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

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.

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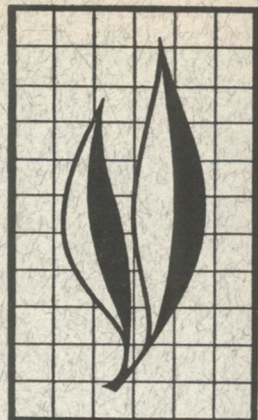
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IV. Biological Control of *Parlatoria oleae* (Colvée) Through the Compensatory Action of Two Introduced Parasites[1,2]

INTRODUCTION AND BIOLOGICAL BACKGROUND

IN 1951, as a result of initiation of a biological control program by the late Professor H. S. Smith and the collecting of foreign parasites by Dean A. M. Boyce, the Division of Biological Control at Albany imported an important parasite of olive scale, *Parlatoria oleae* (Colvée). This parasite, *Aphytis maculicornis* (Masi), became a potent control agent of this serious pest in the Central Valley of California. Almost immediately after the introduction of the parasite, marked declines in the high densities of the pest occurred (Doutt, 1954).

Huffaker, Kennett, and Finney (1962) appraised the results, ecologically and economically. These results and additional data permit the following résumé of this parasite's role.

Aphytis maculicornis is an ectoparasitic aphelinid that has a short life cycle (20 to 30 days) under summer conditions. The adults are intolerant of the hot, dry summers of the Central Valley. Due to its short life cycle, the parasite does not exist in the more resistant, immature stages long enough for it to escape the most severe summer weather conditions.

This parasite, however, has a good searching efficiency even when host densities are low or when many of the scales are concealed beneath several layers of old scale coverings. Parasitization levels as high as 90 per cent in low host densities are common. The parasite also has a high intrinsic power of increase. Under field conditions it normally produces about five fully effective generations during the warm fall and spring months. The increase in numbers is sometimes great in the fall, but this increase often starts from such low levels that an appreciable density of parasites may not be attained until April or May of the following spring. However, there is usually a steeply rising sigmoid increase in the *percentage* of parasitization from mid-March to mid-May (fig. 1). During the summer months the generation time is less, but the adult parasites die so quickly that very few eggs are deposited. Consequently, no effective multiplication of the parasite occurs during the summer; instead, a sharp decimation in parasite numbers takes place from early or mid-June until late August or September.

In certain favorable locations, *A. maculicornis* alone has given good control. This has been the case in groves where summer parasitization by this insect remains as high as 2 to 5 per cent
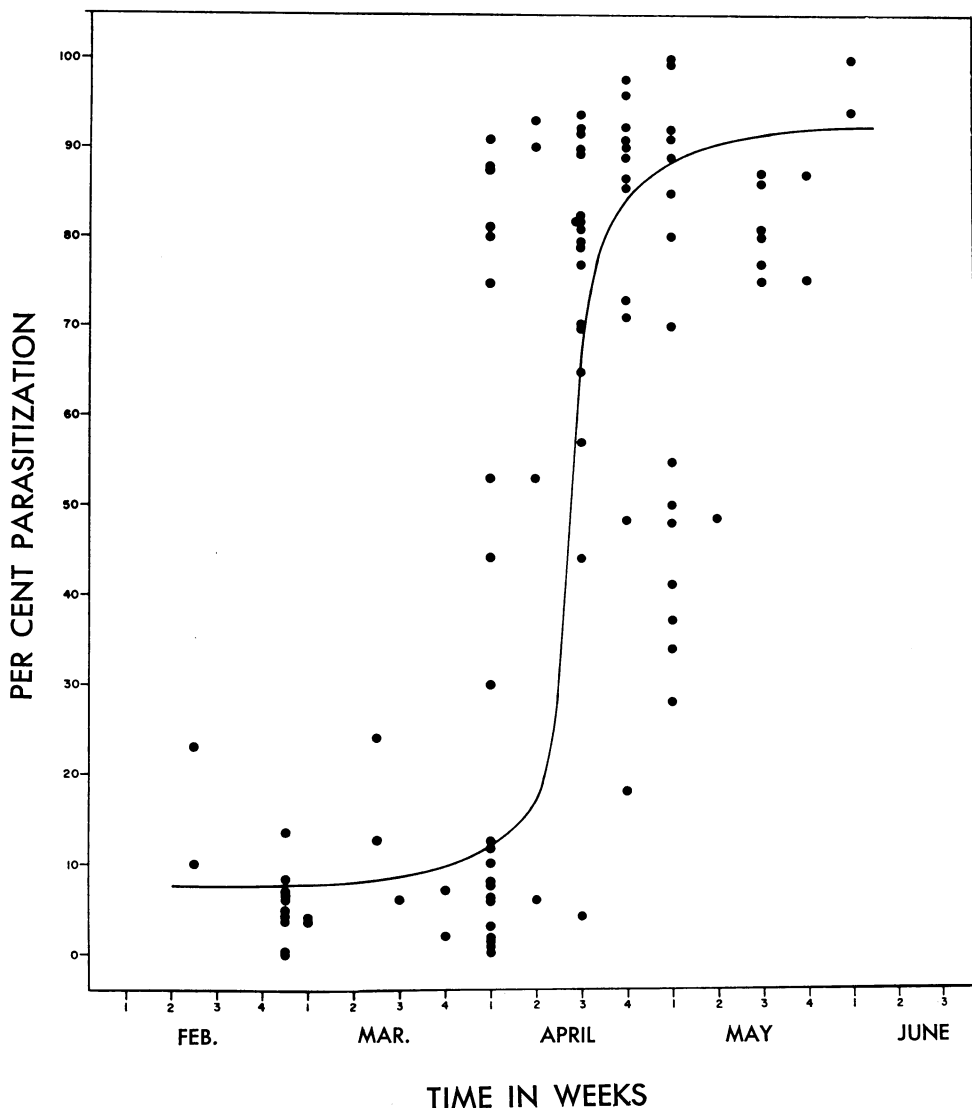
Fig. 1. Parasitization levels achieved by *A. maculicornis* on *P. oleae* at many locations in the Central Valley of California—data accumulated over 12 years: 1953–1964.

and where regular yearly or every-other-year cleanup pruning, good fertilization, and irrigation have been practiced, producing vigorous leader growth and the bearing of fruits far distant from parent scales on the older wood. However, in general, full commercial control has not been achieved with this parasite and the results of using it have been too unreliable for general acceptance. Reasons for the limita-tions in its performance include the concentration of scales on the fruits even under a good level of ecological control, disturbances from drift of insecticides, the decimation of the parasite due to unavailability of hosts in a suitable stage for attack in early summer, and, most important, the severe effect of hot, dry summers on the parasite. Because of these limitations and also because many growers have not

tried biological control, parathion is still used in most groves to control the olive scale, *Parlatoria oleae.*

The performance by *A. maculicornis,* used alone, also varies with location, and seasonal and cultural conditions. Hot, dry summers have a more severe effect on *A. maculicornis* than on *P. oleae,* although the latter, too, is adversely affected. The degree of weather stress on the scale population determines in part the rate of its increase during the summer period of negligible pressure from *A. maculicornis;* and the degree of weather stress on the parasite population, in addition to rendering the parasite ineffective during the summer, determines its capacity to build back its numbers sufficiently early to curtail scale egg deposition by early May.

