratory. As many as four eggs occasionally would be laid on one adult female scale, even when an ample supply of unparasitized suitable scales were present for oviposition. When two eggs were laid on the same scale, both almost always failed to complete development.

Superparasitism may thus be part of

the reason for the discrepancy between the number of eggs laid and the number of adult parasites which later emerged. Furthermore, these tests used different host plants, and it has been shown that the fecundity of *Aphytis* is influenced by the host plant upon which the scale host is grown (DeBach and White, 1960). In our study, the russet potato was not a favorable host for the San Jose scale. Many scales died, and those that survived were small. Wild gourds also may have been unfavorable, either directly or indirectly, to the parasites. The excessive amount of variation between individual females in the progeny production tests is a good indication that conditions in these tests were suboptimal. We must conclude, therefore, that under ideal conditions, a female of this form of *A. aonidiae* is capable of producing about 85 daughters on the average.

This illustrates the large discrepancies different investigators get working with the same species, and even the same investigators get when working with the same species at different times. The precise and reliable measure of fecundity is one of the biggest problems we have had with various species of *Aphytis* over the years. These tiny parasites are extremely sensitive to handling and to other minute differences in environmental conditions. An average potential fecundity of about 85 eggs per female indicates that *A. aonidiae* has a very good capacity to respond rapidly to increases in the San Jose scale population, all other factors being favorable.

Ovipositional behavior

The ovipositional behavior of recently emerged *A. aonidiae* females was observed, using San Jose scale growing on wild gourds. A female was tapped out of a $\frac{1}{4}$ -dram vial directly onto an infested gourd, and then was moved under a dissecting microscope and its

behavior observed. The gourd could be rotated so that a side view of the parasite's ovipositor in action could be obtained.

After being placed on a gourd, the parasite usually remained quiet for a few minutes before beginning to run around on the gourd surface. Then it examined various scales by palpating the scale cover with both antennae. Certain scales were examined more intensely than others, which the parasite abandoned or ignored. The parasite stood on the scale cover with its head pointing toward the periphery of the scale, holding the antennae parallel to each other and rapidly moving them from the inner one-third of the scale cover to its exterior edges. Rotating 360° on the scale cover, the parasite explored completely around the entire scale one to several times. On third-instar and adult female scales, the examination was confined mainly to the exterior two-thirds of the scale cover. From four to 24 seconds may be used for the examination preceding oviposition.

After receiving the proper stimulus, the parasite began the oviposition process. The stylets were bent downward away from the ovipositor sheath until they touched the scale cover. Then they were drawn over a small area of the cover, apparently attempting to locate a suitable penetration spot. Parasites are known to have sense organs at the end of the stylets. Once a suitable spot was found, the drilling process began. By then the parasite had positioned its body at an angle of about 45° to the scale cover. The parasite's body often vibrated during the drilling process with an occasional slow, backward-plunging action of the body. The abdominal tip also moved from side to side. A parasite may suddenly cease drilling and turn around and examine the same scale again with its antennae. One parasite repeated the examination

and drilling process on one scale eight times before successfully penetrating the scale cover. A parasite may also leave a scale entirely after several unsuccessful attempts at drilling the scale cover. It took from 100 to 395 seconds to successfully drill a scale cover. It appears that young scales (first instars) were drilled more easily than older scales (third instars).

The stylets of the ovipositor were inserted into the scale body after the cover was penetrated, and this was followed by some probing action. Venom may be injected at this stage, as it is known that *Aphytis* spp. can "paralyze" the host to prevent further development (Baker, 1976). Then the stylets were withdrawn from within the scale body, and an egg was deposited exteriorly on the scale body beneath the cover. On very rare occasions, parasites were observed drilling male scales from which the adult had already emerged. However, they did not oviposit under these empty scale covers. It appears that the stimulus (or stimuli) for drilling a scale is (or are) present in the scale cover, but that actual host suitability for egg deposition is determined by a chemical and/or physical stimulus perceived by the parasite's ovipositor from the host body, or hemolymph. Quednau and Hubsch (1964), working with *Aphytis coheni* DeBach, stated that "the attractiveness of a scale host was brought about by a stimulating water soluble substance present on the scale cover." They further reported that the tip of the *Aphytis* ovipositor is probably provided with sensitive organs which are able to recognize the scale body, and concluded that "the normal 'cover plus body' stimulus of the natural host is recognized by the ovipositor and must be present in order to stimulate oviposition in *Aphytis*."

