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Studies of Two Parasites of Olive Scale, *Parlatoria oleae* (Colvée)

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I. The genus *Coccophagoides* (Hymenoptera: Aphelinidae) is revised herein and two new species are described. These are *Coccophagoides comperei* Doutt and *Coccophagoides utilis* Doutt. Both *C. utilis* and another new species, *Anthemus inconspicuus* Doutt (Hymenoptera: Encyrtidae), are primary parasites of *Parlatoria oleae* (Colvée). They were collected in Pakistan and have been imported to California to control this olive pest.

II. *Coccophagoides utilis* is arrhenotokous. The females develop as internal primary parasites of *Parlatoria oleae* whereas the males develop adelphoparasitically on the prepupal and pupal stages of their own species. A significant aspect of the life history of *C. utilis* is a mechanism of retarded development in certain female progeny which ensures that the males on emerging meet with females.

(Continued, inside back cover.)

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III. The Role of an Autoparasitic Aphelinid, *Coccophagoides utilis* Doutt, in the Control of *Parlatoria oleae* (Colvée)[1]

INTRODUCTION

THE OLIVE SCALE, *Parlatoria oleae* (Colvée), has been the major pest of olive in California since its establishment near Fresno about 1934. It is also a major pest of many other crops and of ornamental shrubs and trees. It spread rapidly throughout large sections of the state, embracing, by 1961, almost all the San Joaquin and Sacramento valleys and scattered local areas south of the Tehachapi Mountains. Because of the extreme seriousness of infestations by this species, it became the subject of intensive biological control efforts beginning in 1949. The results of the first decade of this work were fully published, first by Doutt (1954), who described the initiation of the work and the preliminary results obtained; and then by Huffaker, Kennett, and Finney (1962), who presented a detailed economic and ecological appraisal of the program, with particular emphasis on the action of the aphelinid parasite *Aphytis maculicornis* (Masi) in olive groves. In the latter paper the introduction and establishment of a second aphelinid parasite, *Coccophagoides* sp. was mentioned, but results with this parasite had not by that time progressed far enough to permit an appraisal of its potential. It is this species which is now designated as *Coccophagoides utilis* Doutt.

THEORETICAL ROLE IN CONTROL

It had become apparent that the Persian *Aphytis maculicornis* is not entirely satisfactory as a control agent, and that it leaves an ecological niche unfilled—that is, it parasitizes, thus utilizes, the host population only to a very slight degree during the summer period (spring host generation). The variable degree of overall control exhibited is a result of this parasite's susceptibility to the hot, dry conditions of summer and the consequent "escape" of the host during one of its two generations each year.

To elaborate, the Persian *Aphytis maculicornis*, first colonized in 1953, had exhibited considerable variation in the degree of control achieved from grove to grove and from year to year. Although often giving satisfactory commercial control, it could not be fully depended on. Undoubtedly, the most important factor contributing to this variability is the effect of extremely high summer temperatures and low humidity on survival of the adult parasite. After reaching peak activity on over-

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wintered female scales in the spring, *A. maculicornis* may be nearly annihilated by extreme summer heat and dryness. Consequently, the adults ensuing from the spring generation of young scales escape with only a trace of parasitization, and are thus able to reproduce again in late summer with no significant deterrence by *A. maculicornis.* Under somewhat ameliorated summer weather conditions, this generation of scales may literally "explode" —that is, increase to much higher densities than those achieved during the normally very hot summers which cause substantial mortality of young scales as well as of adult parasites. With such population "explosions" and the consequent effect of the scales on olives, commercial cullage of fruits increases considerably. Thus, while the host scale gains an immediate advantage from the occurrence of less severe summer conditions, a result which is at once reflected in the fruit crop, the increase in effective control resulting from the parasite's improved survival rate is delayed until the following spring, and does not show up in the fruit crop until the following year.

As the weather stress lessens, *A. maculicornis* achieves some resurgence in numbers during the fall months. The critical aspect of successful control by this parasite is the degree to which it survives the severe summer period and how much resurgence it achieves during the fall months. This depends not only on the severity of summer heat and dryness, but also on a rather normal pattern of fall weather. Unusually early arrival of prolonged cold and continuation of winter conditions into early spring may substantially retard the rate of increase of the *A. maculicornis* population on female scales of the fall generation.

It is thus obvious that there were at least two possibilities open to us in attempting to improve the control being achieved.

First, we attempted to increase the effectiveness of control by *A. maculicornis* through repeated additive colonization of this species in the groves during the fall period, just subsequent to its severe decimation in numbers. This would allow a maximum of time for increase in density of the colonized stock prior to deposition of eggs by the overwintered host scales in the spring. Preliminary results from tests along this line reported by Huffaker, Kennett, and Finney (1962), and additional tests have indicated that some advantage may be gained by this practice. However, such a procedure would be expensive, even if fully effective, perhaps even more expensive than the application of insecticides; and since an alternative course became an immediate, more promising avenue, further tests were suspended.

Secondly, the failure of *A. maculicornis* to tolerate extreme summer heat and dryness and to parasitize the scale population during the summer period emphasized the need for an additional parasite or parasites which could effectively parasitize the scales of the spring generation, thus supplementing the good results of *A. maculicornis* on the fall generation of hosts during the subsequent spring period.

To some (e.g., Turnbull and Chant, 1961) it seemed inadvisable to introduce a second species. Those authors postulate that such an introduction may upset the effectiveness of the earlier introduced species. Nevertheless, we had become convinced, by the logic of Smith's (1929) reasoning, and on the basis of a wealth of experience in biological control, that we should introduce additional species in the hope of obtaining a parasite either generally superior to *A. maculicornis*, or, at the minimum, capable of adding to the degree of total control by effectively parasitizing the spring generation of scales. (See also, DeBach and Sundby, 1963.)

Another tiny aphelinid parasite, which admirably supplements the action of *Aphytis maculicornis* both as to ecological role and economic results, was introduced into California from Pakistan in 1957. This parasite, *Coccophagoides utilis* Doutt (Doutt, 1966). unlike *A. maculicornis,* seems strictly limited to *Parlatoria oleae* as a host, and certainly its life cycle is more perfectly synchronized with that of *Parlatoria oleae* than is the life cycle of *A. maculicornis.* The immature female *C. utilis,* unlike the parasitic *A. maculicornis,* is an internal parasite which develops within the body of the host scale.

The general outlines of this close adaptation to the specific host and the consequences of the parasite's tolerance to the hot, dry summers in California had become apparent, both from earlier observations in the insectary production program and from field studies. The general features were not unexpected in view of the work of Flanders (1937) on species of *Coccophagus* parasitic on lecanine scales and mealybugs. A very interesting, detailed laboratory study of the life history of *Coccophagoides utilis* Doutt and the synchronization of its life cycle with that of its host has been completed by Broodryk and Doutt (1966), and is published herein as a companion paper. The present paper brings up to date the appraisal of prospects for general biological control of olive scale on olives as this is related to the introduction of this new parasite and its ecology in the field.

INITIAL ESTABLISHMENT AND STUDY AREAS

Two releases of *Coccophagoides utilis* were made in olive groves during the fall of 1957. At Herndon, Fresno County, 350 adults were released in September, and at Exeter, Tulare County, 150 were released in November. In 1958 *C. utilis* was released as follows: 300 at Willows in Glenn County, 200 at Brentwood in Contra Costa County, 950 at two sites in Tulare County and 12,550 at one site in Madera, Madera County. Thus, a total of 14,500 *C. utilis* was released in this early colonization.

Because of preoccupation of the insectary facilities and personnel with other work at that time, the stock was then simply maintained until the results indicating promise became available. In 1961 this parasite was found to have become established at two of the above sites, the initial release site at Herndon in Fresno County and the site in Madera County. The field data in this study were obtained principally from the Herndon colonization site, that is, at the Duncan Grove.

Definite proof of establishment of *C. utilis* was not made until early 1961 because of the concurrent releases in 1958 in the same groves of vastly greater numbers of another internal parasite, *Anthemus inconspicuus* Doutt, also imported from Pakistan in 1957. During 1959 and 1960, *A. inconspicuus* was readily recovered from several of the many release sites, including the Herndon and Madera groves, and was considered to be established. However, by early 1961, evidence of internal parasite activity was declining so completely, except at Herndon and the site in Madera County, that additional identifications were made of parasites recovered from these two groves. These examinations confirmed suspicions that the well-established parasite at the two groves was now *Coccophagoides utilis* and no longer *A. inconspicuus.*

A detailed study of the life history of *C. utilis* under field conditions was initiated early in 1962 at the Herndon colonization site. To ensure that an adequate population of *Parlatoria oleae* would be available, from which monthly samples could be drawn over a prolonged period of time, two trees having very high scale densities were selected as the sample source. Scale populations on these two trees had been studied previously as part of check-method studies of DDT-treated (*Aphy-*

tis maculicornis-free) trees (Huffaker, Kennett, and Finney, 1962, p. 619).

After discontinuation of DDT treatments during the late winter of 1960, *Aphytis maculicornis* and *Coccophagoides utilis* were no longer excluded from these two trees. Approximately two years later, on April 10, 1962, the first monthly sample for the life history study was taken. (See tables 1, 2, and 3.) During the intervening two-year period these two trees were sampled semi-annually. The samples revealed a considerable degree of activity by these two parasite species, although not until early 1961 was it determined that the internal parasite was *C. utilis* and not *Anthemus inconspicuus*. Although a large reduction in scale density was evident at the end of this two-year period, the scale population was still much higher than that extant in other trees in the grove. Thus, at the initiation of the life-history study, both *C. utilis* and *A. maculicornis* were present in good numbers in these two trees and the scale population appeared to be experiencing a downward trend.

SAMPLING PROCEDURE

Because a wide variation in scale densities, from twig to twig, would have been encountered in a pure random sampling, the sample twigs were selected each month from among only those twigs which exhibited high scale densities. At the initiation of the study in April, 1962, the sample consisted of 10 twigs, each twig being 12-18 inches in length. As the overall abundance of scales on the sample trees decreased during subsequent months, it became necessary to increase the sample size (number of twigs) to assure the presence of a sufficient number of scales in each monthly sample for making an adequate determination of the life history of *Coccophagoides utilis*. These adjustments in sample size were made at various intervals—whenever it became apparent that there had been a considerable reduction in the density of live scales. However, sample size was held constant throughout each scale generation except in the several instances indicated in tables 1 and 2.

All settled stages of the host scales except male pupae were dissected and examined to determine the presence or absence of *C. utilis*. Dissections were made under a stereoscopic microscope at a magnification of 45×. Immature *C. utilis* were classified in five categories: (1) egg, (2) early larva, (3) intermediate larva, (4) mature larva and prepupa, and (5) pupa.