During a summer of less extreme heat, or of higher humidity, more scales of the spring generation survive. Also, more parasites survive, but the resulting increase of scales is such that their progeny cause an increase in the amount of scaly fruits that same year. On the other hand, the advantage of a less severe summer to *A. maculicornis* does not show up in lower levels of scaly fruits until the following year.

Nevertheless, the powerful action of this parasite has been demonstrated all over California, and in many ways. The success of *A. maculicornis* in removing *Parlatoria oleae* as a major pest of many ornamental shrubs and park and dooryard fruit and shade trees is established. Also, when DDT was used as a check method of analysis, scale densities in olive groves increased 100 to 900 times the densities at which the scale was held by *A. maculicornis* in groves not treated with DDT—this during a period of only two years, or four host generations. Thus, prior to the establishment of a second important parasite, the assignment to *A. maculicornis* of the key role in control of this pest within the existing meteorological environment, was reinforced by results from *A. maculicornis*-free trees growing

side by side with *A. maculicornis*-present trees in six different groves.

We are now doubly fortunate that the recently established parasite *Coccophagoides utilis* Doutt (Doutt, 1966), with its powerful additive value, makes sole reliance on *Aphytis maculicornis* unnecessary. This recently established species is also an aphelinid, one that has a complex life cycle, the females developing only as primary endoparasites of *Parlatoria oleae* and the males developing only as secondaries, ectoparasitically on their own females. The detailed biology of this parasite has been studied in the laboratory by Broodryk and Doutt (1966) and in the field by Kennett, Huffaker, and Finney (1966); results of these studies are published as companion papers to this one.

Here we detail only enough of the biology of *Coccophagoides utilis* Doutt to illustrate the ecological role of this species. Our present concern is an analysis of the competitive population interactions between *A. maculicornis* and *C. utilis* and their roles in control of olive scale.

It had been apparent that an additional parasite was needed, one more tolerant of summer conditions, which would effectively fill an almost unoccupied niche by utilizing scales of the spring generation. Fortunately, Dr. Paul DeBach sent us an ample supply of *C. utilis* Doutt from Pakistan in 1957 (see also, Doutt, 1966). This parasite has proved to have the necessary attributes. Being enclosed in the scale body, and having a life cycle closely synchronized with that of *Parlatoria oleae,* it spends the hottest and driest part of the summer in the immature stages, protected from the severe weather the adult would face.

Coccophagoides utilis is also a good searcher in low host densities and readily finds scales overlapped by old scale coverings. Up to now its usual parasitization has been about 50 to 60 per cent of the available hosts, but these levels have been achieved at host densities

lower than those existing when *A. maculicornis* alone was present.

Operating with *C. utilis, A. maculicornis* still maintains its high level of efficiency during the spring period. Until *C. utilis* reaches a stage of development causing mummification of the host, *A. maculicornis* does not distinguish, but afterwards it does. When both parasites attack the same host, *A. maculicornis* wins. *A. maculicornis* also has six to eight full or partial generations per year, while *C. utilis* has only two basic generations and two additional partial generations. *C. utilis* accepts very small hosts, while *A. maculicornis* does not. *C. utilis* thus gets the first chance at the host, a security factor in its favor which helps equalize the advantage of *A. maculicornis'* higher intrinsic power of increase.

In regard to the potential of *C. utilis,* other things being equal, it would seem that unless the spring period were more favorable to *A. maculicornis* than to such a summer-tolerant species, *C. utilis* would supplant *A. maculicornis,* since *C. utilis* would be present competitively in much greater numbers each fall. The data reveal, however, that other things work in favor of *A. maculicornis'* rebound and dominance on the fall generation of scales (during *A. maculicornis'* spring period of activity), and that *C. utilis* achieves dominance only on the spring generation of scales (during the summer period of activity of both parasites).

(In all discussions of parasite performance, references to the spring generation of the host and to the spring activity of the parasites should be kept clearly in mind. The fall-produced generation of female hosts overwinters in the third stage for the most part. These females may be parasitized in the fall, winter, or spring, up to and including early June. The spring parasitization referred to is on these fall-produced females. On the other hand, the summer parasitization activity is on the spring-produced generation of scales, the females being parasitized to a maximum usually in August.)

Data at two locations over eight- and nine-year periods show that control of *Parlatoria oleae* since establishment of *C. utilis* is superior to that achieved when only *A. maculicornis* was present. Results during 1963, 1964 and 1965, involving some 30 or more additional comparative locations, reveal that where *C. utilis* is also becoming established the same improved control is indicated.

Parasitization records show that in the spring the "indispensable" parasitism by *A. maculicornis* is high and the species dominant. By "indispensable" parasitism we mean that portion of the parasitism which, if it were lacking, would not be replaced by some other cause of death. By "dispensable" parasitism we mean the portion of the parasitism which, if lacking, would be replaced anyway by some other cause of death. Indispensable parasitism implies a corresponding decrease in total host mortality if the parasite were absent; dispensable parasitism implies that no decrease in total host mortality would occur if the parasite were absent. However, a parasite's action usually is not entirely dispensable or indispensable.

While the indispensable fraction of the parasitism by *A. maculicornis* in the spring is high, the indispensable parasitism by *C. utilis* at that season is low, a large portion of the parasitism by this species being dispensable and causing deaths *A. maculicornis* would have caused if *C. utilis* had not been present. On the other hand, during the summer period much of the parasitism by both species is indispensable, but the component furnished by *C. utilis* is overwhelmingly dominant.

Moreover, during years that are less favorable to *A. maculicornis,* the supplementing and meaningful impact of *C. utilis,* even on the fall generation of scales (during the spring period of activity) is very important and acts as a

strong reliability factor, as, of course, the summer activity of *C. utilis* always does act. Estimates of total-generation parasitism or of time-point parasitism by both species at peak activity support these conclusions. "Total-generation" parasitism is the percentage of the initial host generation that has been parasitized by the time the generation ends. "Time-point" parasitization is the percentage of parasitization of the host generation evidenced by a single current sample (i.e., at a point in time). Thus, hosts of the same generation which died of other causes, or from previous parasitization by already emerged parasites, are not included in the population basis for determining the percentage of time-point parasitization. (The evidence is by that time missing.)

Using the parasitism by *A. maculicornis* on *C. utilis*-free hosts, we were able to estimate the searching performance of *A. maculicornis* and to determine its potential for destroying the hosts parasitized by *C. utilis* if the latter had not been present. We also used such data to estimate the dispensable and indispensable fractions of the full parasitism (total recorded parasitism) by *C. utilis* (e.g., table 1, p. 288). The full or total parasitism by *C. utilis* was, in turn, used to estimate the dispensable and indispensabe parasitism by *A. maculicornis*. It is significant that the method is supported by contrasting two groups in 10 locations each: (1) where *C. utilis* is now effective; and (2) where it is ineffective, that is, still rare or not established. During the spring period, *A. maculicornis* performed consistently about as well, or slightly better, on all the hosts in the groves where there were no *C. utilis* (at 82.6 per cent) as it did on the *C. utilis*-free hosts only, in groves where the latter species was effective (at 80.9 per cent). The combined net parasitism of hosts by the two species was 83.6 per cent in the former case, and 88.2 per cent in the latter (table 2, p. 293). By "combined net parasitization" we mean the percentage

of all hosts killed by the two species. Some are killed by one species alone, some by the other; still others are parasitized by both species. In the record of its full or total parasitization, each species is credited with parasitizing such a host; but in the combined net parasitization (mortality) of hosts, the double parasitization is counted as only one host killed. Also, correlation graphs reveal that, in the spring, neither the total parasitism by *A. maculicornis* nor by *C. utilis* is correlated, or is only very slightly correlated, with the combined net parasitization of hosts, whereas the percentage of parasitism by *A. maculicornis* on *C. utilis*-free hosts *is* strongly correlated with the combined net parasitization of hosts. Also, the total parasitism by *C. utilis* is correlated with the indispensable fraction, or control portion, of this species' parasitism. The detailed data reveal the overlapping and mutually compensatory action of the two parasites (see pp. 295–99).