Baker (1976), in a more thorough study on the influence of scale covers and bodies in host discrimination by

Aphytis, was able to show that both the scale cover and its body were important in host selection. The observations made here on *A. aonidiae* seem to support the contentions of both Quednau and Hubsch (1964) and Baker (1976).

The egg placement by *A. aonidiae* is of interest. Of the seven cases observed where female parasites drilled suitable prepupal male scales, all the eggs were laid ventrally on the male prepupa between the scale body and the gourd surface. When oviposition was on third-instar and adult female scales, the eggs were laid dorsally on the scale body between the scale cover and the scale body. However, a female parasite would occasionally lay an egg ventrally on a third-instar or adult female scale. Also, one parasite oviposited on the venter of a live, winged, adult male scale which was still under the scale cover.

One case of apparent "aborted oviposition" was noteworthy. A female parasite spent some three minutes or more attempting to drill through the cover of an adult female scale. The stylets had not penetrated the scale cover when the egg began making its way down the ovipositor (this probably reflects an intense ovipositional pressure). Because the egg was exterior to the scale cover, it remained attached to the tip of the ovipositor. The parasite then began running around on the gourd surface with the egg still adhering to the ovipositor. The ovipositor was repeatedly bent downward to touch the gourd surface in what appeared to be futile attempts to dislodge the egg. Both hind legs were used and, finally, the egg was pulled off and became attached to the gourd surface.

The ovipositional behavior of *A. aonidiae* as described above is similar to that described for *A. lepidosaphes* by DeBach and Landi (1961), for *A. melinus* by Abdelrahman (1974), and for members of the *A. lingnanensis* complex by Gordh and DeBach (1977).

Host-feeding behavior

During field studies on population dynamics of the San Jose scale in southern California, an appreciable amount of unexplained scale mortality usually showed up on life-table field counts. Host-feeding, unfavorable crawler-settling sites, unfavorable climate or combinations of these may have been responsible. Host-feeding, however, has been found to be the greatest cause of "unexplained" mortality in the black scale, *Saissetia oleae* (Bern.), the California red scale, *Aonidiella aurantii* (Maskell), the purple scale, *Lepidosaphes beckii* (Newman), and others (DeBach, 1943, 1969; DeBach and Landi, 1961). Tests were then devised to evaluate the host-feeding behavior of *A. aonidiae*.

Host-feeding and host-mutilation behavior in the genus *Aphytis* has been reported by several authors (Flanders, 1953; DeBach and White, 1960; DeBach and Landi, 1961; DeBach and Sundby, 1963; Quednau, 1964; Bartlett, 1964; Abdelrahman, 1974). DeBach and Landi (1961), working with *A. lepidosaphes*, a parasite of the purple scale *Cornuaspis Lepidosaphes beckii* (Newman), reported that "adult female parasites feed extensively on the hemolymph (body juices) of the host, causing considerable scale mortality. This is necessary for continued, sustained egg production during the life of the female." They further stated that "within a period of two or three days after host-feeding has occurred, the scale body is shriveled and dead. Such parasite caused mortality is an appreciable factor in the field, but it may be overlooked unless this habit of the parasite is recognized."

Even if the host-feeding habit of an *Aphytis* is recognized, it is still difficult to quantify mortality generated by this behavior. As reported above, scales that are fed upon shrivel and dry up, and it is thus difficult to tell precisely how

a scale died. This is especially true when young scales are found dead.

Host-feeding behavior of *A. aonidiae* was observed in the same manner as was its ovipositional behavior. Individual females, recently emerged, were gently tapped out of $\frac{1}{4}$ -dram vials directly onto a gourd infested with San Jose scale. As soon as a parasite showed some interest in a scale and began to examine it, the gourd was placed under a binocular microscope for examination.

Host-feeding behavior of *A. aonidiae* essentially followed the same general pattern as that described by DeBach and Landi (1961) for *A. lepidosaphes*, and by Abdelrahman (1974) for *A. melinus*. A female parasite would drill the scale cover as if to oviposit. The ovipositor was then thrust into the scale body, and a waxy material was secreted along the length of the ovipositor. This material hardened into a tube, and the ovipositor was withdrawn. The parasite would then turn around and imbibe the host hemolymph which oozed out.