LIFE HISTORY AND ECOLOGY IN THE FIELD

General

Coccophagoides utilis is not affected to a great extent by extreme summer heat and dryness. This is perhaps largely due to the fact that its life cycle, like that of its host and unlike that of *Aphytis maculicornis,* is adapted in a way whereby the most susceptible stage (for the parasite, the adult) is not present as an entire brood at the most severe period—that is, in midsummer. It thus spans the unfavorable period much more successfully than does *A. maculicornis,* even though the adults may be equally intolerant of such conditions.

Insectary and field data have revealed that the life cycle of *C. utilis* is extremely well synchronized with that of its host. Peak emergence occurs shortly after the host begins reproduction: that is, in May, when the fall generation of hosts is reproducing, and in September, when the spring generation of hosts is reproducing (see Huffaker, Kennett, and Finney, 1962, p. 549). *C. utilis* has a long developmental period within the host; and this, plus a delay in emergence, to be discussed later, ensures the continuous presence of adult parasites in the field environment during the occurrence of the susceptible immature stages of the host from late spring to late fall.

Basically, *C. utilis* is synchronized to produce one "full" generation on each host generation, that is, two such "full" generations per year. However, a partial second generation of the parasite may be produced on each host generation because those parasites which develop and emerge from male scales *may* also parasitize female scales of the same generation. Thus, *C. utilis* has somewhat fewer than four generations per year.

C. utilis develops internally within the body of the host scale. A female *C. utilis* which has been impregnated by a male produces eggs of the female sex which develop as primary endoparasites in both male and female scales. The mated female parasite oviposits in all immature settled stages of the host except the male prepupa and pupa.

The mated female parasite first pierces the scale armor with its ovipositor, after which it pierces the scale integument and deposits a single egg per host. Of the more than 1,700 scales containing female *C. utilis* in the egg and early larval stages in field-collected samples during 1962, 1963, and 1964, only two contained two first-instar parasite larvae, and in only one instance were a parasite egg and first-instar larva encountered in a single host. Thus superparasitism appears to be of rare occurrence under field conditions.

While *C. utilis* is in the egg and first-larval instar, the host scale exhibits no abnormalities. As the parasite larva reaches an intermediate stage (second and third instars) in its development, the scale body becomes flaccid and assumes a very pale pinkish, milky appearance. At this time the parasite larva is clearly visible within the scale body. Shortly before the parasite larva completely consumes the body contents of the host, the scale integument changes color from a pale pink to a pale yellow. The scale body becomes quite inflated at this time and is no longer flaccid. By the time the parasite larva has completely consumed the body contents of the host, the scale integument has turned yellowish brown and has become rigid and parchment-like. Scales in this condition, containing a mature larva, prepupa, or pupa of *C. utilis,* are referred to hereinafter as "scale mummies."

A female *C. utilis* which has not been impregnated by a male produces eggs of the male sex only (arrhenotokous reproduction). The male parasite egg is deposited externally on a female *C. utilis* prepupa or pupa within the host scale mummy and develops ectoparasitically as an obligate hyperparasite. This phenomenon was first studied in detail for certain species of the related genus *Coccophagus* (Flanders, 1937). The most recent study of an aphelinid species exhibiting a similar autoparasitic habit is that of Zinna (1962) on *Coccophagoides similis* (Masi).

C. utilis exhibits a marked discrimination in its oviposition habits, even though it does accept a wide range of stages of the host scale. This discriminatory behavior has several aspects: (1) Only very rarely is a second female egg deposited in a host, whereas (2) all male eggs are presumably deposited in hosts already containing a female parasite prepupa or pupa; and (3) there is an avoidance of hosts that have progressed too far in their development, that is, either prepupal or pupal males and gravid females.

Because of the very complex reproductive habits of *C. utilis* as a parasite of olive scale, a detailed description of its life cycle will be presented. Rather than give this in a purely seasonal or chronological sequence, we shall emphasize the relationship of the life cycle of *C. utilis* to each of the scale generations.

TABLE 1

AGE DISTRIBUTION OF IMMATURE *COCCOPHAGOIDES UTILIS* DOUTT DEVELOPING IN FEMALE *PARLATORIA OLEAE* (COLVÉE)

(Duncan Grove, Herndon, Fresno County, California: 1962, 1963, and 1964)

Date of sampling	Scale generation	No. twigs	Total no. immature *C. utilis**	Parasite stage									
				Egg		Early larval		Intermediate larval		Mature larval and prepupal		Pupal	
				no.	*per cent*	*no.*	*per cent*	*no.*	*per cent*	*no.*	*per cent*	*no.*	*per cent*
4/10/62........	Spring, 1961	10	124†	0	....	0	....	0	....	94	75.8	30	24.2
4/10/62........	Fall, 1961	10	284	0	....	36	12.7	248	87.3	0	....	0	....
5/11/62........	Spring, 1961, and Fall, 1961 combined	10	224‡	0	....	0	....	3	1.3	105	46.9	116	51.8
6/12/62........	Spring, 1961 and Fall, 1961 combined	10	108‡	0	....	0	....	1	0.9	82	75.9	25	23.2
7/12/62........	Spring, 1961, and Fall, 1961, combined	12	81‡	0	....	0	....	0	....	69	85.2	12	14.8
7/12/62........	Spring, 1962	12	151	12	8.0	62	41.1	77	50.9	0	....	0	....
8/10/62........	Spring, 1962	12	183	0	....	13	7.1	46	25.1	75	41.0	49	26.8
9/14/62........	Spring, 1962	20	115	0	....	0	....	11	9.6	74	64.3	30	26.1
10/12/62.......	Spring, 1962	20	55	0	....	0	....	3	5.5	46	83.6	6	10.9
11/15/62.......	Spring, 1962	20	67†	0	....	0	....	0	....	65	97.0	2	3.0
12/13/62.......	Spring, 1962	20	49†	0	....	0	....	0	....	49	100.0	0	....
1/15/63........	Spring, 1962	20	53†	0	....	0	....	0	....	53	100.0	0	....
2/14/63........	Spring, 1962	20	47†	0	....	0	....	0	....	46	97.9	1	2.1
3/14/63........	Spring, 1962	20	63†	0	....	0	....	0	....	57	90.5	6	9.5
4/15/63........	Spring, 1962	20	47†	0	....	0	....	0	....	21	44.6	26	55.4
9/14/62........	Fall, 1962	20	87	3	3.4	84	96.6	0	....	0	....	0	....
10/12/62.......	Fall, 1962	20	95	5	5.3	89	93.6	1	1.1	0	....	0	....
11/15/62.......	Fall, 1962	20	84	5	6.0	72	85.7	7	8.3	0	....	0	....
12/13/62.......	Fall, 1962	20	73	3	4.1	68	93.2	2	2.7	0	....	0	....
1/15/63........	Fall, 1962	20	64	5	7.8	58	90.6	1	1.6	0	....	0	....
2/14/63........	Fall, 1962	20	91	0	....	70	76.9	21	23.1	0	....	0	....
3/14/63........	Fall, 1962	20	84	0	....	18	21.4	66	78.6	0	....	0	....
4/15/63........	Fall, 1962	20	52	0	....	0	....	18	34.6	34	65.4	0	....

5/10/63........	Spring, 1962, and Fall, 1962 combined	24	108‡	0	....	0	....	2	1.9	28	25.9	78	72.2
6/13/63........	Spring, 1962, and Fall, 1962 combined	24	19‡	0	....	0	....	1	5.3	9	47.35	9§	47.35
7/11/63........	Spring, 1962, and Fall, 1962, combined	24	10‡	0	....	0	....	0	....	7	70.0	3¶	30.0
7/11/63........	Spring, 1963	24	42	0	....	30	71.4	12	28.6	0	....	0	....
8/8/63.........	Spring, 1963	24	86	1	1.2	13	15.1	24	27.9	18	20.9	30	34.9
9/11/63........	Spring, 1963	24	43	0	....	0	....	4	9.3	17	39.5	22	51.2
10/15/63.......	Spring, 1963	24	31	0	....	0	....	1	3.3	17	54.8	13	41.9
11/15/63.......	Spring, 1963	24	23†	0	....	0	....	0	....	21	91.3	2	8.7
12/17/63.......	Spring, 1963	24	15†	0	....	0	....	0	....	15	100.0	0	....
1/16/64........	Spring, 1963	24	17†	0	....	0	....	0	....	17	100.0	0	....
2/14/64........	Spring, 1963	24	5†	0	....	0	....	0	....	5	100.0	0	....
3/13/64........	Spring, 1963	24	6†	0	....	0	....	0	....	6	100.0	0	....
4/14/64........	Spring, 1963	24	8†	0	....	0	....	0	....	4	50.0	4	50.0
9/11/63........	Fall, 1963	24	55	9	16.4	44	80.0	2	3.6	0	....	0	....
10/15/63.......	Fall, 1963	24	112	16	14.3	75	66.9	21	18.8	0	....	0	....
11/15/63.......	Fall, 1963	24	81	6	7.4	50	61.7	23	28.4	2	2.5	0	....
12/17/63.......	Fall, 1963	24	96	6	6.3	57	59.4	13	13.5	10	10.4	10	10.4
1/16/64........	Fall, 1963	24	93	9	9.7	45	48.4	12	12.9	20	21.5	7	7.5
2/14/64........	Fall, 1963	24	79	6	7.6	46	58.3	5	6.3	8	10.1	14	17.7
3/13/64........	Fall, 1963	24	60	1	1.7	26	43.3	15	25.0	6	10.0	12	20.0
4/14/64........	Fall, 1963	24	72	0	....	3	4.2	22	30.5	29	40.3	18	25.0

* Figures without symbols indicate all parasites are females.

† Principally mature male *C. utilis* larvae in diapause; see table 5 for male and female percentages in 1963.

‡ Here, for May, June, and July samples, it is not possible to determine whether the hosts are of the spring or fall generation, since the parasitized scales of the fall generation had become mummified and were indistinguishable from the overwintered mummified scales of the previous spring generation.

§ Of the 9 female parasite pupae present, 7 were found to be hyperparasitized by male *C. utilis* larvae.

¶ Of the 3 female parasite pupae present, 1 was found to be hyperparasitized by a male *C. utilis* larva.

Preliminary Explanation of Tables

Table 1 presents the data relating to the developmental stages of *Coccophagoides utilis* in female scales of each generation. The number of immature parasites in each stage and their respective percentage of the total present are given for each monthly sample. The May, June, and July samples include, where indicated, the scale mummies of the previous spring and fall generation scales, because host generation source could not be determined for mummified scales during those months (see footnote ‡, table 1). For example, the April 10, 1962, sample contained 124 overwintered female scale mummies of the previous spring (1961) generation containing 124 *C. utilis* (principally males) in the mature larval, prepupal, and pupal stages. Also in this sample were 284 female scales of the fall generation of 1961, containing 284 female *C. utilis* in the early and intermediate larval stages. One month later, on May 11, 1962, all but three of the *C. utilis* developing in female scales of the fall generation had reached the prepupal, and pupal stages, and had caused the host scales to become mummified. Thus these scales could no longer be separated from scale mummies which originated from the previous spring generation; hence a distinction in host generation source was no longer possible.