Last and most significant, tests using patterns of DDT applied as a check-method for interfering (1) more with *A. maculicornis;* (2) more with *C. utilis;* and (3) with both species; compared to (4) plots where both species were left undisturbed, support the general conclusions that *A. maculicornis* is the superior single parasite; that *C. utilis* alone would not be as effective, but that it adds a much needed element of reliability; and that the two parasites combined maintain a higher degree of control.

In table 1 we see the contrast in performance of the two parasites during the critical months of each host generation. The parasitization of the fall generation of scales is shown at two periods: in November and December, prior to the winter period, when activity nearly ceases; and again in March and April, when activity by *A. maculicornis* is much intensified but that by *C. utilis* is largely a simple holdover of the parasitization status achieved during the fall months.

TABLE 1

TIME-POINT PARASITIZATION* OF *PARLATORIA OLEAE* BY *APHYTIS MACULICORNIS* AND *COCCOPHAGOIDES UTILIS* DURING CRITICAL MONTHS OF EACH HOST GENERATION

(Duncan Grove, Herndon, California)

Host generation and dates of testing	Female hosts†	Hosts parasitized by *A. maculicornis*					Hosts parasitized by *C. utilis*			Combined net parasitization of hosts by the two species‖
		Total	C. *utilis*-free hosts	C. *utilis*-parasitized hosts	Dispensable amount‡	Indispensable amount‡,§	Total	Dispensable amount‡	Indispensable amount‡	
	no.	*per cent*						*per cent*		
Fall generation:										
1962 November..........	301	36.2	42.9	25.0	9.3	26.9	37.2	16.0	21.2	64.1
December..........	291	32.3	39.2	16.1	4.5	27.8	29.9	11.4	18.5	57.7
1963 March..........	242	23.9	30.0	15.2	6.2	17.7	40.9	12.3	28.6	58.6
April..........	168	46.4	66.1	7.1	2.3	44.1	33.3	22.0	11.3	77.4
1963 November..........	300	21.3	21.3	21.4	7.3	14.0	34.3	7.3	27.0	48.3
December..........	297	22.9	29.3	11.9	4.4	18.5	37.1	10.8	26.3	55.6
1964 March..........	221	12.7	17.4	0.0	0.0	12.7	27.1	4.7	22.4	39.8
April..........	201	53.2	82.3	6.5	2.5	50.7	38.3	31.6	6.7	89.0
Spring generation:										
1962 July..........	432	3.9	4.9	2.0¶	0.7	3.2	35.0	1.7	33.3	38.2
August..........	277	2.9	8.5	0.0¶	0.0	2.9	66.1	5.6	60.5	69.0
1963 July..........	217	2.8	2.9	2.3	0.5	2.3	19.4	0.6	18.8	21.7
August..........	165	4.2	8.9	0.0	0.0	4.2	52.1	4.7	47.4	56.3

* Percentage of parasitization evidenced by a single current sample. (For details, see p. 287.)
† In 1963, no special selectiveness was needed to obtain twigs with enough scales; in 1964 selection was intensified.
‡ Dispensable and indispensable parasitization or parasitism are defined on p. 286.
§ In this case we have given *C. utilis* credit for all hosts also attacked by *A. maculicornis*.
‖ Combined net parasitization is defined on p. 287.
¶ Estimated.

The performance of *A. maculicornis* during the fall and spring months with respect to its possible rejection of hosts already parasitized by *C. utilis* is of importance in the analysis of the results. When the immature *C. utilis* has progressed in its development to the point of turning the host's body material to a milky stage, ovipositing *A. maculicornis* females reject the host (Broodryk and Doutt 1966).

For example, taking a preliminary look at the data of table 1, in November of 1962, *C. utilis* evidently had developed sufficiently for some of the hosts it parasitized to be unacceptable at that early period to *A. maculicornis,* for the latter had parasitized 42.9 per cent of the *C. utilis*-free hosts and only 25.0 per cent of the *C. utilis*-parasitized hosts in the samples. By December the contrast was greater: 39.2 per cent and 16.1 per cent, respectively. No substantial change from this status occurred until late February or early March. At that time, overwintering *A. maculicornis* would have been emerging, and delayed or unsuccessful oviposition by these adults tends to reduce the percentage of parasitization by *A. maculicornis.* The result of this emergence is seen in the April sample, when *A. maculicornis* parasitization on *C. utilis*-free hosts increased greatly. This new parasitization also shows the sharp rejection by ovipositing *A. maculicornis* of the now largely-mummified hosts previously parasitized by *C. utilis.*

At the time of the sampling in November, 1963 (table 1), few *C. utilis* had developed sufficiently to render the hosts they had parasitized unacceptable to *A. maculicornis.* The data for November show that *C. utilis*-parasitized and *C. utilis*-free hosts were attacked equally at 21.3 per cent and 21.4 per cent by the ovipositing *A. maculicornis* females. By December, however, the increase in *A. maculicornis* activity had caused an increase in the parasitization level on *C. utilis*-free hosts. This more than made up for the emergence of adult *A. maculicornis,* which latter would lower the parasitization level in the December sample, because the old parasitized hosts of this generation can no longer be distinguished from those of previous generations. At the same time there was a decline in the *A. maculicornis* parasitization level of *C. utilis*-parasitized hosts, because more of these hosts had developed to the stage where *A. maculicornis* rejects them.

The usual upsurge of parasitization rate near this period, mainly on the acceptable *C. utilis*-free hosts, had occurred by the time of sampling in April, 1964—the level at that time being 82.3 per cent on *C. utilis*-free hosts. This again shows the sharp rejection of the hosts by *A. maculicornis* when the *C. utilis* in the hosts have progressed to a certain stage of development.

In regard to *C. utilis* parasitization of the spring generation of hosts during the summer period, the critical data are for August. In August, 1962, the total parasitization by *C. utilis* was 66.1 per cent, while in August, 1963, it was 52.1 per cent (table 1). Since there is very little action by either *A. maculicornis* or *C. utilis* during the development of the host at this season, the highest combined net parasitization by the two species in August is roughly the total host-generation mortality of the spring generation from parasitization.