When *A. aonidiae* host-feeds on young scales, the feeding tube can sometimes be seen connecting the scale cover to the scale body by very carefully lifting the scale cover. However, when this parasite host-feeds on adult female scales, no feeding tube can be observed. Adult female scales have their bodies closely appressed to the scale cover, and apparently all that the parasite has to do for the host hemolymph to exude is pierce the scale body. A few days after a female scale has been fed upon, its body becomes firmly attached to the scale cover at the point where the feeding puncture was made.

Variations in this behavior were observed. For example, a female parasite formed a feeding tube on a pupal male scale, and host-fed at this tube for 20 seconds. She then turned around, and, with the tip of the ovipositor, explored the scale cover in a rapid manner in the immediate vicinity of the old feeding

tube. When the tube was found, the ovipositor was inserted, the parasite, by vigorous probing actions, reinitiated the flow of the host hemolymph after 60 seconds. She then turned around and host-fed at this tube again for five seconds. Possibly the flow of hemolymph was inadequate, because she turned around again, reinserted her ovipositor into the old feeding tube, and vigorously probed for 90 seconds. Again she turned around and fed at the tube for 100 seconds, after which she reprobbed the tube for another 60 seconds. After feeding at the tube for an additional 80 seconds, the parasite finally left the scale. This female parasite thus fed at the same tube four times, reopening the tube three times in doing so.

Another female parasite drilled a first-instar scale and formed a feeding tube in 100 seconds. She then fed at the tube for 20 seconds. The parasite attempted to redrill the feeding tube, but failed to locate the puncture with her ovipositor. After 15 seconds of futile effort, she turned around, located, and again fed at the tube for 18 seconds. Again she sought to redrill the tube with her ovipositor, but again failed to locate the tube orifice. She then turned around and began examining the same scale with her antennae. Following this examination, she proceeded to drill the scale again at another location, taking 50 seconds to do so. She formed a new feeding tube, host-fed at it for 63 seconds, then left the scale. This female had thus host-fed twice on the same scale, doing so by forming two separate feeding tubes.

The discussion of host-feeding by *A. aonidiae* included no mention of host mutilation. Flanders (1953) described host mutilation as the repeated puncture of the host by a parasite's ovipositor, without any attempt to oviposit or to ingest body fluids. We did not observe this type of behavior in the lab-

oratory. In the field, scales are commonly found whose bodies bear necrotic marks, but it is not known whether these are host-feeding or mutilation marks, because host-feeding also produces necrotic spots. DeBach and White (1960) and Quednau (1964) reported host mutilation in *A. lingnanensis*, and Abdelrahman (1974) also reported the phenomenon in *A. melinus*.

That *A. aonidiae* does host-feed has been well established. This host-feeding habit may thus be responsible for a large portion of the unexplained scale mortality found under natural conditions.

Priority of host-feeding over oviposition

DeBach and Landi (1961), working with the purple scale parasite, *A. lepidosaphes*, stated that "it is not necessary for the newly emerged females to host-feed prior to oviposition." However, in other parasites, the opposite is true; thus, it became of interest to check the behavior of *A. aonidiae*.

The technique previously used in observing host-feeding behavior was used again. Data were gathered on six specimens. All previously unfed females host-fed on the first scale they drilled. Five out of the six parasites observed subsequently oviposited on another scale, and one parasite oviposited on the same scale it had host-fed on. It appears that with this species, host-feeding initially takes preference over oviposition.

Because the recently emerged female *A. aonidiae* tends to host-feed on the first scale it drills, we needed to determine the effect previous feeding of water or honey would have on this behavior. Elimination or reduction of host-feeding in laboratory cultures, or in the field, could reduce host "waste" and increase parasite efficiency.

In three small experiments, parasites were fed water alone, honey alone, or

both, before they were placed with hosts. With water, two of five females oviposited before host-feeding; with honey, two of seven oviposited first; and with honey plus water, three of six oviposited first. As previously noted, six out of six host-fed first when not pre-fed. Although the number tested was too small to show statistical differences, there is some indication that prefeeding newly emerged females honey plus water may reduce the initial tendency to host-feed.