Table 2 presents the data relating to the developmental stages of *C. utilis* in male scales of each generation. The data are presented in the same manner as for the female scales in table 1. Because sex of young scales in the first instar and early second instar stages cannot be readily determined, data concerning parasitization by *C. utilis* during the early stages of the scale generations (June for the spring generation, August for the fall generation) are not included in tables 1 and 2.

Table 3 shows the total number of female scales present in each monthly sample, the average number of females per twig, and the percentage of female scales successfully parasitized by *C. utilis*. The percentage of female scales successfully parasitized by *Aphytis maculicornis* is also included in table 3, as is the percentage of female scales parasitized by the two parasite species combined. An important inclusion in this table is the column entitled "Unparasitized female scales per twig." This column shows the trend in female scale densities during the period covered by this study.

While the data presented in table 4 are of secondary importance as regards trends in scale densities, they are included in this paper to show the degree of parasitization achieved by *C. utilis* and *A. maculicornis* on male scales of each generation.

Figure 1 presents a schematic illustration of the life history of *C. utilis* on its host, *Parlatoria oleae,* as it occurred under field conditions at Herndon, Fresno County, California.

Parasitization of Spring-Generation Scales

Young *Parlatoria oleae* make their appearance as crawlers in early May, the eggs being produced by overwintered females of the fall generation. Hatching of the crawlers continues throughout May and into early June. During this period and until shortly before egg production is again initiated in late July, the immature scales are susceptible to parasitization by *Coccophagoides utilis.* (See fig. 1.)

Overwintered male and female *C. utilis* commence emergence as adults shortly after scale reproduction is initiated in May. On emergence, the virgin female *C. utilis* may deposit male eggs on female parasites in the prepupal and pupal stages still in the scale mummies. (See fig. 1.) The male parasites resulting from this hyperparasitization emerge during the summer months. Once mated, the female parasite deposits only female eggs in the young male and female scales of the spring

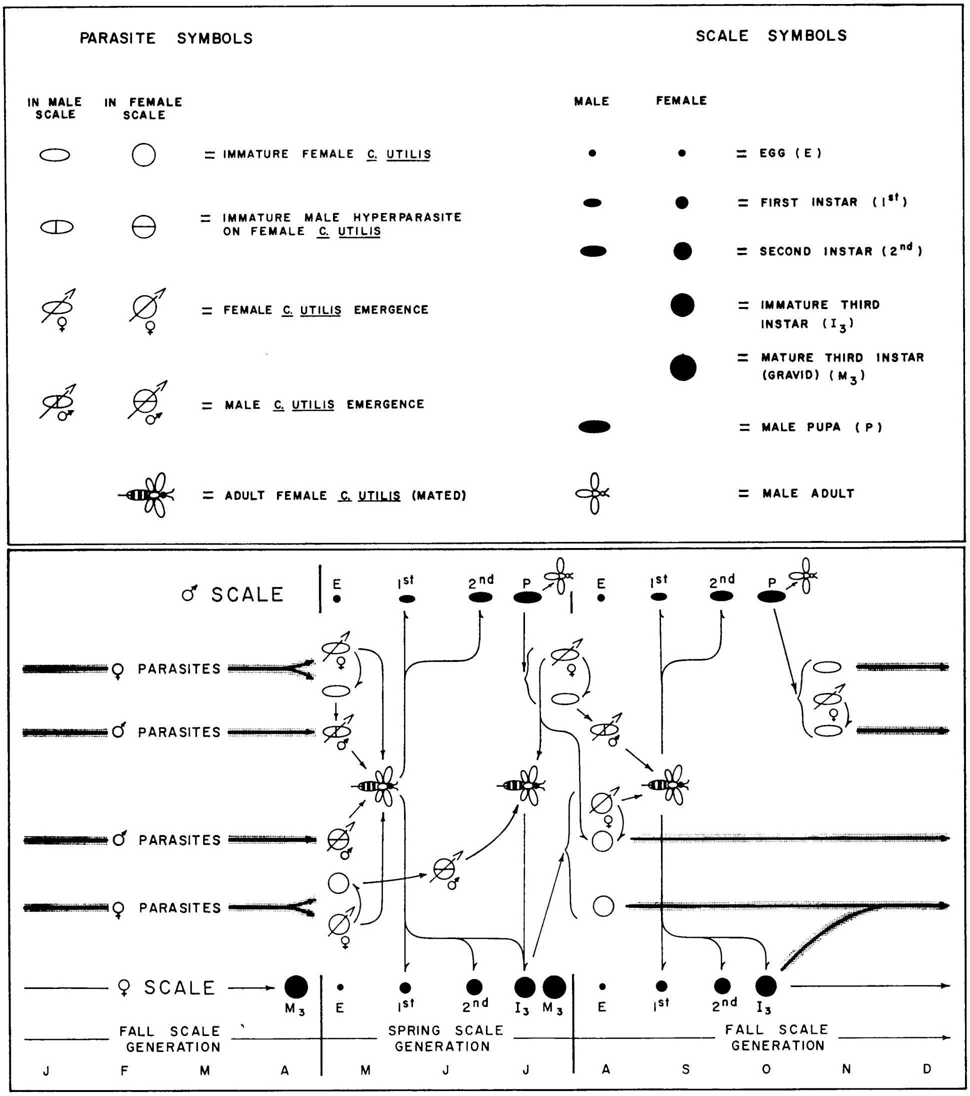

Fig. 1. Life history of *Coccophagoides utilis* Doutt on *Parlatoria oleae* (Colvée) at Herndon, Fresno County, California. Stages of development of *P. oleae* are shown by solid ovals for males and solid circles for females. Immature stages of development of *C. utilis* are shown by open ovals for parasites in male scales and by open circles for those in female scales. Adult female *C. utilis* (mated) are shown by schematic symbols of a wasp in the center of the diagram. The half-arrows from the symbols for mated female *C. utilis* indicate primary parasitization (female parasite egg deposited in male or female scale). The half-arrows from the symbols representing female parasite emergence indicate hyperparasitization by unmated females (male eggs deposited on female parasite prepupae or pupae in male and female scales). The full arrows from symbols representing female parasite emergence indicate the source of females which become mated. The full arrows from symbols representing male parasite emergence indicate the source of males which impregnate females. The full arrows from solid ovals and solid circles indicate host generation source of parasitized scales. The shaded arrows indicate the overwintering period of immature stages of *C. utilis*. Months of the year are shown along the bottom of the diagram.

TABLE 2

AGE DISTRIBUTION OF IMMATURE *COCCOPHAGOIDES UTILIS* DOUTT DEVELOPING IN MALE *PARLATORIA OLEAE* (COLVÉE)

(Duncan Grove, Herndon, Fresno County, California: 1962, 1963, and 1964)

Date of sampling	Scale generation	No. twigs	Total no. immature *C. utilis**	Parasite stage: Egg		Early larval		Intermediate larval		Mature larval and prepupal		Pupal	
				no.	*per cent*	*no.*	*per cent*	*no.*	*per cent*	*no.*	*per cent*	*no.*	*per cent*
4/10/62	Fall, 1961	10	15†	0	....	0	....	0	....	12	80.0	3	20.0
5/11/62	Fall, 1961	10	9†	0	....	0	....	0	....	0	....	9	100.0
6/12/62	Fall, 1961	10	1†	0	....	0	....	0	....	0	....	1	100.0
7/12/62	Spring, 1962	12	87	0	....	5	5.8	21	24.1	47	54.0	14	16.1
8/10/62	Spring, 1962	12	17‡	0	....	0	....	0	....	10	58.8	7	41.2
9/14/62	Spring, 1962	20	3‡	0	....	0	....	0	....	2	66.7	1	33.3
9/14/62	Fall, 1962	20	116	1	0.8	22	19.0	93	80.2	0	....	0	....
10/12/62	Fall, 1962	20	77	2	2.6	5	6.5	12	15.6	42	54.5	16	20.8
11/15/62	Fall, 1962	20	84	0	....	0	....	0	....	62	73.8	22	26.2
12/13/62	Fall, 1962	20	46†	0	....	0	....	2	4.3	31	67.4	13	28.3
1/15/63	Fall, 1962	20	48†	0	....	0	....	1	2.1	41	85.4	6	12.5
2/14/63	Fall, 1962	20	40†	0	....	1	2.6	0	....	27	69.2	11	28.2
3/14/63	Fall, 1962	20	34†	0	....	0	....	0	....	29	85.3	5	14.7
4/15/63	Fall, 1962	20	26†	0	....	0	....	0	....	19	73.1	7	26.9
5/10/63	Fall, 1962	24	25†	0	....	0	....	0	....	6	24.0	19	76.0
6/13/63	Fall, 1962	24	0	0	....	0	....	0	....	0	....	0	....
7/11/63	Spring, 1963	24	60	0	....	2	3.3	14	23.3	25	41.7	19	31.7
8/8/63	Spring, 1963	24	6‡	0	....	0	....	1	16.7	2	33.3	3	50.0
9/11/63	Spring, 1963	24	3‡	0	....	0	....	0	....	1	33.3	2	66.7
9/11/63	Fall, 1963	24	12	1	8.3	8	66.7	3	25.0	0	....	0	....
10/15/63	Fall, 1963	24	20	0	....	1	5.0	5	25.0	7	35.0	7	35.0
11/15/63	Fall, 1963	24	18	0	....	0	....	1	5.6	9	50.0	8	44.4
12/17/63	Fall, 1963	24	11†	0	....	0	....	2	18.2	3	27.3	6	54.5
1/16/64	Fall, 1963	24	15†	0	....	1	6.7	0	....	6	40.0	8	53.3
2/14/64	Fall, 1963	24	4†	0	....	0	....	1	25.0	0	....	3	75.0
3/13/64	Fall, 1963	24	4†	0	....	0	....	0	....	2	50.0	2	50.0
4/14/64	Fall, 1963	24	6†	0	....	0	....	0	....	1	16.7	5	83.3

* Figures without symbols indicate all parasites are females.
† Principally male *C. utilis* prepupae and pupae in diapause; see table 7 for male and female percentages for 1963.
‡ Principally male *C. utilis* and pupae *not* in diapause,

generation. (See fig. 1.) Oviposition in male hosts continues into June and in female hosts into July.

Reflecting the close synchronization between *C. utilis* and its host, the female parasite develops in a male host in a considerably shorter time than does the female *C. utilis* parasitizing a young female host of equal age. Broodryk and Doutt (1966) have shown, in laboratory studies, that the male scale up to 17 days of age is the preferred host. They attribute this preference to the fact that the male scales develop more rapidly than do the females.