DOMINANCE OF *Aphytis maculicornis* ON THE FALL-PRODUCED GENERATION OF SCALES

General Features of the Data

An explanation of our means of estimating the dispensable and indispensable fraction of the parasitization by each parasite as presented in tables 1, 3, 4, and 7 is essential. To do this, we compare the percentage of parasitization by *A. maculicornis,* based on the total number of hosts at the time of sampling, with the percentage of parasitization by this species based on only those hosts that were available to it— that is, those not previously parasitized and rendered unacceptable by *C. utilis.* It is reasonable to assume that the parasitization of the *C. utilis*-free hosts is a proper measure of the capacity of *A. maculicornis* for finding and parasitizing hosts during the late spring period. After biological control has become relatively effective and the density of hosts has been reduced, the ratio of searching *A. maculicornis* adults to suitable unparasitized scales in late April or early May is nearly always sufficiently high that parasitization by the population of *A. maculicornis* females would probably be very little limited by short supply of *A. maculicornis* eggs. At this time there are more *A. maculicornis* females searching than there are hosts still unparasitized. Consequently, *A. maculicornis* females would not lack eggs to parasitize the hosts rendered unacceptable to them by *C. utilis.* This searching efficiency of *A. maculicornis* is a key to (1) its potential effectiveness at control levels within the existing meteorological pattern; and (2) it shows the degree to which mortality caused by *C. utilis* in late April or early May is dispensable to the final level of host mortality.

Using the data for November, 1962 (table 1), as representing a significant time, we see that *A. maculicornis* parasitized 42.9 per cent of the *C. utilis*-free hosts. If, then, *A. maculicornis* had

been acting, alone, and disregarding here any modification due to the density-dependent aspect of the functional response, we estimate that it would have parasitized 129 of the 301 hosts (i.e., 42.9 per cent) rather than the 109 (i.e., 36.2 per cent) it actually parasitized. Since at this time the combined net mortality from the two species of parasites was only 64.1 per cent, this means that the indispensable mortality caused by *C. utilis*—mortality that would have been lacking if *A. maculicornis* were operating alone—was 21.2 per cent (64.1–42.9). Actually, however, *C. utilis* parasitized 112, or 37.2 per cent of the 301 hosts. Of the 112 hosts which *C. utilis* attacked, 28 (that is, 25.0 per cent) were also attacked by *A. maculicornis;* and on the basis of our assumption, *A. maculicornis* would have attacked 20 more than the 109 it did attack, had they not been rendered unacceptable by *C. utilis.* We are here simply attempting to appraise the additional value assignable to the new factor, *C. utilis.*

We may also look at the same data from the standpoint of considering the additional value coming from *A. maculicornis,* after giving full credit to *C. utilis*—as if the latter had been established first. Here we note, however, that appraisal of the additional value of *C. utilis* is more realistic, since *A. maculicornis* has the last opportunity to attack hosts; and, if both species attack, *A. maculicornis* wins. Since the *C. utilis* females had already deposited their eggs before the hosts reached a stage of development acceptable to *A. maculicornis,* the number of hosts actually attacked by *C. utilis* would not have been greater if *A. maculicornis* had been absent. Thus, in this sense the total *C. utilis*-caused mortality in November, 1962, and in fact up to the following spring (since *C. utilis* would not

produce a new generation till the following May) is 37.2 per cent. The indispensable mortality caused by *A. maculicornis* in November alone, then, is 26.9 per cent (64.1 – 37.2). The other comparable values are given in table 1.

Although the indispensable mortality caused by *C. utilis* in this generation is normally lower than that caused by *A. maculicornis*, it would be erroneous to play down *any* degree of indispensable mortality by the latter. Such additional mortality, as total-generation mortality moves closer to 100 per cent or to the requirement for equilibrium,[3] is vital to economic control. For example, where fecundity is 25 per female, a 92 per cent total-generation mortality will permit no population increase, whereas an 88 per cent mortality would permit a 50 per cent increase *each* generation, indefinitely. Thus, if we consider merely the fall generation of scales alone, the evidence indicates economic advantage from the introduction of *C. utilis*. This is based on the assumption that *A. maculicornis* has not been so reduced in numbers as a result of competition with *C. utilis* that its control efficiency, as represented by these data, is lessened. This question cannot be answered directly or conclusively, but so far *A. maculicornis* has continued to perform almost as well in groves where *C. utilis* is abundant as in those where *C. utilis* is absent (see table 2).

It is an interesting, although not a strictly verifiable method of appraisal, to consider data from places where only *A. maculicornis* and where both species are now quite effective. These data show that the searching efficiency of the *A. maculicornis* population is far greater than is indicated by the parasitization level if *C. utilis* is present. *Aphytis maculicornis* achieved this level of performance by late spring in the *C. utilis*-present groves, in spite of the fact that by the end of the summer their numbers are reduced by perhaps half because of the utilization of hosts by *C. utilis*. The mean level of total parasitization by *A. maculicornis* during the spring at ten locations in 1964 where *C. utilis* was effective was only 50.3 per cent, whereas it was 82.6 per cent in the groves where there were few or no *C. utilis* (table 2). This latter figure is only 1.7 points more than the *A. maculicornis* parasitization on *C. utilis*-free hosts in the groves where *C. utilis* was effective (table 2). The criterion here is that the percentage of *C. utilis*-free hosts parasitized by *A. maculicornis* was very much greater than the percentage of all the hosts, taken together, that *A. maculicornis* parasitized. *A. maculicornis* must therefore have searched sufficiently well to have found equal proportions of the *C. utilis*-parasitized hosts, but simply rejected them. This is expected only during the spring period, and, in fact, the early fall data do not exhibit this feature. All these data on parasitization during different time periods are discussed in detail in the following section.

Records of Time-Point Parasitism (Parasitism Evidenced by a Single Sample)

While estimates of net effects on generation mortality as seen in tables 4 and 6 are more meaningful, we wish to point out that data on parasitization at a single point in time are also useful, and may illustrate the sharp contrast between performance of the two parasites in regard to either the fall or the spring host generations. In fact, much can be learned about the effectiveness of these two parasites by obtaining data at a single proper time for each host generation even though, for *A. maculicornis* in particular, such a record may include only a part of the hosts of a

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[3] For an insect having equal numbers of males and females, the required mortalities for equilibrium would be 98 per cent if the fecundity is 100 live-born or eggs per female; and 92 per cent if fecundity is 25 per female. Average fecundity (no. of eggs) of olive scales is near 25, but in some situations it may be nearer 50.

TABLE 2

TIME-POINT PARASITIZATION* OF *PARLATORIA OLEAE* BY *APHYTIS MACULICORNIS* AND/OR *COCCOPHAGOIDES UTILIS* AT 10 LOCATIONS IN CALIFORNIA WHERE *C. UTILIS* IS EFFECTIVE AND AT 10 LOCATIONS WHERE IT IS NONEFFECTIVE: LATE APRIL–EARLY MAY, 1964

C. utilis-effective groves

Grove	Female hosts	Net parasitization of hosts by:			A. maculi-cornis on C. utilis-free hosts
		A. maculi-cornis	C. utilis	2 species combined†	
	no.	per cent			
Duncan	201	53.2	35.8	89.0	82.3
Sheeler	63	43.7	40.2	83.9	78.7
Greer-Lucca	50	36.0	54.0	90.0	78.3
Oberti (Martinelli)	191	60.2	29.3	89.5	85.2
Oberti (River)	101	66.3	25.7	92.0	89.3
Dambrosio	331	56.8	25.7	82.5	76.4
Kirkpatrick-Holworthy	38	28.9	55.3	84.2	64.7
Kennedy	120	41.7	52.5	94.2	87.7
Bell	59	64.4	22.0	86.4	82.6
Shimaji	335	51.9	37.9	89.8	83.7
Mean		50.3	38.1	88.2	80.9