Mortality caused by host-feeding on San Jose scale

Field material that is being dissected in the laboratory to determine the extent of parasitization often includes many dead scales (Gulmahamad and DeBach, 1978). A large proportion of these dead scales may have been host-fed on, but usually causes of this mortality cannot be easily determined after the fact. Host-fed scales usually shrivel and dry in a few days. This is particularly true of first-instar scales, some of which are sucked dry by the parasite. On older scales, host-feeding sometimes shows up as brownish-black spots on the scale body; and these are usually apparent for some time after the scale has died.

Host-feeding or mutilation in the genus *Aphytis* has been recognized as important in the regulation of host population densities (DeBach and Landi, 1961; DeBach, 1969; Quednau, 1964). Quednau (1964) stated that "for an assessment of the utility of an *Aphytis* species for the biological control of scale pests, not only its fecundity is a factor, but also its controlling influence on the scales by host mutilation activities." According to DeBach (1969), host-feeding mortality of the California red scale actually is much greater than life-table counts indicate; but accurate measurement of it in the field is impossible, because within a day or so after

host-feeding, the scale dies and dries up.

The following laboratory experiments were set up in an attempt to collect data on the mortality caused by host-feeding per individual *A. aonidiae* that were isolated separately with surpluses of different stages of San Jose scale.

The first set of experiments utilized a citron melon (*Citrullus* sp.) uniformly infested with San Jose scale in the "white cap" stage (usually 12- to 18-hour-old scales were used). By using such scales, and holding the temperature at $23.9 \pm 1.1^\circ\text{C}$ and the relative humidity at 60 ± 5 percent, the scales would remain in the first-instar stage for about four days. It was thus necessary to transfer a set of parasites every four days to new scales. As carbon dioxide was used to anesthetize the parasites when transferring them, the least number of transfers was desirable. Also, moving these tiny parasitic wasps necessitates very careful handling so as to avoid injuring or losing them.

The experimental set-up was as follows: Polystyrene cages made of half petri dishes (35×10 mm) were used to confine the parasites on the melon surface. A hole for introduction of the parasites was cut in the center of each dish and plugged with cotton. A cage was then placed over an area on the melon surface having an adequate number of scales, and the enclosed area was marked into eight equal, pie-shaped sections numbered 1 to 8. The scales in each section were counted and totaled. A total of 550 scales was left in the entire circular area.

The use of 550 scales meant that an average of 27.5 scales were available to each parasite per day, as five females were used for four days. Quednau (1964), studying the host-feeding behavior of *A. lingnanensis*, reported that 20 scales were adequate for one female parasite per day. Our observations revealed that 550 scales were ample. Five recently emerged parasites were intro-

duced into the cage which was supplied with honey as adult food.

The melon bearing the caged parasites was placed on a rack in a room where it received approximately 10 hours of light and 14 hours of darkness. Another cage enclosing 550 scales, prepared in the same way, was set up on the same melon at the same time as the one mentioned above. No parasites were added to this control dish.

Four days after parasites were introduced, the experiment was ended by anesthetizing the parasites with CO_2 , removing the cage, and collecting the parasites. These were then transferred to a new cage containing scales. This procedure was repeated every four days until all the parasites had died.

Once the parasites were transferred to a new cage, the surface area which was enclosed on the melon by the previous cage was carefully excised, and the scales were examined under a microscope.

First-stage scales which were fed upon had one or more of the following characteristics: 1) scales fed upon in the early stages of development died, and thus were smaller, in comparison with normal living scales, at the end of the experiment; 2) scales fed upon were dessicated, and their bodies became brownish or blackish. As first-instar San Jose scale has a whitish scale cover, it was easy to see the darker appearance of dead scales through the scale cover from above; and 3) the hole made by the parasite ovipositor through the scale cover was conspicuous once the scale body had dried up. The hole appears as a small black spot on the scale cover. Older scales (second and third stages) also have characteristic necrotic feeding spots.

All scales with any of the above characteristics were first turned over and examined so as to be sure of the cause of death. The remaining scales were then rapidly turned over, examined,

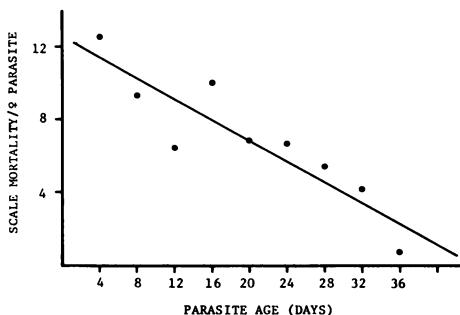


Fig. 3. Relation between adult parasite age (days) and mean first-instar scale mortality due to host-feeding by a single female *Aphytis aonidiae* during 4-day intervals throughout her lifetime.

and deaths recorded. The control was treated in the same way. The number of dead scales in the control was subtracted from the number of total dead scales in the experiment to estimate the mortality actually caused by the five parasites.