Sexual differentiation of the young scales has not developed enough by early June to permit determination of the percentage of parasitization of the scales by sex. However, by mid-July more than two-thirds of the female parasites in male scales had reached the prepupal and pupal stages. (See July, 1962, and July, 1963, spring-generation samples, table 2.) These female *C. utilis* matured and emerged as adults during July and early August. While of virgin status, these adult females hyperparasitized female prepupae and pupae—in other words, their "sisters"—which were still developing in male and female scales of the current generation. Thus, male parasites developed and emerged during the late summer and early fall, when they were required to ensure the presence of mated females to parasitize the fall-generation scales (see fig. 1).

Considering scales of the spring generation only, the greatest degree of hyperparasitization during July appears to have occurred on female prepupae and pupae in *male* scale mummies, since the female parasites developing in *female* scales did not reach the stages of development susceptible to hyperparasitization, in any numbers, until early August.

Female parasites which emerge from male hosts in July and early August may, however, be impregnated by male *C. utilis* which developed from hyperparasitization on overwintered female *C. utilis* prepupae and pupae during the spring and early summer. (See June 13, 1963, and July 11, 1963, samples, table 1. Also, see fig. 1.) Such mated females may contribute additional primary parasitization of immature female scales (see fig. 1). However, most of the oviposition in female scales by female *C. utilis* (the latter derived from the male scales of the spring generation) must occur prior to late July. This is because of the near-maturity or maturity, and consequent unacceptability, of a great majority of the female scales after late July. That primary parasitization of female scales does occur after mid-July is shown by the data in table 1. The sample of July 11, 1963, for the spring generation of scales revealed 42 female scales containing 42 female *C. utilis* (1 egg per host). The August 8, 1963, sample shows an increase of over 100 per cent in the number of female scales containing female *C. utilis* (constant twig sample size). An increase in the number of parasitized female scales also occurred between the July and August samples in 1962, but this increase did not approach the magnitude of that which occurred in 1963.

As previously stated, the developmental period of the primary female parasite in the female scale is generally much longer than in the male scale when very young scales are parasitized. However, because of the physiological synchronization of host and parasite development, the time required for development of female parasites is shortened considerably when parasitization takes place in female scales more advanced in development. Broodryk and Doutt (1966) have shown in laboratory studies that when female scales are parasitized at ages 25 and 29 days, the developmental period of the parasite is shorter than that obtained with male scales of any age.

By mid-July, female parasites developing in female scales of the spring generation were in the egg, early larval,

TABLE 3

PARASITIZATION OF FEMALE *PARLATORIA OLEAE* (COLVÉE) BY *COCCOPHAGOIDES UTILIS* DOUTT AND BY *APHYTIS MACULICORNIS* (MASI)
(Duncan Grove, Herndon, Fresno County, California: 1962, 1963, 1964)*

Date of sampling	Scale generation	Live female scales†	No. of twigs	Live female scales per twig	Female scales successfully parasitized by *C. utilis*	Female scales successfully parasitized by *A. maculicornis*	Female scales successfully parasitized by both parasites	Unparasitized female scales per twig
		no.		*no.*	*per cent*	*per cent*	*per cent*	*no.*
4/10/62..........	Fall, 1961	957	10	95.7	29.7	8.4	38.1	59.3
5/11/62..........	Fall, 1961	446	10	44.6	50.2	22.8	73.0	12.1
7/12/62..........	Spring, 1962	432	12	36.7	35.0	3.9	38.9	22.0
8/10/62..........	Spring, 1962	277	12	23.1	66.1	2.9	69.0	7.2
9/14/62..........	Fall, 1962	229	20	11.5	37.9	0.0‡	37.9	7.1
10/12/62..........	Fall, 1962	243	20	12.2	39.1	9.9	49.0	6.2
11/15/62..........	Fall, 1962	301	20	15.1	27.9	36.2	64.1	5.4
12/13/62..........	Fall, 1962	291	20	14.6	25.4	32.3	57.7	6.2
1/15/63..........	Fall, 1962	241	20	12.1	26.6	32.4	59.0	4.9
2/14/63..........	Fall, 1962	243	20	12.2	37.4	23.5	60.9	4.8
3/14/63..........	Fall, 1962	242	20	12.1	34.7	23.9	58.6	5.0
4/15/63..........	Fall, 1962	168	22	7.6	31.0	46.4	77.4	1.7
5/10/63..........	Fall, 1962	113	24	4.7	29.2	48.7	77.9	1.0
7/11/63..........	Spring, 1963	217	24	9.0	19.4	2.8	22.2	7.0
8/8/63..........	Spring, 1963	165	24	6.9	52.1	4.2	56.3	3.0
9/11/63..........	Fall, 1963	223	24	9.3	20.2	0.0‡	20.2	7.0
10/15/63..........	Fall, 1963	296	24	12.3	37.8	8.8	46.6	6.6
11/15/63..........	Fall, 1963	300	24	12.5	27.0	21.3	48.3	6.5
12/17/63..........	Fall, 1963	297	24	12.4	32.3	22.9	55.2	5.5
1/16/64..........	Fall, 1963	282	24	11.7	32.9	15.9	48.8	6.0
2/14/64..........	Fall, 1963	260	24	10.8	30.4	10.4	40.8	6.4
3/13/64..........	Fall, 1963	221	24	9.2	27.1	12.7	39.8	5.5
4/14/64..........	Fall, 1963	201	24	8.4	35.8	53.2	89.0	0.9

* Not based on total-brood mortality but only on the "non-defunct" portion of the brood present at the time of sampling.
† Live female scale category includes, in addition to unparasitized scales, those scales parasitized by immature *C. utilis* and *A. maculicornis*, some of which have consumed the entire host body contents at the time of sampling.
‡ Female scales are too small to be parasitized by *A. maculicornis* in September.

and intermediate larval stages. For the spring host generation of 1962 the predominant female parasite stage on July 12 was the intermediate larval, at 50.9 per cent (table 1). For the same host generation in 1963 the predominant stage on July 11 was the early larval, at 71.4 per cent. Not until sometime after mid-August of both 1962 and 1963 did female *C. utilis* in female scales reach a concentration in the prepupal and pupal stages equal to that reached by the female parasites in male scales a month or more earlier. (For a comparison of female parasite development in male and female scales of the spring generation, see July and August samples for the spring generations of both 1962 and 1963 in tables 1 and 2.) Emergence of adult female *C. utilis* from female scales commenced shortly after mid-August. These females, before being impregnated, may hyperparasitize their "sisters" still developing in female scales. (See fig. 1.)

In both 1962 and 1963, a good percentage of the female parasites present as prepupae and pupae in female hosts of the spring generation was hyperparasitized during August and September. The resulting male parasites, after developing on the female prepupae or pupae, remained in the female scale mummies as mature larvae until the fol-

TABLE 4

PARASITIZATION OF MALE *PARLATORIA OLEAE* (COLVÉE) BY *COCCOPHAGOIDES UTILIS* DOUTT AND BY *APHYTIS MACULICORNIS* (MASI)
(Duncan Grove, Herndon, Fresno County, California: 1962-1963)*

Date of sampling	Scale generation	Live male scales†	No. of twigs	Live male scales per twig	Male scales successfully parasitized by *C. utilis*	Male scales successfully parasitized by *A. maculicornis*	Male scales successfully parasitized by both parasites	Unparasitized male scales per twig
		no.		*no.*	*per cent*	*per cent*	*per cent*	*no.*
7/12/62..........	Spring, 1962	149	12	12.4	58.4	16.8	75.2	3.1
9/14/62..........	Fall, 1962	298	20	14.9	39.9	4.7	44.6	8.3
10/12/62.........	Fall, 1962	143	20	7.2	53.8	20.9	74.7	1.8
7/11/63..........	Spring, 1963	192	24	8.0	31.3	10.4	41.7	4.7
9/11/63..........	Fall, 1963	159	24	6.6	7.5	8.2	15.7	5.6
10/15/63.........	Fall, 1963	75	24	3.1	26.7	4.0	30.7	2.2

* Not based on total brood mortality, but only on the "non-defunct" portion of the brood present at the time of sampling.
† Live male scale category includes, in addition to unparasitized scales, those scales parasitized by immature *C. utilis* and *A. maculicornis*, some of which have consumed the entire host body contents at the time of sampling.

lowing spring. This period of arrested development of the male parasite extends from late summer until late March or early April, a span of approximately six to seven months under the conditions studied. (See fig. 1.) In 1963, results also showed that, of these mummified spring-generation female scales containing *C. utilis* which diapause until the following spring, an average of approximately 94 per cent was found to contain male parasites and 7 per cent, female parasites (see table 5). This period of arrested development thus applies to both male and female parasites, although females were but a small percentage of the total. No attempt is made here to assign the type of diapause involved. Male larvae of *C. utilis* remained inactive until sometime after mid-February. By mid-March only 10 per cent of the population, approximately, consisted of pupae, but by mid-April over half were pupae. (See table 1, spring generation of 1962, samples for February, March, and April, 1963.)

Since there was an average of nearly 46 per cent premature mortality of *C. utilis* in the late immature stages occurring in female hosts in the field in 1962–1963 (table 6), there is a possibility that female *C. utilis* originally constituted a greater portion than 7 per cent of the parasites entering the overwintering diapause, and that a greater precentage of females than males may have suffered premature mortality. If this were the case, then the percentage of overwintering male parasites would be less than indicated from the material that emerged in the laboratory (see table 5).

Determination of premature mortality in *C. utilis* under field conditions was made by examination of scales showing evidence of *past* parasitization. Scale mummies were classified as exhibiting either successful parasite development and emergence or unsuccessful development and premature mortality. Of the 12,042 female scale mummies examined between 1962 and 1963 (see table 6), 45.5 per cent contained dead *C. utilis* in late stages of development (nearly mature larva, mature larva, prepupa and pupa). Premature mortality of *C. utilis* in male scales was slightly higher, at 49.1 per cent (see table 6).

Parasitization of Fall-Generation Scales

Oviposition by female scales of the

TABLE 5

SEX OF OVERWINTERING *COCCOPHAGOIDES UTILIS* DOUTT EMERGED IN THE LABORATORY FROM FIELD-COLLECTED MATURE LARVAE, PREPUPAE, AND PUPAE PARASITIZING FEMALE *PARLATORIA OLEAE* (COLVÉE) OF THE 1962 SPRING GENERATION

(Duncan Grove, Herndon, Fresno County, California)

Month of sampling	Prepupae and pupae recovered	Adult *C. utilis* emerged	♀♀ emerged	♂♂ emerged	Per cent emerged as ♂♂
	no.	*no.*	*no.*	*no.*	
November, 1962	65	34	0	34	100.0
January, 1963	48	36	0	36	100.0
February, 1963	40	29	4	25	86.2
March, 1963	47	31	5	26	83.9
Total	200	130	9	121	Av. of total: 93.1

spring generation is initiated in late July, and by mid-August some eggs have hatched and young scales in settled stages are present. (See fig. 1.) Oviposition continues throughout August and into September, a small percentage of the females producing eggs as late as early October.