C. utilis-noneffective groves

Grove	Female hosts	Net parasitization of hosts by:			A. maculi-cornis on C. utilis-free hosts
		A. maculi-cornis	C. utilis	2 species combined†	
	no.	per cent			
Hatakeda-Yebisu	33	78.8	0.0	78.8	78.8
Paregien	115	78.3	4.3	82.6	81.8
Owensby	48	89.6	0.0	89.6	89.6
McKellar	258	82.9	0.0	82.9	82.9
Workman	80	78.8	0.0	78.8	78.8
Glenn	52	86.5	0.0	86.5	86.5
Kirkpatrick	92	84.8	5.4	90.2	89.7
Ransome	30	83.3	0.0	83.3	83.3
Bell	61	85.2	0.0	85.2	85.2
Fox-Winton	165	77.6	0.6	78.2	78.0
Mean		82.6	1.0	83.6	83.5

* Percentage of parasitization evidenced by a single current sample. Further explained on p. 287.
† Net parasitization by the two species combined is defined on p. 287.

given generation that the parasite kills. As seen in table 1 for the fall generation studied at the Duncan Grove, the total parasitization by *C. utilis* in November, 1962, was 37.2 per cent, but the meaningful, or indispensable mortality *C. utilis* caused was only 21.2 per cent. In December, the total was 29.9 per cent and the indispensable amount was 18.5 per cent; and at the end of the host generation in April, 1963, these statistics were 33.3 per cent and 11.3 per cent, respectively. The figures for the fall-generation mortality caused by *C. utilis* the following year were, respectively: total parasitization, 34.3 per cent, and the indispensable amount 27.0 per cent, in November (1963); 37.1 per cent and 26.3 per cent, respectively, in December; and 38.3 per cent and 6.7 per cent, respectively, at the end of the host generation in April (1964). Thus, the amount of indispensable parasitization by *C. utilis* becomes decidedly lower by April. It is only at that season that the compensating potential of *A. maculicornis* for destroying these same hosts is attained. It is thus seen that the percentage of indispensable mortality of the fall generation from *C. utilis* attack was, month by month, considerably less than the total percentage of observed parasitization by this species. This was especially true at the end of the generation in April. By that time, *A. maculicornis* had become so active that it would (presumably) have parasitized most of the hosts attacked by *C. utilis* if the latter had not been present.

Still considering the fall generation, we see that the indispensable mortality caused by *A. maculicornis*, month by month (table 1), was somewhat more nearly equivalent to the observed total parasitization by this species. This was especially true by the end of the host generation in April, the figures at that time being 46.4 per cent total parasitization by *A. maculicornis* and 44.1 per cent indispensable parasitization, in April, 1963; and 53.2 per cent and 50.7

per cent, respectively, in April, 1964. (See also table 4 and pp. 307 and 308.)

Note that in table 1 the total parasitization by *C. utilis*, plus the indispensable parasitization by *A. maculicornis*, gives the observed combined net parasitization. The maximal potential parasitization (that on *C. utilis*-free hosts) by *A. maculicornis*, plus the indispensable parasitization by *C. utilis*, also gives the combined net parasitization.

In table 3 we present data that show the progress of *C. utilis* in 12 groves that formerly had only *A. maculicornis*. In most of these locations, and in parts of others, *C. utilis* was not colonized in large numbers until 1962. Exceptions were the Duncan Grove and part of the Oberti-H Grove. As may be seen from the data, in the Duncan Grove there was no substantial difference between the total parasitization by *C. utilis* for 1963 and for 1964. However, because of lower *A. maculicornis* activity in 1963, the indispensable activity of *C. utilis* was substantially higher in 1964.

At all the other locations, there was a marked increase in the total parasitization by *C. utilis* in 1964; and the indispensable component by *C. utilis*, on the average, increased also. This was because the mean potential or compensating parasitization by *A. maculicornis* (judged by *A. maculicornis* parasitization of *C. utilis*-free hosts) was lower in 1964 than in 1963. As suggested on page 294, this may well be due to an overall competitive pressure from *C. utilis*, this slightly reducing *A. maculicornis'* searching performance as a population.

In the 12 groves where samples were taken in 1963 and 1964, the mean combined net parasitization of the two species did not increase as much in 1964 as did the indispensable component contributed by *C. utilis*. This was because the *A. maculicornis* contribution in 1964 was lower. The actual increase in combined net parasitization was only 3.3 per cent, *i.e.*, from 84.0 per cent in 1963 to 87.3 per cent in 1964 (table 3).

TABLE 3

TIME-POINT PARASITIZATION* BY APHYTIS MACULICORNIS AND COCCOPHAGOIDES UTILIS ON PARLATORIA OLEAE AT 12 LOCATIONS IN THE SAN JOAQUIN VALLEY, SHOWING THE PROGRESS OF C. UTILIS: APRIL–MAY, 1963–1964†

Grove	Parasitization, 1963							Parasitization, 1964						
	Mature female scales	A. maculicornis		C. utilis			Combined net	Mature female scales	A. maculicornis		C. utilis			Combined net
		Total	On C. utilis-free hosts*‡	Total	Dispensable	Indispensable			Total	On C. utilis-free hosts*‡	Total	Dispensable	Indispensable	
	no.	per cent	per cent	per cent	per cent	per cent	per cent	no.	per cent	per cent	per cent	per cent	per cent	per cent
Duncan........	168	44.1	66.1	33.3	22.0	11.3	77.4	201	53.2	82.3	35.8	6.7	29.1	89.0
Sheeler........	231	76.2	78.6	3.0	2.4	0.6	79.2	63	47.6	76.9	38.1	29.3	8.8	85.7
Greer........	70	57.1	64.5	11.4	7.4	4.0	68.5	15	33.3	71.4	53.3	38.1	15.2	86.6
Oberti (H.)........	185	80.0	83.1	3.8	3.1	0.7	83.8	164	64.0	85.4	25.0	21.4	3.6	89.0
Oberti (R.)........	119	90.7	90.7	0.0	....	....	90.7	101	66.3	89.3	25.7	23.0	2.7	92.0
Lucca........	83	62.7	74.3	15.6	11.6	4.0	78.3	35	37.1	81.3	54.3	44.2	10.1	91.4
Dambrosio........	67	53.8	63.2	14.9	9.4	5.5	68.7	331	56.8	76.4	25.7	19.6	6.1	82.5
Kirkpatrick........	217	87.5	93.1	6.0	5.6	0.4	93.5	23	30.4	77.8	60.9	47.4	13.5	91.3
Holworthy........	247	97.2	98.0	0.8	0.8	0.0	98.0	15	26.7	50.0	46.7	23.3	23.4	73.4
Kennedy........	258	82.9	93.4	11.3	10.5	0.8	94.2	120	41.7	87.7	52.5	46.0	6.5	94.2
Hills Valley........	300	80.0§	83.3§	4.0§	3.3§	0.7§	84.0§	30	60.0	78.3	23.3	18.2	5.1	83.3
Clovis........	70	91.4	91.4	0.0	....	....	91.4	29	68.9	86.9	20.6	17.9	2.7	89.6
Mean........	....	75.3	81.6	8.7	6.3	2.3	84.0	....	48.8	78.6	38.5	27.9	10.6	87.3

* Time-point parasitization refers to the percentage of currently available hosts on which parasites were present at time of observation.
† At most of these locations and in parts of the others, C. utilis was just released in substantial numbers in 1962. Note that numbers of scales do not indicate densities—selective sampling.
‡ This percentage is also the portion of total C. utilis parasitization that is dispensable; and 100 less this amount gives the portion that is indispensable.
§ Estimated.