There were four replicates, each consisting initially of five parasites, for a total of 2,200 scales exposed to 20 parasites during the first interval. At 4-day intervals, the surviving parasites of each replicate were transferred to a new petri dish containing 550 scales. This was repeated until all parasites were dead. Thus, total host-feeding mortality per female lifetime was obtained. The results were computed as follows: The scale mortality due to host-feeding for each 4-day transfer increment for each replicate was divided by the number of live parasites at the end of that increment. This gave the number of scales killed due to host-feeding by one parasite during the 4-day period. This figure was added to that of all the other replicates, and divided by four to give the mean scale mortality caused by one female parasite for each 4-day interval. The results from this experiment are shown in Fig. 3.

The second set of experiments used second-instar and prepupal male scales. San Jose scale reaches the early second-

instar stage in about 10 days when reared at $26.7 \pm 1.1^\circ\text{C}$ and 50 ± 5 percent R.H. These scales remain in the second-instar for about three days if kept at $23.9 \pm 1.1^\circ\text{C}$ and 60 ± 5 percent R.H. Thus, the parasites were transferred every three days during this experiment.

The experimental setup in this experiment was essentially the same as that used when first-instar San Jose scale was studied, except for the following modifications. Only 500 scales were used per cage, and parasite transfer was made every three days instead of four. Also, there were only two replicates, each consisting of five parasites. The melon bearing the caged parasites was kept at the same temperature, humidity, and photoperiod as stated for the first set of experiments. The results obtained from this experiment were computed in the same way as outlined for the previous test, and are shown in Fig. 4.

The third set of experiments used third-instar and noncrawler-producing adult female scales. The 30-day-old scales were raised on citron melon at $26.7 \pm 1.1^\circ\text{C}$ and 50 ± 5 percent R.H. The experimental setup had to be changed somewhat from that previously

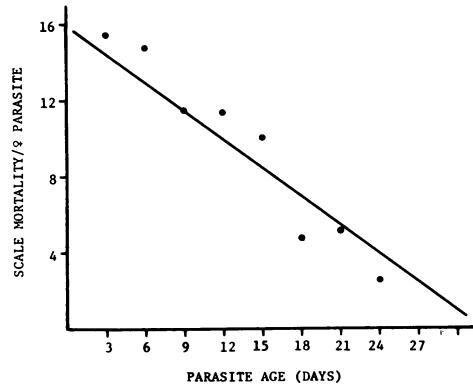


Fig. 4. Relation between adult parasite age (days) and mean second-instar and prepupal male scale mortality due to host-feeding by a single female *Aphytis aonidiae* during 3-day intervals over her lifetime.

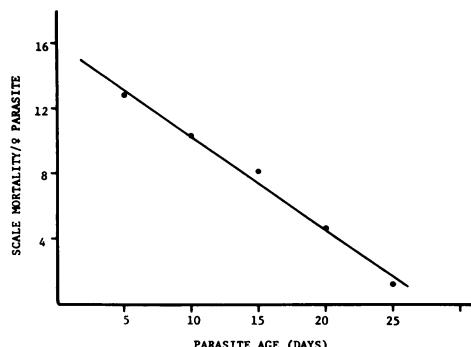


Fig. 5. Relation between adult parasite age (days) and mean mortality of third-stage scales due to host-feeding by a single female *Aphytis aonidiae* during 5-day intervals throughout her lifetime.

described. Larger, plastic 60×15 -mm cages were used as the 35×10 -mm cages were too small to enclose an adequate number of these larger scales. About 300 30-day-old scales could be enclosed within a 60-mm dish. Three female parasites were set up in each of four experimental cages for five days, because the third stage lasts longer. This represented a surplus of scales available to each parasite per day for host-feeding, oviposition, or both. Four control cages were also set up without parasites.

Handling the cages, transferring parasites to subsequent hosts, and recording host-feeding mortality were done as described previously. Temperature, humidity, and photoperiod were kept the same as in the first set of experiments. Data were analyzed in the same way as described before, and results are shown in Fig. 5.