From mid-August through the fall months, young scales are susceptible to parasitization by *Coccophagoides utilis* as the adult female parasites emerge from female scales of the spring generation. These female parasites may, before being impregnated by male *C. utilis,* hyperparasitize their "sisters" still present in female scales as prepupae and pupae (see discussion, p. 266). The male parasites which impregnate these females during late summer and early fall are derived principally from hyperparasitization on the male scales of the spring generation (see p. 265).

The development of female *C. utilis* in male scales of the fall generation is, as was the case with the spring generation, closely synchronized with host development. By September 14, 1962, 80.2 per cent of the female parasites had reached an intermediate larval stage, and by October 12 the parasites were predominantly in the mature larval, prepupal, and pupal stages (75.3 per cent; see table 2). On this latter date, a majority of the unparasitized male scales had completed their development and emerged as adults.

Although all immature female *C. utilis* developing in male hosts were in the prepupal and pupal stages by November, 1962, the December, January, and February, 1963, samples each contained one or two male scales parasitized by a female *C. utilis* larva in the early or intermediate stages of development (table 2). The complete absence of adult parasites during the winter months precludes any possibility of male hyperparasitization on these females, and thus we see that some overwintering of female parasites in male scales does occur. (See fig. 1, and also table 2.)

Female *C. utilis* developing in male scales of the fall generation of 1963 were not so advanced in development by mid-September as were those of the fall generation of 1962. On September 11, 1963, only 25.0 per cent of the females had reached the intermediate larval stage, whereas on September 14, 1962, 80.2 per cent had reached the same stage. However, by October 15, 1963, the percentage of female *C. utilis* in the mature larval, prepupal, and pupal stages (70.0 per cent) was nearly equal to the percentage (75.3 per cent) in those stages on October 12, 1962 (see table 2).

During October and November of

TABLE 6
MORTALITY IN LATE DEVELOPMENTAL STAGES OF IMMATURE *COCCOPHAGOIDES UTILIS* DOUTT IN MUMMIFIED HOSTS
(Duncan Grove, Herndon, Fresno County, California: 1962-1963)

Date of sampling	♀♀ scale mummies		♂♂ scale mummies	
	No. examined	Premature mortality of parasites	No. examined	Premature mortality of parasites
		per cent		*per cent*
1/10/62	533	48.8	104	50.0
4/10/62	328	55.5	54	53.7
5/11/62	502	53.4	101	61.2
6/12/62	592	47.6	42	50.0
7/12/62	716	51.5	114	45.6
8/10/62	674	45.1	195	47.7
9/14/62	1,538	41.5	281	35.9
10/12/62	1,088	40.3	265	48.7
11/15/62	1,235	44.8	352	53.2
12/13/62	934	51.6	276	54.7
1/15/63	1,158	45.3	317	42.6
2/14/63	1,609	44.7	379	55.7
3/14/63	1,135	39.7	357	47.3
	Total: 12,042*	Av. of total: 45.5*	Total: 2,837*	Av. of total: 49.1*

* Total no. male and female scales: 14,879. Av. mortality of parasites (male and female) in scales: 46.2 per cent.

1962, virgin female *C. utilis* emerged from male scale mummies and accomplished considerable hyperparasitization of their "sisters" still developing in male hosts (see fig. 1). The male parasites which resulted from this hyperparasitization overwintered as prepupae and pupae. (See table 2, 1962, fall scale generation.)

If the female *C. utilis* which emerge from male hosts principally during October and November become impregnated, primary parasitization may occur on female and late-developing male scales. However, the data obtained during the fall months of 1962 and 1963 support the conclusion that very few of these females become impregnated. As seen in table 2 (September samples, spring generations, 1962 and 1963), male parasites which developed on male scales of the spring generations of 1962 and 1963 have nearly completed adult emergence by mid-September, whereas female parasites on male scales of the fall generation have not progressed beyond the intermediate larval stage by that time. Thus, there is little chance of overlap in adult emergence of parasites of the two generations. Also, as seen in table 1, female parasites which developed in female scales of the spring generation had essentially completed adult emergence prior to mid-October, the remaining parasites in subsequent monthly samples being principally males in diapause. (See discussion, p. 267.)

The data do not entirely eliminate the possibility that male diapause may be terminated prematurely in certain individuals, or may not occur in some individuals. Still, the relatively constant numbers of female scale mummies (constant twig sample size) containing male parasites from October to April would seem to preclude the possibility that these males emerge as adults during October and November.

Thus, although it has been recognized that limited mating and consequent primary parasitization of female scales may be accomplished by female parasites which develop on male scales of the fall generation, it was considered inappropriate to include such supposition in figure 1.

Fall emergence of female parasites from male hosts was essentially completed prior to mid-December in both 1962 and 1963 (see table 2). Samples taken throughout the winter of 1963 (constant twig sample size) revealed a fairly constant number of male scale mummies. (See table 2, 1962, fall scale generation.) The gradual reduction in the number of male scale mummies during the winter and early spring months of 1963 and 1964 may be a reflection of the premature mortality known to occur in this parasite.

Emergence of adult parasites in the laboratory during the winter from field-collected male scale mummies of the fall scale generation of 1962 consisted of approximately 90 per cent male and 10 per cent female *C. utilis* (table 7). Hence, that portion (90 per cent) of the male scales of the fall generation which contained overwintering parasites were hyperparasitized during the late fall months, principally by the earliest-emerging virgin females which developed on male scales of the same fall generation, and to a much lesser extent by virgin females from the last of the emergence from female scales of the spring generation. Thus, overwintering male *C. utilis* are derived from both scale generations: from male scales of the fall generation and from female scales of the spring generation.

The remaining overwintering parasites in male scales, approximately 10 per cent, were females which escaped hyperparasitization during the fall and were delayed in adult emergence until mid-spring.

Female scales of the fall generation are parasitized during late summer and early fall by female *C. utilis* which emerge during this period from the previous generation of scales (see fig. 1). As was the case with *C. utilis* developing in the spring-generation scales, female parasites developing in female hosts of the fall generation lag behind in their development, compared to female parasites developing in male scales. Whereas a high percentage of the female *C. utilis* in male hosts complete their development and emerge as adults during the fall months, female *C. utilis* developing in female hosts remain principally in the egg, early larval, and intermediate larval stages throughout the fall and early winter. (See table 1, fall generations of 1962 and 1963.)

During the fall and early winter of 1962–1963, female *C. utilis* developing in female hosts of the fall generation were principally in the egg and early larval stages until sometime after mid-January of 1963. A small percentage of *C. utilis* in the intermediate larval stages occurred in each monthly sample during the fall and early winter. The highest level observed was 8.3 per cent on November 15, 1962. (See table 1, 1962 fall generation.) During the fall of 1963 there was considerable acceleration in the development of female *C. utilis* occurring in female scales. On October 15, 1963, 18.8 per cent of the female parasites in fall-generation scales had reached the intermediate larval stage, and by November 15, 1963, 28.4 per cent were in the intermediate larval stage, and 2.5 per cent in the mature larval stage.

This contrast between 1962 and 1963 in development of the immature stages of *C. utilis* may have been the result of differences in synchronization between the emergence of adult parasites from spring-generation scales and the appearance of susceptible male and female scales of the fall generation. In July of 1963 the predominant stage of female parasites in female scales was the early larval, whereas in July of 1962 the predominant stage was the intermediate larval (see table 1). Thus the late summer and early fall emergence period of adult female *C. utilis* may have occurred somewhat later in 1963. The possibility of a later emer-

TABLE 7

SEX OF OVERWINTERING *COCCOPHAGOIDES UTILIS* DOUTT EMERGED IN THE LABORATORY FROM FIELD-COLLECTED PREPUPAE AND PUPAE PARASITIZING MALE *PARLATORIA OLEAE* (COLVÉE) OF THE 1962 FALL GENERATION

(Duncan Grove, Herndon, Fresno County, California)

Month of sampling	Prepupae and pupae recovered	Adult *C. utilis* emerged	♀♀ emerged	♂♂ emerged	Per cent emerged as ♂♂
	no.	*no.*	*no.*	*no.*	
January, 1963	30	16	3	13	81.3
February, 1963	34	15	1	14	93.3
March, 1963	30	20	1	19	95.0
Total	94	51	5	46	Av. of total: 90.2

gence period is also indicated by the low level of parasitization achieved on the male scales of the fall generation of 1963 (see table 4). The male scales usually experience a higher degree of parasitization than do the females during the early part of the scale generation (see p. 265). If such a delay in adult parasite emergence occurred, then parasitization may have been intensified on somewhat older female scales of the fall generation with a resultant acceleration in parasite development. (See table 1, 1963 fall generation.) This explanation is in accord with the laboratory observations of Broodryk and Doutt (1966, p. 243).

It thus appears that when parasite emergence is well synchronized with the appearance of very young scales in late summer, parasitization of the young female scales (first and second instars) results in a high percentage of the parasite brood remaining in the egg and early larval stages throughout the fall and early winter. Conversely, when parasite emergence is not well synchronized with the appearance of very young scales, parasitization of older female scales (early third instar) results in a considerable percentage of the parasite brood continuing its development throughout the fall and early winter months.

Female *C. utilis* parasitizing the 1962 fall generation of scales had resumed development by mid-February of 1963; and, although over three-fourths of the brood was still in the early larval stage, the remaining one-fourth had developed to the intermediate larval stage. By mid-March the percentages of female parasites in these two larval stages were very nearly reversed. Higher temperatures during early spring accelerated larval development, and by mid-April approximately two-thirds of the female *C. utilis* had reached the mature larval and prepupal stages. One month later (mid-May) female parasite emergence was well under way. (See fig. 1 and table 1.) However, emergence of a small percentage of females was delayed, and these were still in the pupal stage as late as July, 1963. Emergence in the laboratory of adults from female scale mummies of the July, 1963, sample showed 36 per cent of the parasites to be females.

Emergence of adult male *C. utilis* which overwintered principally as mature larvae also began in May (see fig. 1). Those males which developed as hyperparasites on male scales of the fall generation had completed emergence by mid-June. (See sample for June 13, 1963, table 2.) It is most probable that male *C. utilis* which developed as hyperparasites on female scales of the previous spring generation (1962) had also emerged by mid-June. However, it was not possible to separate parasites occurring in female scales as to source of the host generation during June, since by mid-June all parasitized female scales of the fall generation had also become mummified and the immature parasites were in the mature larval, prepupal, and pupal stages (see footnote ‡, for June 13, 1963, sample in table 1).