The mean levels for these 12 groves show that the total parasitization by *A. maculicornis* fell from 75.3 per cent in 1963 to only 48.8 per cent in 1964, while the total parasitization by *C. utilis* increased from a low 8.7 per cent in 1963 to 38.5 per cent in 1964. Yet, because of the still high performance of *A. maculicornis* on *C. utilis*-free hosts in 1964, 78.6 per cent of this 38.5 per cent was dispensable, involving 27.9 per cent of the total number of hosts.

It is difficult to precisely compare the mean total parasitization by *C. utilis* with that by *A. maculicornis* in these 12 groves in 1964 (table 3) beyond showing the marked contrasts with 1963. In five of the groves, parasitism by *C. utilis* exceeded that by *A. maculicornis* in 1964. From time to time such a result is to be expected, despite the fact that when both attack the same host, *A. maculicornis* wins and, in addition, it has a greater ability to find hosts in the first place than does *C. utilis*. The reason for *C. utilis'* superior performance when it occurs in such cases is due to the advantage it gains as first invader, which enables it to render many hosts unacceptable to *A. maculicornis*.

While the results from grove to grove vary, the data present a picture of the steadying role and improved natural control that *C. utilis* may exert, even on the fall generation of hosts. This role would be more pronounced under conditions more adverse to *A. maculicornis* than occurred in the experimental groves during either 1963 or 1964. The extent to which parasitization by *A. maculicornis* on *C. utilis*-free hosts, plus the total parasitization by *C. utilis* exceeds 100 per cent, is a measure of the improved reliability in having both parasites rather than just one of them. When we also consider the spring generation of hosts, this reliability aspect is vastly better. In the spring of 1964 these two statistics considerably exceeded 100 per cent in many of the groves under study (table 3).

No significant differences between the means appear when we compare the critical time-point parasitization by *A. maculicornis* on *C. utilis*-free hosts in groves where *C. utilis* is very effective with the parasitization by *A. maculicornis* in groves where *C. utilis* is as yet ineffective (table 2).

Parasitization by *A. maculicornis* on *C. utilis*-free hosts in the groves where *C. utilis* was effective was about 81 per cent, on the average; and in those groves where this species was rare or absent, it was about 83.5 per cent. The variation is in the direction which *could* signify that the competition with *C. utilis* reduced to some extent the densities of *A. maculicornis,* and did in fact slightly reduce the performance of *A. maculicornis.* However, many more data would be required to substantiate this. The main point is that when *A. maculicornis* performed almost alone in the environments, it was still able to parasitize at least the same, if not a slightly higher, percentage of the hosts available to it than it parasitized in the groves having *C. utilis* (table 2). The basic feature of the data in table 2 is that the combined net time-point parasitization of over-wintered females by the two species during the spring period of 1964, was rather uniform for all groves, whether or not *C. utilis* was effective.

The dominance of *A. maculicornis* over *C. utilis,* as to compensating ability and correlation of inherent performance with combined net parasitization by the two species (total combined effect), is revealed further by the data in figures 2 to 6, inclusive. In figure 6 the total percentage of parasitization by *C. utilis,* plotted against the combined net parasitization by the two species, revealed no suggestion of a correlation. On the other hand, in the data of figures 3 and 5, there is a good correlation between the percentage of parasitization by *A. maculicornis* on *C. utilis*-free hosts and the combined net parasitization. This is superficially surprising. One might expect that if the

total parasitization by *A. maculicornis* is not correlated with the combined net parasitization, as is seen in figure 4, then the parasitization performance by this species (*A. maculicornis*) also would be unrelated to this combined control effect. This, however, would not be a proper conclusion.

It is also probable that in spite of the lack of correlation between the parasitization by *C. utilis* and the combined net parasitization as presented by these data, (fig. 6) *C. utilis*, as well as *A. maculicornis,* has some meaningful role in the combined control effect during this spring period (see p. 308 for discussion of the role of *C. utilis* on the spring generation—summer activity). The lack of an obvious correlation may be due, in part, to the inadequacy and variability of the data. Many variables enter into the performances of the two species of parasites at different locations. Perhaps if we had enough data from each of several locations under the same orchard management and under the same climatic or weather picture, the data might exhibit stronger correlation.

However, there is a more important explanation that is clearly elucidated by these data. It concerns dispensable and indispensable parasitization. Considering many different groves, we might expect each component accounting for the combined net parasitization by the two species to be correlated with the combined effect itself. However, such a correlation would be nullified if, as happens, one of the parasites (*C. utilis*) exhibits a varying performance in different groves, and renders some hosts unacceptable to the second species (*A. maculicornis*); and if the second species has the capacity to destroy those hosts the first species attacked, if they had not in fact been previously attacked, i.e., if *C. utilis* were not even present in the grove. It is obvious from the data at hand that during the spring period *A. maculicornis* does perform in this way. It

would not be expected, however, that it would *completely* or uniformly compensate for the greater or lesser intensity of attack by *C. utilis* in the various groves. Therefore, a low degree of correlation between the attack by *C. utilis* and the combined net parasitization would remain after removal of the contribution due to the dominant *A. maculicornis.* We would expect, then, what the data show—that the percentage of parasitization by *A. maculicornis* on *C. utilis*-free hosts in the spring is somewhat less than the percentage of combined net parasitization by the two species on all hosts; and that the combined net parasitization where both species are markedly active, is far greater than the total parasitization by either species (table 2). The extent to which the percentage of parasitization by *A. maculicornis* on *C. utilis*-free hosts exceeds the percentage of total parasitization by *A. maculicornis* is a measure of the capacity of *A. maculicornis* to compensate for the variability of performance by *C. utilis.* Likewise, the extent to which the combined net parasitization exceeds the parasitization by *A. maculicornis* on *C. utilis*-free hosts is a measure of the indispensable or meaningful parasitization by *C. utilis.*

Considering in detail the spring, 1963, results at 12 locations, the total parasitization by *A. maculicornis* (fig. 2) was fairly well correlated with the combined net parasitization of the two species, as it must be where nearly all the parasitization is by that species alone (table 3, 1963 results). In 1963 the mean total parasitization by *C. utilis* was only 8.7 per cent, and the range was from 0.8 per cent to 15.6 per cent, for those places were *C. utilis* occurred. Hence *C. utilis* parasitization in 1963 could only have lessened somewhat the perfect correlation between the total performance of *A. maculicornis* and the combined net parasitization of the two species. On the other hand, *C. utilis* parasitization completely

negated or obscured the correlation between the total parasitization by *A. maculicornis* and the combined net parasitization of the two species in 10 locations in the spring of 1964 (fig. 4).

An important point in these graphs is the departure of trend lines from 100 per cent hypothetical correlation as the percentage of parasitization by the species plotted on the abscissa decreases from 100 per cent. This departure is, of course, a measure of the action of the *other* species. In figure 2, this departure encompasses both a simple disturbing or obscuring effect and a portion representing its indispensable contribution to combined net parasitization. In figure 3 the departure of the trend line from the 100 per cent correlation line is entirely associated with the indispensable parasitism by *C. utilis*, which in 1963 was low at each of the 12 locations plotted, *C. utilis* having been only recently established there.