Using first-instar San Jose scale (Fig. 3), the mean number of scales killed by host-feeding by one female *A. aonidiae* during her lifetime was 62.0, with a range of 47.7 to 83.7. These figures indicate that a relatively large number of first-instar scales can be killed by host-feeding by *A. aonidiae* in the laboratory

and, presumably, in the field as well. However, caution must be taken when attempting to extrapolate these results to field conditions. It should be borne in mind that these parasites were not given a choice of scale stages, but were confined to the same stage of scale throughout their lifetime. Although first-instar San Jose scale is not at all preferred for oviposition by *A. aonidiae*, and is not suitable for development, some of the scales may have been killed by frustrated oviposition attempts rather than by actual host-feeding because of the absence of suitable scale stages. Actually, a few eggs were laid on the first-instar scales.

As the parasites became older, they killed progressively fewer first-instar scales (Fig. 3). Nine transfers, involving a total of 36 days, were made during the experiment. Such survival indicates that the handling of the parasites during the transfers did not drastically affect their longevity, as previous studies have indicated that the average longevity of *A. aonidiae* females kept at $25.6 \pm 1.1^\circ\text{C}$ and 50 ± 5 percent R.H. is about 35.5 days.

In the host-feeding experiment involving second-instar and prepupal male San Jose scales (Fig. 4), the mean number of scales killed by a single female *A. aonidiae* during her lifetime was 75.3, and the range was 52.1 to 77.5. Again, host-feeding was shown to be a very important cause of scale mortality.

Figure 4 shows the same general trend as in the first experiment (Fig. 3), in that as the parasites became older, they killed progressively fewer scales by host-feeding. Eight transfers to new hosts, comprising a total of 24 days, were made during this experiment; thus, the parasites in this test lived for a shorter period of time than did those in the first experiment. This was probably due to the fact that 10- to 13-day-old second-stage scales were used. This age range included some scales, which,

although not the preferred stage for egg deposition by *A. aonidiae*, are readily oviposited on, in contrast to the first-instar scales used in the first test. Thus, some eggs were laid by these parasites during this experiment. Egg laying constitutes an important energy drain on the parasites, and probably was responsible for their reduced longevity.

Measurement of mortality caused by host-feeding became a little less precise when third-instar and noncrawler-producing females (30- to 35-day-old scales) were used. Although a scale body may bear several host-feeding marks, such a large scale does not always die rapidly. Some few adult female scales whose bodies bore host-feeding marks subsequently even went on to produce crawlers. However, because these were exceptions, in this experiment a scale was recorded as dead if its body bore one or more host-feeding marks. Some scales had as many as eight host-feeding scars on their bodies.

In this experiment (Fig. 5), the mean number of scales killed by host-feeding by a single female *A. aonidiae* during her lifetime was 37.4, with a range of 18.4 to 44.7. These figures are lower than those of the other two experiments. This is probably an indication that, if given the most suitable stage for oviposition, this parasite would kill fewer scales by host-feeding, and also an indication that it can obtain more nutrient from larger scales, and thus needs to host-feed less. Again, however, the total scale mortality per female parasite is impressive.

Figure 5 shows, as do Figs. 3 and 4, that as the parasites became older, they progressively killed fewer scales by host-feeding. Five transfers, covering a total of 25 days, were made. Here again, as in Fig. 4, longevity was reduced when the parasites were kept with older scales, probably because of extensive oviposition.

Influence of scale density on host-feeding

The concept of a functional response to prey density by parasites and predators is now largely accepted by most ecologists. The idea was apparently first stated by Solomon (1949):

To be density dependent, the enemy must respond to changes in numbers of the host. The nature of this response is commonly twofold. First, there must be a functional response to (say) an increase in the host density, because of the increased availability of victims: as host density rises, each enemy will attack more host individuals, or it will attack a fixed number more rapidly.

The idea of a functional response was later studied in detail by Holling (1959a, 1959b, 1961, 1965, 1966) and Takahashi (1968). Other studies showing clear functional responses of parasites to prey density are those of DeBach and Smith (1941), Ulliyett (1949a, 1949b), and Burnett (1951).

DeBach (1943), working with *Metaphycus helvolus* Compere, a parasite of the black scale, was apparently the first to study the effect of increasing host densities on the host-feeding of this parasite. He found that percentage host-feeding mortality decreased rather rapidly with increases in host density. Thus, an inverse density-dependent relationship between percentage host-feeding and host density was established for *M. helvolus*.