Mummified scales containing *C. utilis* larvae and pupae in the June sample were held for parasite emergence to determine if males were still present. Also, dissections showed male larvae hyperparasitizing female pupae (see footnote §, for June 13, 1963, sample in table 1). Virgin female *C. utilis* emerging prior to mid-June hyperparasitized some of their "sisters" and thus precluded determination of the source of male parasites at that time (see fig. 1). Had this hyperparasitization not occurred, any males which emerged from female scale mummies of the June sample must have originated from female scales of the previous spring generation.

Hyperparasitization

Although it was not possible to determine the exact degree of hyperparasitization which occurs under field conditions, a rough approximation is here presented. Taking the July and August, 1962, totals for female *Coccophagoides utilis* developing in the spring generation of female scales at 151 and 183, respectively (table 1), the average population of female parasites present and susceptible to hyperparasitization was 167, or 13.9 per twig (12-twig sample). Of this population, the female parasites not subsequently hyperparasitized emerged as adults during late summer and early fall. However, those female parasite prepupae and pupae which were hyperparasitized produced overwintering male *C. utilis,* which passed the fall and winter months as mature larvae (see fig. 1). The total number of female scale mummies containing *C. utilis* in the monthly samples from October 12, 1962, to April 15, 1963, was 381 (table 1). The average number of mummies per monthly sample was thus 54; and with a constant sample size of 20 twigs, the average number of mummies was 2.7 per twig. Since approximately 7 per cent of the *C. utilis* in these mummies were females (see table 5), the number of scale mummies containing male *C. utilis* was reduced to an average of 2.5 mummies per twig. Since the generation started with 13.9 female scales per twig containing female parasites susceptible to hyperparasitization, and since we obtained an average of 2.5 scale mummies per twig containing male *C. utilis* for the overwintering period after the female parasites had emerged, we found the approximate degree of hyperparasitization to be 18.0 per cent.

Hyperparasitization on female parasites in female scales of the fall generation occurs during late spring as the overwintered female *C. utilis* begin adult emergence (see fig. 1). Since there is continuous development (no diapause) of the male hyperparasite during the spring, it was difficult to obtain data on the degree of hyperparasitization. However, the May and June, 1963, samples (table 1) give an indication of the degree of hyperparasitization achieved. Of 108 female scale mummies containing 108 *C. utilis* in the sample for May, 1963, roughly one-half contained male *C. utilis* derived from female scales of the spring generation of 1962. The remaining half contained female *C. utilis* which had parasitized female scales of the fall generation of 1962. These female parasites in the prepupal and pupal stages in the scale mummies were susceptible to hyperparasitization, as stated above. The sample for June, 1963, showed that of the 19 female scale mummies containing *C. utilis,* 18 were in a stage of development susceptible to hyperparasitization. Of these 18, seven were currently hyperparasitized by male *C. utilis* larvae. (See footnote §, table 1.) If roughly one-half, or 54 of the 108 *C. utilis* in female scale mummies in May, 1963, were female *C. utilis* and seven subsequently contained male *C. utilis,* the degree of hyperparasitization was approximately 12.5 per cent as shown by the June sample.

Hyperparasitization on the male scales of the fall generation was considerably higher than that occurring on the female scales of the spring and fall generations. For the fall generation of 1962, the total number of male scales containing female *C. utilis* was 116 on September 14 (see table 2). This gave an average of 5.8 parasitized male scales per twig (20-twig sample). The average number of male scale mummies containing *C. utilis* in the samples for December, 1962, and January and February, 1963, was 2.2 male scale mummies per twig (constant sample size, 20 twigs). The number of male scale mummies for the months of March, April, and May, 1963, was not used in computing the average, because premature mortality may have been responsible for the reduced number of male scale mummies during those months. Since approximately 10 per cent of the male scale mummies in early 1963 contained female parasites (see table 7), the number of scale mummies containing male parasites was reduced from 2.2 to an average of 2.0 per twig. Since the generation started with 5.8 male scales per twig containing female *C. utilis* subsequently susceptible to hyperparasitization, and since we obtained an average of 2.0 scale mummies per twig containing male *C. utilis* for the overwintering period after the female parasites emerged, the approximate degree of hyperparasitization was found to be 34.5 per cent.

Hyperparasitization on female parasites in male scales of the spring generation was the most difficult to determine. The July samples in both 1962 and 1963 were taken too early for determination of hyperparasitization, and by August the samples showed that a very high percentage of the parasites had emerged from the male scale mummies (see July and August samples for above years, table 2). Assuming that all the remaining male scale mummies in the August samples contained male *C. utilis,* hyperparasitization for 1962 and 1963 was 19.5 and 10.0 per cent, respectively.

APPRAISAL OF ECOLOGICAL ROLE

Although *Coccophagoides utilis* does not attain the high degree of parasitization which *Aphytis maculicornis* often achieves in the spring, it does successfully parasitize both generations of scales and to about the same degree. This is shown, for the Duncan Grove, in tables 3 and 4. Table 3 shows that by April 10, 1962, 29.7 per cent of the overwintered female scales of the 1961–1962 fall generation had been parasitized by *C. utilis,* and that by July 12, 1962, 35.0 per cent of the female scales of the spring generation had been parasitized. For the fall generation of 1962 *C. utilis* achieved a parasitization of 39.1 per cent of the female scales by October 12, 1962. Of the female scales of the 1963 spring generation, 19.4 per cent had been parasitized by *C. utilis* by July 11, 1963; and by October 15, 1963, 37.8 per cent of the female scales of the 1963 fall generation had been parasitized by *C. utilis.*

Primary parasitization of female scales of the spring generation was somewhat belated in 1963 when contrasted with the 1962 parasitization figures. By July 11, 1963, only 19.4 per cent of the female scales had been parasitized, whereas the July, 1962, figure was 35.0 per cent. Also, the female parasites were not as far along in development in 1963 as they were in 1962 (see discussion, p. 266).

The low percentage of parasitization

of female scales by July 11, 1963, and the relatively slow development of the immature stages of the parasite may be explained possibly by the fact that there was considerable mortality of overwintering female *C. utilis* developing in female scales of the fall generation; this mortality was due to parasitization of the host scales by *A. maculicornis* (see section on Multiple Parasitization, pp. 275 ff.). Thus there were fewer female *C. utilis*, derived from overwintered scales, available to parasitize the spring-generation scales during May, June, and July. The increase in the number of female scales showing parasitization by *C. utilis* in the sample for August, 1963, over that of July may have been due, in part, to parasitization by female *C. utilis* which emerged in July from male scales of the spring generation (see p. 265). The August samples for both 1962 and 1963 indicate that primary parasitization continued into late July.

The level of parasitization by *C. utilis* on female scales of the fall generation was somewhat lower in the September sample of 1963 than it was for the same sample of 1962. However, by mid-October of 1963, the level of parasitization was roughly equal to that observed for mid-October of 1962. (See table 3.)

Since there may be some emergence of female parasites after mid-October, and since female scales are susceptible to parasitization during the entire fall season, evidence of additional parasitization might be expected to appear in subsequent samples. However, the level of *successful* parasitization by *C. utilis*, as shown in table 3, was slightly lower in the November and December samples in both 1962 and 1963 than for the October samples of the same years. These reductions were due to *A. maculicornis* parasitization of female scales containing eggs and young larvae of *C. utilis*.

The degree of parasitization of the male scales by *C. utilis* is shown in table 4. In all scale generations studied, *C. utilis* achieved a higher initial parasitization of male scales than of females, except on the fall-generation scales of 1963.

We feel that since the male scales have a considerably faster rate of development than do the females, *C. utilis* preferentially parasitizes the more advanced scales (males) during the early part of each scale generation. Broodryk and Doutt (1966; see figure 12 therein) have shown this to be the case in laboratory populations. While the initial parasitization under field conditions is usually higher on the male scales, as the scale generation progresses parasitization on the female scales may reach a higher level than that achieved on the males. This may be explained by the fact that although the male is the more desirable host early in the scale generation, it is susceptible to parasitization for a much shorter period of time than the female.

We feel that the low degree of parasitization of the male scales of the fall generation observed on September 11, 1963, at the Duncan Grove (7.5 per cent; see table 4) may have been due, at least in part, to poor synchronization between the emergence of adult female parasites from spring-generation female scales and the occurrence of susceptible stages of the male scales. Also, possibly poor synchronization between emergence of adult male and female parasites, or a shortage of male parasites, resulting in a reduced incidence of mating during the period of male scale susceptibility, may have been factors contributing to the low degree of parasitization of male scales (see also discussion, p. 271).

As was the case with female scales of the spring generation, there was a considerable difference in the level of *C. utilis* parasitization of male scales of the spring generations of 1962 and 1963 as shown by the July samples (table 4). However, the age distribution of immature *C. utilis* in the July, 1963, sample was quite similar to that of the

July, 1962, sample (table 2). Thus, although *C. utilis* apparently was not as successful in parasitizing male scales of the spring generation in 1963 as in 1962, the data show that the parasitization occurred at about the same period in both years. The lower level of parasitization on the male scales in July of 1963 may have been due to the same causes considered possibly responsible for the reduced parasitization of female scales in July, 1963 (see p. 274).

The increase in percentage of parasitization of male scales of the fall generation between September and October in both 1962 and 1963 (table 4) is not meaningful, since there was considerable emergence of unparasitized adult male scales during the period between samples. That this emergence occurred is apparent from the significant difference in the number of immature male scales (parasitized and unparasitized) in the samples for September and October.

Multiple Parasitization

Multiple parasitization of the host occurs when a scale containing a female egg or young larva of *Coccophagoides utilis* is also parasitized by *Aphytis maculicornis*. The ectoparasitic larva of *A. maculicornis* is intrinsically superior and, as such, destroys the scale host and the young *C. utilis* within.

The ovipositional instincts of *A. maculicornis* apparently preclude the deposition of its eggs on scales containing *C. utilis* larvae in an intermediate stage of development (i.e., when host scales are flaccid and lacteal), as this was not observed during the course of this study.