Taking now the more meaningful data of 1964, we are able to show more clearly that in situations where more than one species is effective, plotting the percentage of total parasitization by a given species does not depict a meaningful performance in natural control. We also can illustrate that plotting parasitization expressed in other ways—in this case parasitization by *A. maculicornis* on *C. utilis*-free hosts—does depict a meaningful performance, despite great variations in conditions, and despite the fact that there was only a narrow range of variation in combined net parasitization from location to location (see fig. 5). This procedure is also sound from the standpoint of the comparative biologies of the two species.

The results for 1964 in *C. utilis*-effective groves indicate a strong compensatory ability in both parasites. Each species varied from grove to grove in the percentages of its parasitization of all the hosts, the variation extending from 36.0 per cent to 66.3 per cent for *A. maculicornis*, and from 22.0 per cent to

55.3 per cent for *C. utilis* (table 2). The combined net time-point parasitization approached 90 per cent, and the total net parasitization of the whole female generation reaching the third stage was probably near 94 per cent to 96 per cent. Figures 4 and 6, showing results for the spring of 1964, depict the absence of correlation between the total parasitization by *A. maculicornis* or by *C. utilis*, respectively, and the combined net parasitization. Yet, when the performance of *A. maculicornis* on *C. utilis*-free hosts is plotted instead, as in fig. 5 (also representing 1964 results), a fair correlation is seen. Here the indicated trend line departs noticeably from the 100 per cent correlation line, and this departure is a measure of the indispensable parasitism by *C. utilis*; thus, the latter's influence, too, is shown. Since, during the spring of 1964, *A. maculicornis* performed so very efficiently almost everywhere, compared with its usually somewhat lesser efficiency (Huffaker, Kennett, and Finney, 1962), all the points fall in the upper right-hand corner of the graph. After the return of more normal weather patterns, we may obtain data extending this pattern into portions of the graph representing a lower efficiency on the part of *A. maculicornis*. In such an event, it is obvious that the importance of the parasitism by *C. utilis* and its correlation with the combined net parasitization would be greater. Hence, the outlook for *C. utilis'* role, even in regard to the fall-produced generation of scales, is even brighter than the data in figure 5 indicate. (See also section describing the role of *C. utilis* in parasitizing the spring generation of hosts, p. 308.)

We may also graphically illustrate the meaningful role of *C. utilis* in parasitizing this same fall generation of scales (spring period of activity) by plotting the data so as to depict the correlation between the total amount of *C. utilis* parasitization and that portion of the total paratization of the matur-
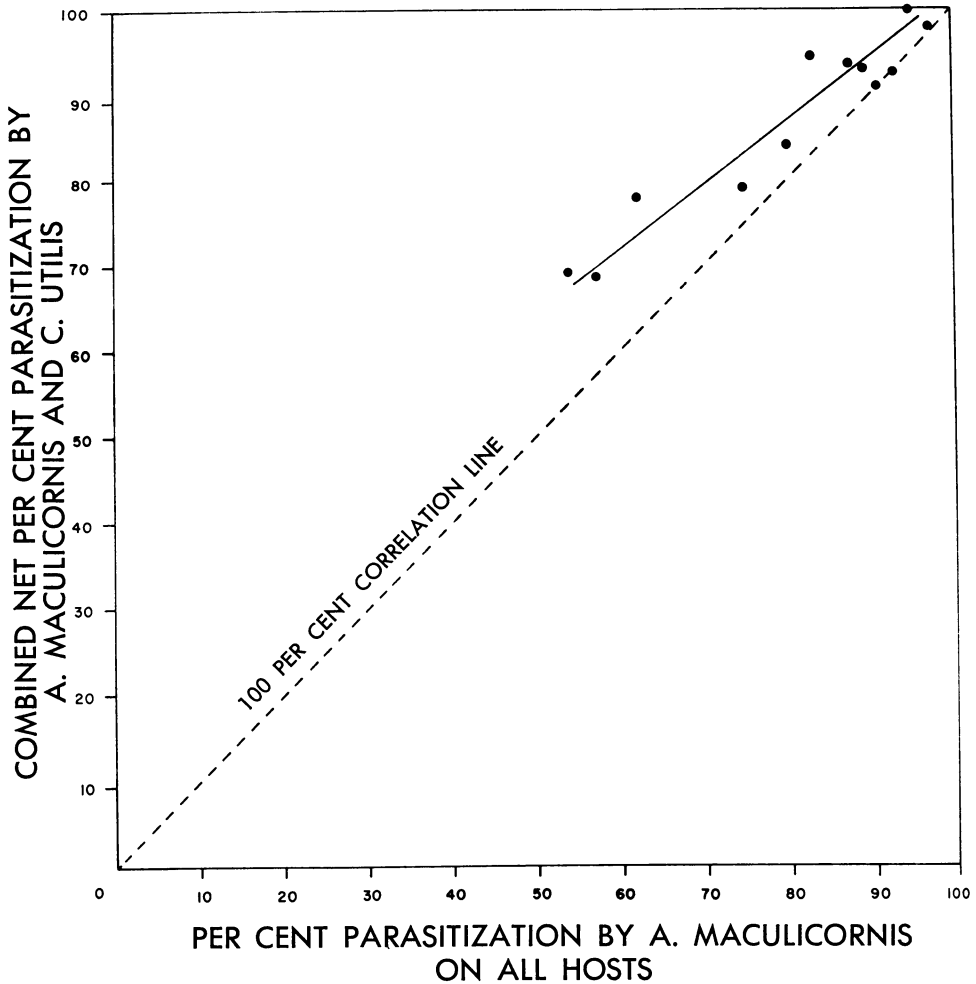
Fig. 2. Correlation between total parasitization by *A. maculicornis* and combined net parasitization by this species and by *C. utilis* on *P. oleae* at 12 locations—spring, 1963.

ing brood which was indispensably parasitized by *C. utilis*. Figure 7 shows this relationship. There is obviously fairly good correlation here, but there is so much spread between the points that the indicated trend line is rather indefinite, and the range is shown by shading. The wasted or dispensable component of the total parasitization by *C. utilis* (hosts which would have been parasitized by *A. maculicornis* anyway) would inherently account for some of this spread. Since *A. maculicornis* can parasitize over *C. utilis*, and not the reverse, we cannot assume a corresponding potential parasitization of *A. maculicornis*-attacked hosts by *C. utilis* (as if *A. maculicornis* were not present).