The purpose of the following experiment was to check the host-feeding response of *A. aonidiae* to various densities of San Jose scale. First-instar San Jose scales, growing on citron melons, were enclosed in 35 × 10-mm cages as previously described in the section on host-feeding. The following scale densities were used: 500, 1,000, 1,500, 2,000, and 2,500. Two cages were set up for each scale density, and five recently emerged female *A. aonidiae* were added

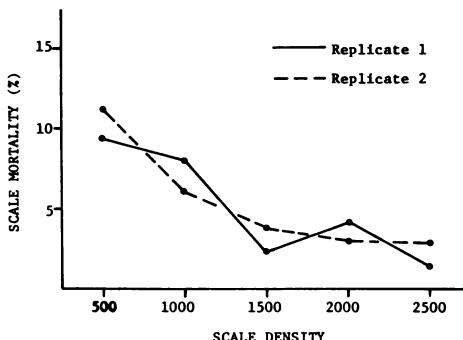


Fig. 6. Relation between first-instar San Jose scale density and percent scale mortality due to host-feeding by five female *Aphytis aonidiae* during four days.

to one cage at each density. No parasites were added to the other dish, which served as a control. The melons bearing the petri dishes were kept at $25.6 \pm 1.1^\circ\text{C}$ and 50 ± 5 percent R.H. The photoperiod was approximately 10 hours light and 14 hours darkness. After four days, the experiment was terminated, and the dead scales were counted in both the experimental and control dishes as described in the section "Mortality caused by host-feeding on San Jose scale." The difference between the two totals gave the mortality due to host-feeding by the parasites. Replicated twice, the results are presented in Fig. 6. Results were similar in both replicates. It is apparent that as the density of scales increased, the percentage scales killed by host-feeding by five female *A. aonidiae* progressively decreased. This relationship fits Poole's (1974) type-2 response, that is, the percentage predation (in this case host-feeding) declines continuously with increasing prey density. The results obtained here for *A. aonidiae* are similar to those obtained by DeBach (1943) for *M. helvolus*.

It should be noted, however, that there is no clear-cut trend in total number of scales killed per parasite at different scale densities. Apparently, suf-

ficient scales were present at the lowest density to satisfy host-feeding needs, so no greater numbers were fed on at the higher densities.

Influence of parasite density on host-feeding

DeBach (1943) also was apparently the first to examine the relationship between parasite density and host-feeding. He found that as the parasite density increased, the percentage of scales killed by host-feeding also increased. This relationship was examined for *A. aonidiae*.

First-instar San Jose scale was used under the same test conditions as for the scale density experiment. Six of 12 cages, each enclosing a total of 500 scales, were used as controls. To each of the other six cages were added 1, 3, 5, 7, 9, and 11 recently emerged parasites, respectively. After three days, the experiment was terminated, and the number of dead scales in each of the experimental and control dishes was recorded. The difference between the two totals gave the mortality due to host-feeding by the parasite. The results obtained from this experiment are shown in Fig. 7.

As parasite density increased on a fixed scale density, the percentage of

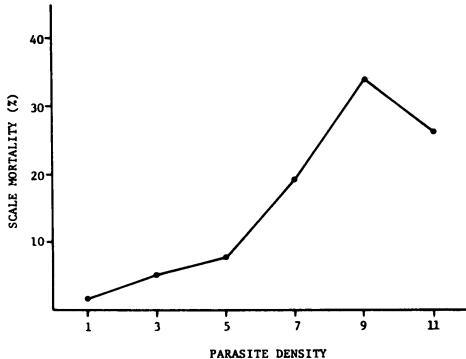


Fig. 7. Relation between the number of parasites per 500 scales and percent of first-instar San Jose scales killed by host-feeding by *Aphytis aonidiae* during three days.

first-instar San Jose scale killed by host-feeding also increased. This increased mortality reached a peak at a parasite density of nine females, when 34 percent of the scales were killed. It subsequently decreased at the next higher level of parasite density. If actual numbers of scales killed per parasite are considered in relation to parasite density, it appears that fewer hosts (seven to 10) per parasite were killed at the low parasite densities of one, three, and five; more (14 to 19) were killed at the

intermediate parasite densities of seven and nine; and 12 were killed at the highest parasite density of 11. It appears that at a parasite density above nine, increased intraspecific interference resulted in a decreased percentage, or number, of scales killed due to parasite host-feeding. This may indicate a feedback mechanism that acts to prevent parasites, when abundant relative to the host, from achieving "overkill" of the host, and subsequently eliminating their own populations.