A. maculicornis parasitization of scales containing *C. utilis* is of little consequence to female scales of the spring generation because of the very low densities of *A. maculicornis* during the development of the spring-generation scales. In the Duncan Grove, on July 11, 1963, only 2.3 per cent of the female scales of the spring generation, containing immature female *C. utilis*, were also parasitized by *A. maculicornis.*

The data in table 8 show the effect of multiple parasitization on the success of *C. utilis* in parasitizing female scales of the fall generations of 1962 and 1963. In both years *A. maculicornis* survived the summer period at levels considerably higher than usual (see tables 3 and 4, spring-generation scales), and was able subsequently, during the fall months, to increase to parasitization levels much higher than it achieves on fall-generation scales in most years. Because of the relatively high densities of *A. maculicornis*, considerable multiple parasitization resulted during the fall of both 1962 and 1963. For example, the total number of immature female *C. utilis* in the sample of November 15, 1962, was 112, the total parasitization by *C. utilis* being 37.2 per cent (see table 8). Of the 112 female eggs and young larvae of *C. utilis* present, 28 occurred in scales also parasitized by *A. maculicornis.* Thus 25.0 per cent of the immature *C. utilis* population was subsequently eliminated by *A. maculicornis* and the resultant current successful parasitization by *C. utilis* (table 8, column G) was obtained by reducing the observed parasitization in column D by one-quarter, from 37.2 per cent to 27.9 per cent, for the November sample. The highest degree of instantaneous multiple parasitization during the fall months occurred in November of both 1962 and 1963. The levels for November, 1962, and November, 1963, were 25.0 per cent and 21.4 per cent, respectively (see table 8).

It should also be mentioned that while there is only one generation of female *C. utilis* parasitizing female scales of the fall generation, *A. maculicornis* may have as many as three or more generations parasitizing this host generation during the fall, winter, and spring. Thus multiple parasitization during the fall months is only part of the total. The net effect of multiple

TABLE 8

EFFECT OF MULTIPLE PARASITIZATION ON THE DGEREE OF SUCCESSFUL PARASITIZATION BY FEMALE *COCCOPHAGOIDES UTILIS* DOUTT ON FEMALE *PARLATORIA OLEAE* (COLVÉE) OF THE FALL GENERATIONS OF 1962 AND 1963

(Duncan Grove, Herndon, Fresno County, California)

Month of sampling	A Live female scales	B Immature female *C. utilis*	C Immature *A. maculicornis*	D Parasitization by *C. utilis*	E Parasitization by *A. maculicornis*	F Multiple parasitization: Female scales parasitized by both *C. utilis* and *A. maculicornis*		G† Currently successful parasitization by *C. utilis*	
	no.	*total no.*	*total no.*	*per cent*	*per cent*	*no.*	*per cent**	*no. scales parasitized*	*per cent scales parasitized*
October, 1962......	243	87	24	35.8	9.9	..	....	..	....
November, 1962......	301	112	109	37.2	36.2	28	25.0	84	27.9
December, 1962......	291	87	94	29.9	32.3	14	16.1	73	25.4
March, 1963......	242	99	58	40.9	23.9	15	15.2	84	34.7
April, 1963......	168	56	78	33.3	46.4	4	7.1	52	31.0
October, 1963......	296	126	26	42.6	8.8	14	11.1	112	37.8
November, 1963......	300	103	64	34.3	21.3	22	21.4	81	27.0
December, 1963......	297	109	68	37.1	22.9	13	11.9	96	32.7
March, 1964......	221	60	28	27.1	12.7	0	0.0	60	27.1
April, 1964......	201	77	107	38.3	53.2	5	6.5	72	35.8

* The percentage of multiple parasitization is that fraction of the total number of *C. utilis* present (Column B) also parasitized by *A. maculicornis* as shown in column F.

† For an explanation of the way currently successful parasitization by *C. utilis* is arrived at, see p. 275.

parasitization by *A. maculicornis* is reflected in the number of *C. utilis* which mature successfully in April, compared to the number present in October and November, excluding, of course, those parasites which experience premature mortality from other causes.

In the fall of 1962, the average number of immature female *C. utilis* for October and November combined was 99.5 (see table 8, column B). The April, 1963, sample showed 52 female *C. utilis* present (see table 8, column G). The reduction in successful parasitization by *C. utilis* during the fall scale generation was thus 47.7 per cent. For the 1963 fall scale generation. *C. utilis* experienced a 37.4 per cent reduction. The lower figure for 1963 was principally due to less multiple parasitization by *A. maculicornis* (see table 8, column F).

Since *A. maculicornis* reaches its highest level of parasitization during early spring, a higher degree of multiple parasitization on female scales of the fall generation might be expected to occur during the spring than during the fall. However, this was not the case for the 1962 and 1963 fall-generation scales. Although *A. maculicornis* began emerging in late February and early March of 1963 at the Duncan Grove, and there was a relatively high number of *A. maculicornis* eggs present by the mid-March sample (see table 9), this new parasitization did not result in an increase in the percentage of multiple parasitization (see table 8, column F). By the time *A. maculicornis* activ-

TABLE 9

AGE DISTRIBUTION OF IMMATURE *APHYTIS MACULICORNIS* (MASI) DEVELOPING ON FEMALE *PARLATORIA OLEAE* (COLVÉE) OF THE FALL GENERATIONS OF 1962 AND 1963

(Duncan Grove, Herndon, Fresno County, California)

Month of sampling	Parasite stage						Total parasites
	Egg		Larval		Pupal		
	no.	*per cent of total*	*no.*	*per cent of total*	*no.*	*per cent of total*	*no.*
October, 1962	6	25.0	13	54.2	5	20.8	24
November, 1962	17	15.6	63	57.8	29	26.6	109
December, 1962	4	4.3	59	62.8	31	32.9	94
March, 1963	27	46.6	15	25.8	16	27.6	58
April, 1963	11	14.1	50	64.1	17	21.8	78
October, 1963	11	42.3	14	53.9	1	3.8	26
November, 1963	8	12.5	42	65.6	14	21.9	64
December, 1963	4	5.9	47	69.1	17	25 0	68
March, 1964	2	7.1	5	17.9	21	75.0	28
April, 1964	37	34.6	70	65.4	0	0.0	107

ity became intensified in March and early April, a high proportion of the female scales containing immature *C. utilis* was no longer susceptible to attack by *A. maculicornis*. (See p. 275.) Thus the level of multiple parasitization in March, 1963, was only 15.2 per cent, slightly below that observed for December, 1962. By mid-April, 1963, the level of multiple parasitization had dropped to 7.1 per cent (table 8). This was a result of most of the scales parasitized by *C. utilis* having become mummified and being no longer susceptible to parasitization by *A. maculicornis*.

In 1964 the spring activity of *A. maculicornis* was retarded as shown by the presence of only 2 eggs in the mid-March sample (see table 9). Multiple parasitization at this time was 0.0 per cent (see table 8, column F). This absence of evidence of multiple parasitization was the result of very few *A. maculicornis* eggs being deposited. Also, since the remaining 26 immature *A. maculicornis* in the sample (see table 9) were in the mature larval or pupal stages on March 13, 1964, determination of multiple parasitization on those host scales was precluded. Parasitization by *A. maculicornis* in late March and early April resulted in a large increase in the number of eggs present, and this resulted in an increase in multiple parasitization to 6.5 per cent (see table 8, column F).

Unfortunately from one point of interest, the degree of multiple parasitization on female scales of the fall generations in the Duncan Grove was quite similar during the fall months of both 1962 and 1963. Had *A. maculicornis* survived the summer period at a more typical low density in either of these two years, a significant contrast in the degree of multiple parasitization would probably have occurred during the fall months of those years.

Very little information was obtained regarding the degree of multiple parasitization occurring on male scales. There are several explanations for this. First, male scales of both the spring and fall generations are of a susceptible age during the period when *A. maculicornis* is at its low ebb (mid-June through September). Thus the male scales of both generations normally experience very little parasitization by *A. maculicornis* (see table 4). Secondly, parasitization of male scales by *A. maculicornis* could not be determined for the June samples, because the scales have not reached a discernible sexual differentiation at that time. Third, although male scales were sexually differentiated at the time of the September samples, the degree of parasitization by *A. maculicornis* was very low (see table 4) and multiple parasitization was not observed. Lastly, the samples taken in mid-July and mid-October revealed that a high percentage of the *A. maculicornis* parasitizing male scales had already reached the pupal stage. Once *A. maculicornis* has consumed the scale body, evidence of parasitization by *C. utilis* is no longer present.

For the spring-generation scales of 1963, the observed incidence of multiple parasitization of the male scales was 1.6 per cent on July 11, when only one of 61 male scales containing eggs or young larvae of *C. utilis* was also parasitized by a larva of *A. maculicornis*. Of the 20 *A. maculicornis* occurring on male scales on this date, 14 were in the pupal stage and six were in the larval stage. Hence, determination of the presence of *C. utilis* was possible on only six of the 20 scales. Undoubtedly a higher degree of multiple parasitization of male scales occurred; but because most *A. maculicornis* were in the pupal stage, the total degree was not discernible.

THE QUESTION OF COMPETITIVE DISPLACEMENT OR USEFUL COEXISTENCE

The question occurs as to whether or not olive scale on olives presents an unfilled and separate niche to be occupied by another parasite, even when *Aphytis maculicornis* is present. Theoretical considerations and the data and observations since the introduction of *Coccophagoides utilis* in 1957 indicate that the two species of parasites will continue to coexist, and in such numbers that each will remain a significant factor in the control and regulation of the host species. Various facts suggest this. First, of course, *A. maculicornis* is ill-adapted to exploit the spring generation of the host species, and hence leaves available a largely unutilized resource. Secondly, *C. utilis* has demonstrated a remarkable adaptiveness to the hot summer period and effectively parasitizes the scale—thus it effectively exploits the available food and reduces the host population. Third, as a parasite of olive scales during seasons when the weather is favorable to both parasites, *C. utilis* is inherently at a disadvanage compared to *A. maculicornis*.

This inferior status of *C. utilis* is probably due to various factors, concerning some of which we have no data or only inadequate data. Both species are effective searchers for olive scales at low densities; however, since no comparative data are available, this aspect is not considered here. An important feature is that *A. maculicornis* appears to have a considerably higher power of population increase than does *C. utilis* under weather conditions favorable to both species. This higher power of increase is based in part on the fact that, under favorable conditions, *A. maculicornis* may complete a full generation in about 20–25 days, while *C. utilis* has only two basic generations a year, both synchronized with those of the host. *C. utilis* also has one additional partial increase phase which may be associated with each such full generation (see p. 259).

Regarding another facet of power of increase — fecundity — Maddox (cited from Huffaker, Kennett, and Finney, 1962, p. 576) found that female *A. maculicornis* held at 81°F and 55 per cent relative humidity deposited an average of 30 eggs during an average ovulation period of 20 days. On the other hand, Broodryk and Doutt (1966) found that female *C. utilis* deposited an average of 26 eggs during an average ovulation period of 12 days under insectary conditions. An additional basis of the comparison is that *A. maculicornis* has exhibited in the field a phenomenally rapid increase in numbers within a short period during April and early May (Doutt, 1954; Huffaker, Kennett, and Finney, 1962, p. 577), whereas *C. utilis* has never exhibited such a rapid increase. One further reason why *C. utilis* does not exhibit so rapid an increase under field conditions may be that, as discussed previously, it suffers a rather substantial mortality from unknown but apparently density-independent causes (see table 6), whereas *A. maculicornis* has never been observed to suffer an appreciable mortality during its development (see table 10). This differential in mortality thus adds to the inherent disadvantage of *C. utilis* when the climatic condition during summer (adverse to *A. maculicornis*) is excluded.