DISCUSSION AND CONCLUSIONS

Previous biological control attempts against the San Jose scale largely ignored parasites identified as *A. mytilaspidis* (Rosen and DeBach, 1974), probably because the importance of these parasites as natural enemies of this diaspine scale had not been evaluated. As we now know, these yellow *Aphytis* also include—perhaps predominantly—*A. aonidiae*. The preceding article in the present publication, "Biological Control of the San Jose Scale *Quadraspidiotus perniciosus* (Comstock) (Homoptera: Diaspididae) in Southern California" has shown that *A. aonidiae* is the dominant and most widely distributed of the natural enemies which attack the San Jose scale in southern California, and is mainly responsible for control of that scale.

Our studies indicate that this parasite has a high fecundity. For biological control purposes, not only should the

potential rate of increase of *A. aonidiae* be considered, but also its host-feeding behavior. This parasite generates a very substantial amount of scale mortality by host-feeding, a trait generally overlooked in the field. Total host mortality caused by this parasite is much greater than would be expected from a measure of the degree of field parasitization only.

We recommend that serious consideration be given to importation of this parasite against the San Jose scale wherever the parasite does not exist. It is possible that biotypes or sibling species, or even the present form, occur in areas other than southern California. Additionally, periodic colonization of *A. aonidiae* or sibling forms should be compared experimentally with similar colonization of *Prospaltella perniciosi*, which is now mass-produced and colonized in many countries. *Aphytis aonidiae* might well be superior.

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ACKNOWLEDGMENTS

Both articles in this publication were based on studies made possible through the financial support of Grant No. GB 30843X of the National Science Foun-

dation. This support is gratefully acknowledged. Acknowledgment is also made to Max Badgley for the photographs in both papers.

(Continued from inside front cover)

were responsible for the generally low scale population densities observed in the field in southern California, and that climate was permissive for scale development. These tests showed that *A. aonidiae*, acting alone, can regulate San Jose scale populations at low levels.

Based on these studies, we suggest that the potential of *A. aonidiae* for biological control of San Jose scale should be reexamined in all countries where this scale is a problem.

Biological Studies on *Aphytis aonidiae* (Mercet) (Hymenoptera: Aphelinidae), an Important Parasite of the San Jose Scale

Aphytis aonidiae (Mercet) is the major parasite of the San Jose scale, *Quadraspidiotus perniciosus* (Comstock) in southern California. It reproduces by thelytoky; however, occasionally a rare male occurs. Adult females of *A. aonidiae* lived an average of 35.4 ± 6.9 days in the laboratory when fed honey and kept at $25.6 \pm 1.1^\circ\text{C}$ and 50 ± 5 percent relative humidity. The mean fecundity was 85.1 eggs per female. The ovipositional and host-feeding behavior of *A. aonidiae* is generally similar to other species of *Aphytis*. *Aphytis aonidiae* host-feeds and forms a feeding tube. Immediately after adult emergence, host-feeding appeared to take preference over oviposition. The average number of first-instar scales killed by host-feeding by a single female *A. aonidiae* during her lifetime was 62.0. The average number of second-instar and prepupal male scales killed per female was 75.3. The number of third-instar and noncrawler-producing mated female scales killed per female averaged 37.1. Host-feeding mortality per female parasite was impressive for all scale stages, but less host-feeding occurred on the older scales, as compared to the younger ones. In all such experiments, a progressively smaller number of scales was killed by host-feeding as the parasites became older. The percentage of scales killed per female *A. aonidiae* declined as a function of increasing first-instar host density. Also, given a fixed density of first-instar scales, increasing the number of parasites increased the percentage of scales killed up to a point, after which further parasite increase resulted in a decrease in the percentage of hosts killed by host-feeding. This may be one mechanism for maintaining host-parasite population balance. The potential for using *A. aonidiae* as a biological control agent of the San Jose scale in other countries is considered to be good.

The journal HILGARDIA is published irregularly. Number of pages and number of issues vary per annually numbered volume. Address: Agricultural Sciences Publications, University of California, Berkeley, CA 94720.