A. maculicornis is an ectoparasite, while the female of *C. utilis* is an endoparasite. Only *A. maculicornis* survives when multiple parasitism occurs. Thus, *C. utilis* is further retarded in its power of increase because of the mortality caused by *A. maculicornis.* On the other hand, it is known that *C. utilis* causes little, if any, direct mortality of *A. maculicornis*. However, the situation is more complex than this: *C. utilis* has the first opportunity to parasitize host scales, since it attacks very young scales as well as older ones. *A. maculicornis,* by contrast, attacks mainly the nearly mature scales. This situation would not operate against *A. maculicornis* were it not for the fact that, beyond a certain point in the development of *C. utilis,* the host scales appear to be rendered less attractive (presumably unsuitable) to the ovipositing *A. maculicornis* females. Under field conditions, in fact, multiple parasitism is not nearly as common as would otherwise be expected. This is because the early stages of the host (whether or not parasitized by *C. utilis*), and those stages in which *C. utilis* in the host has developed beyond a certain point, are both unacceptable to *A. maculicornis.* Nevertheless, some conflict of interest or ecological overlap (competition) does exist, and this results perhaps in a net advantage to *C. utilis,* because of its acceptance of the youngest stages of the host.

Thus the overall effect of the competition experienced up to the present in the two olive groves studied—the Duncan Grove at Herndon and the grove at Madera—has been such that *A. maculicornis* loses ground during the summer. At this time *C. utilis* has the host almost to itself; then, during the fall and subsequent spring periods, by virtue of its greater rate of increase and its survival when the two species attack the same host, *A. maculicornis* regains the ground lost. A higher mortality rate in *C. utilis* during developmental stages is also indicated. It is also possible that the greater rate of increase demonstrated by *A. maculicornis* in the spring is a result of a more effective searching capacity, although no data on this possibility have been obtained.

Regarding differences in mortality rate between the two species during developmental stages under field conditions, a preliminary comparison indicates that failure of parasites which have reached a nearly mature larval stage to complete their development and emerge as adults, is much more pronounced in *C. utilis.* During 1962 and 1963 at the Herndon location, only 53.8 per cent of such nearly mature larvae completed their development and emerged, the other 46.2 per cent dying either prior to pupation, in the pupal stage, or as adults which failed to emerge from the scale mummies (table 6). On the other hand, an average of only 17.1 per cent of the *A. maculicornis* suffered a similar mortality (table 10). No data on the mortality occurring earlier in the life cycle of

TABLE 10

MORTALITY IN LATE DEVELOPMENTAL STAGES OF IMMATURE *APHYTIS MACULICORNIS* (MASI)

(Duncan Grove, Herndon, Fresno County, California: 1962–1963)

Date of sampling	On female scales		On male scales	
	No. *A. maculicornis* examined	Per cent mortality	No. *A. maculicornis* examined	Per cent mortality
11/15/62	465	20.0	98	20.4
12/13/62	450	15.6	90	15.6
1/15/63	567	16.6	83	16.9
2/14/63	554	16.8	47	12.8
3/14/63	504	17.9	67	11.9
	Total: 2,540*	Av. of total: 17.2*	Total: 385*	Av. of total: 16.1*

* Total no. male and female scales: 2,925. Av. mortality of parasites (male and female combined) in scales: 17.1 per cent.

C. utilis have been obtained. It is known, however, that *A. maculicornis* suffers only a very low mortality in its early stages (extensive observations from dissections).

Whether a gradual displacement of *A. maculicornis* may occur as *C. utilis* becomes more widespread and abundant generally, cannot be known at present. Since *A. maculicornis* was already very abundant when *C. utilis* was introduced, it seems unlikely that *C. utilis* could have become so readily established and of significance if *A. maculicornis* were sufficiently superior overall as to be capable of replacing *C. utilis* entirely. It is not felt that these two species are exact ecological homologues,[2] and we do not expect either one to exclude the other, as occurred with parasites of red scale studied by DeBach and Sundby (1963).

EVALUATION OF EFFECTIVENESS OF *Coccophagoides utilis*

A preliminary evaluation of the success of *Coccophagoides utilis* in supplementing the economic control previously achieved by *Aphytis maculicornis* alone is now possible. At the Duncan Grove, which consists of a 4-acre planting of olives, the single release of only 350 *C. utilis* was made in the early fall of 1957. Although this grove had been considered to be under satisfactory control by *A. maculicornis* during most years since biological control was initiated in 1953, it was not until *C. utilis* became well established throughout the grove that a very high level of consistently effective control was achieved. In 1960 the level of fruit marking, the final criterion of successful control, was brought below 1 per cent for the first time. Since that time, as a result of continuing action by both *A. maculicornis* and *C. utilis,* the amount of scale-marked fruit has remained below 1 per cent each year. This is particularly significant in view of the fact that in groves in the area where *C. utilis* is not established there was, in 1962, a phenomenal increase in scales because of a summer very favorable for their increase.

A second grove, at Madera, consists of some 40 acres, of which approximately two acres were placed under biological control with the colonization of *A. maculicornis* in 1957 and of *C. utilis* in 1958. *A. maculicornis* was unable to achieve control immediately, and in 1958 scale-marked fruit in-

[2] No such insects really exist in an exact sense.

creased to a high level. As a result of excellent survival of *A. malicornis* during the summer of 1958, however, satisfactory biological control was achieved in 1959, with fruit marking at 4.4 per cent. The remaining acreage of the grove was treated with chemicals (Volck oil) for the last time in 1960, and *A. maculicornis* and *C. utilis* have since been able to move into the remainder of the grove. To assist the natural spread, prunings from two experimentally established, high scale-density trees (containing parasites) were spread throughout the grove in March, 1961. By the spring of 1962, both parasites had become well established throughout the grove. However, because of the large acreage involved and possibly as a result of neighboring insecticidal interference, only three-fourths of the grove was under satisfactory control by 1962. But the results in the 2-acre portion, where both parasites have been established for at least five years, have been entirely satisfactory, the number of scale-marked fruits being again less than 1 per cent during the most favorable year (1962) for scale increase among the last eight years. In 1963, the entire 40-acre grove exhibited excellent control, the level of fruit marking being rated at 0.4 per cent.

In addition, a third olive grove of approximately 40 acres, located one-eighth mile south of the Madera grove just discussed, has been under observation since 1961. Parasite colonization has never been attempted in this grove. Prior to 1962 this grove was treated annually with oil to control olive scale. Although control measures were considered adequate, treatment was discontinued after a summer oil application in 1961. Even though olive scale was found to have increased considerably by early spring of 1962, the levels of *A. maculicornis* and *C. utilis* present at that time were considered entirely capable of reducing the scale density to a satisfactory level by late spring. Excellent control resulted in 1962 and again in 1963, with fruit marking below 1 per cent both years. Thus *A. maculicornis* and *C. utilis* became established in this grove by natural dispersion from the nearby Madera grove, in spite of annual oil treatments, and successfully controlled the scale during the first and second years under biological control.

It is obvious that if the two parasites can operate together in a manner giving such a high degree of control throughout the olive-growing areas of the state, this program will be a remarkable success. On the basis of the first years of observation at three groves, there is a good chance that they can. There is no doubt that such an event would be of great value also regarding the many host plants other than olive which this scale attacks. Consequently, we have greatly increased the program of insectary production and widespread colonization of *C. utilis*.

EXPANDED COLONIZATION PROGRAM

After the findings in 1961 that *Coccophagoides utilis* had become well established in the Duncan Grove at Herndon and in the Madera olive grove, it was decided to expand the colonization of this parasite. During 1961, the insectary stock of scales was increased as rapidly as possible, and parasite production was timed to coincide with the spring hatch from overwintered female scales. By late spring of 1962, parasite production had reached approximately 100,000 insects per week.

Colonizations were discontinued for the winter on November 30, 1962, and were resumed in May, 1963. By the time liberations were again discontinued on December 3, 1963, a total slightly in excess of 4,000,000 *C. utilis* had been colonized at more than 170 sites in 24 counties. The releases were concentrated in those counties where olive scale is the greatest threat to the olive industry—Tulare County receiving 1,580,000 *C. utilis* at 48 sites; Fresno County 646,000 at 16 sites; and Madera County 278,000 at 5 sites.

Other counties in which *C. utilis* was colonized during 1962 and 1963 are as follows:

County	Number colonized	Year(s)
Merced	44,000	1962
Kings	50,000	1962, 1963
Kern	88,000	1962
Glenn	166,000	1962, 1963
Butte	293,000	1962, 1963
Sutter	149,000	1962, 1963
Yuba	43,000	1962
Tehama	129,000	1962, 1963
Colusa	32,000	1962
Yolo	36,000	1962
Contra Costa	36,000	1962
San Joaquin	49,000	1962
San Bernardino	60,000	1962
San Diego	63,000	1962
Los Angeles	91,000	1962, 1963
Stanislaus	40,000	1962, 1963
Placer	43,000	1962
Orange	39,000	1962, 1963
Inyo	33,000	1963
Tuolumne	5,000	1963
Riverside	28,000	1963

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III. The olive scale, *Parlatoria oleae,* was first found in California in 1934 and has since become a major pest. Attempts to control this insect by biological means began with the introduction of the external parasite, *Aphytis maculicornis,* from Iran in 1952. Inconsistent control by *A. maculicornis* led to the introduction of two additional parasites from Pakistan in 1957. One of these, *Coccophagoides utilis,* became established in California.

Coccophagoides utilis is an internal parasite which attacks both scale generations which *P. oleae* produces each year. Adult female *C. utilis* which have been mated deposit female eggs only. Unmated females deposit male eggs only. Field results show *C. utilis* capable of destroying up to 50 per cent of each host generation. The two species of parasites working together have exhibited the ability to give excellent control of olive scale.

IV. The competitive population interactions between *Aphytis maculicornis* and *Coccophagoides utilis* were analyzed in order to determine their roles in controlling olive scale, *Parlatoria oleae,* in California olive groves. There is strong evidence that the two parasites working together give better control of olive scale than does *A. maculicornis* working alone. Conclusions are based on observations of parasite populations at selected groves over a period of five years.

K-values for various factors affecting olive scale mortality were developed in order to measure and assess the controlling effects of these two parasites on olive scale from generation to generation.

V. In 1961 the large-scale production of the aphelinid parasite *Coccophagoides utilis* was initiated. During the seasons of 1962 and 1963, over four million were made available for release against the olive scale, *Parlatoria oleae,* in colonization sites throughout California.

The factors involved in the production of *P. oleae* and *C. utilis* are briefly discussed and the methods and equipment used in the insectary are described and illustrated.

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