However, one aspect tending to lower the indicated performance by *C. utilis* needs to be mentioned. The presently discussed data are based on time-point parasitization. By April, 1964, when the data were taken, a substantial number of the hosts previously attacked by *C. utilis* would also have been attacked by *A. maculicornis*, the adult *A. maculicornis* would have emerged, and no evidence would be left as to the exis-
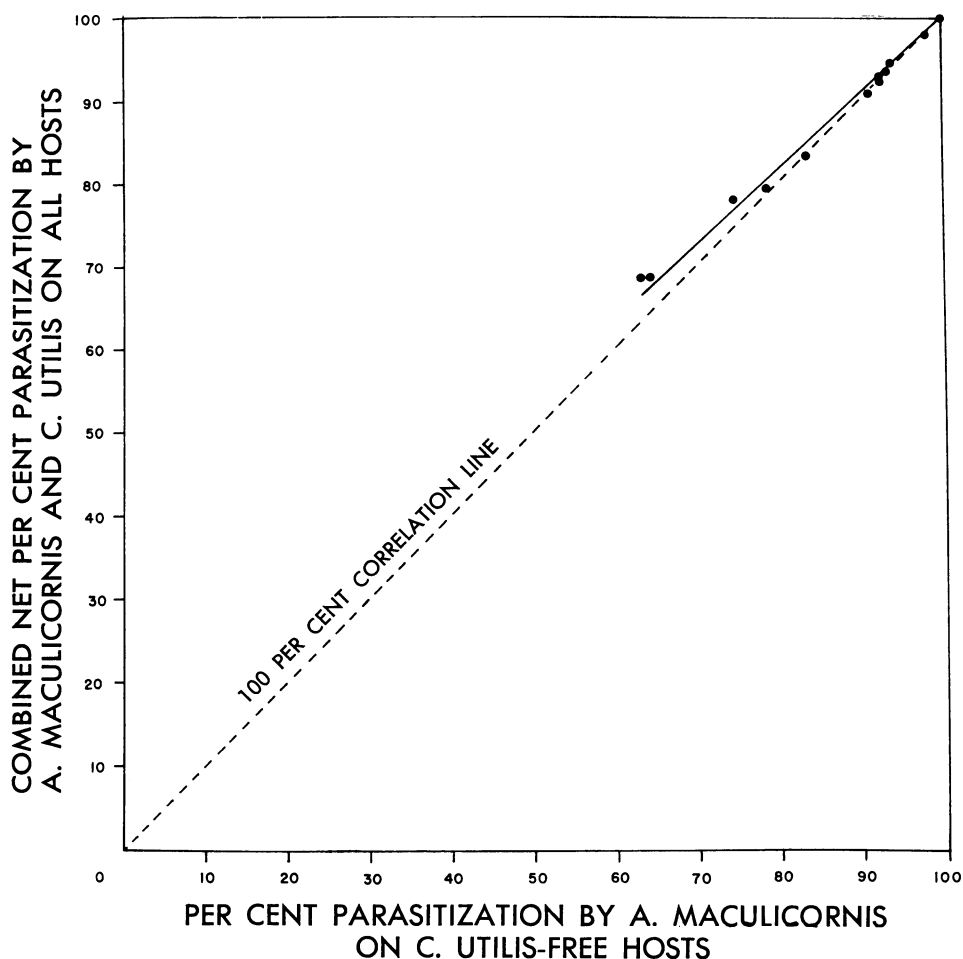
Fig. 3. Correlation between parasitization by *A. maculicornis* on *C. utilis*-free hosts, and combined net parasitization by this species and by *C. utilis* on *P. oleae* at 12 locations—spring, 1963.

tence of these hosts *or* the previous attacks by either the *C. utilis* or *A. maculicornis*. (*A. maculicornis* would have destroyed the hosts and the *C. utilis* therein.) Records of this previous period of dynamics on the same host generation are lacking in these data. Also, in some examples of multiple parasitism by the two species, the *A. maculicornis* would still be recognizable at the time of the sampling, while *C. utilis* would not be.

Estimates of Total-Generation Parasitism

As a means of more realistically appraising total-generation mortality due to parasitism, we used some rather arbitrary rule-of-thumb treatments of the monthly data and estimated accumulated mortalities. Taking 300 hosts, an appropriate sample size for the data concerned, as the beginning fall female-host population, we made rough but very conservative estimates of the mortality caused by *A. maculicornis* at the Duncan Grove at various times. Certainly, all individual hosts parasitized by *A. maculicornis* in October, November, December, January, and February would no longer appear in the parasitization data for April, nor would those
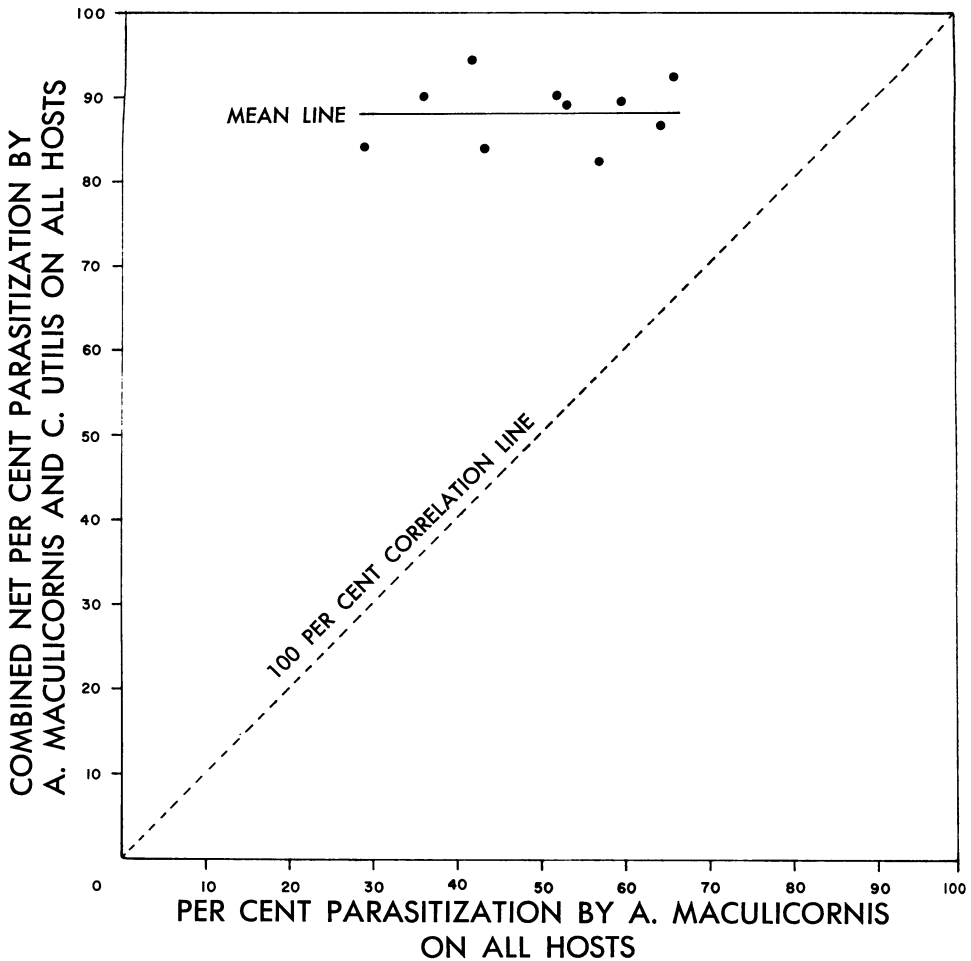
Fig. 4. Absence of correlation between parasitization by *A. maculicornis* and combined net parasitization by this species and *C. utilis* on *P. oleae* at 10 locations—spring, 1964.

parasitized during the first half of March, normally. The data for parasitization for consecutive months are based on the immature parasites that simply had not matured and emerged at the particular time. Some may be present for one sample date only; others for two or more sample dates. Therefore, we cannot assume that the records for each month represent entirely new or distinct parasitizations for use in estimating accumulated total-generation parasitization.

Instead, we used extensive independent records indicating the general rate of development of *A. maculicornis*

under field conditions, its retarded development in winter, and its general emergence in early spring, as a means of estimating the amount of host mortality that we can assume to have already occurred prior to the April sampling. Thus, we used all the parasitization by *A. maculicornis* in October and half that in November to represent one distinct element of mortality, and, again, all the parasitization in February and half of that in March as still additional generation mortality occurring prior to and distinct from the time-point parasitization record of the April sampling (see table 4, column 2).
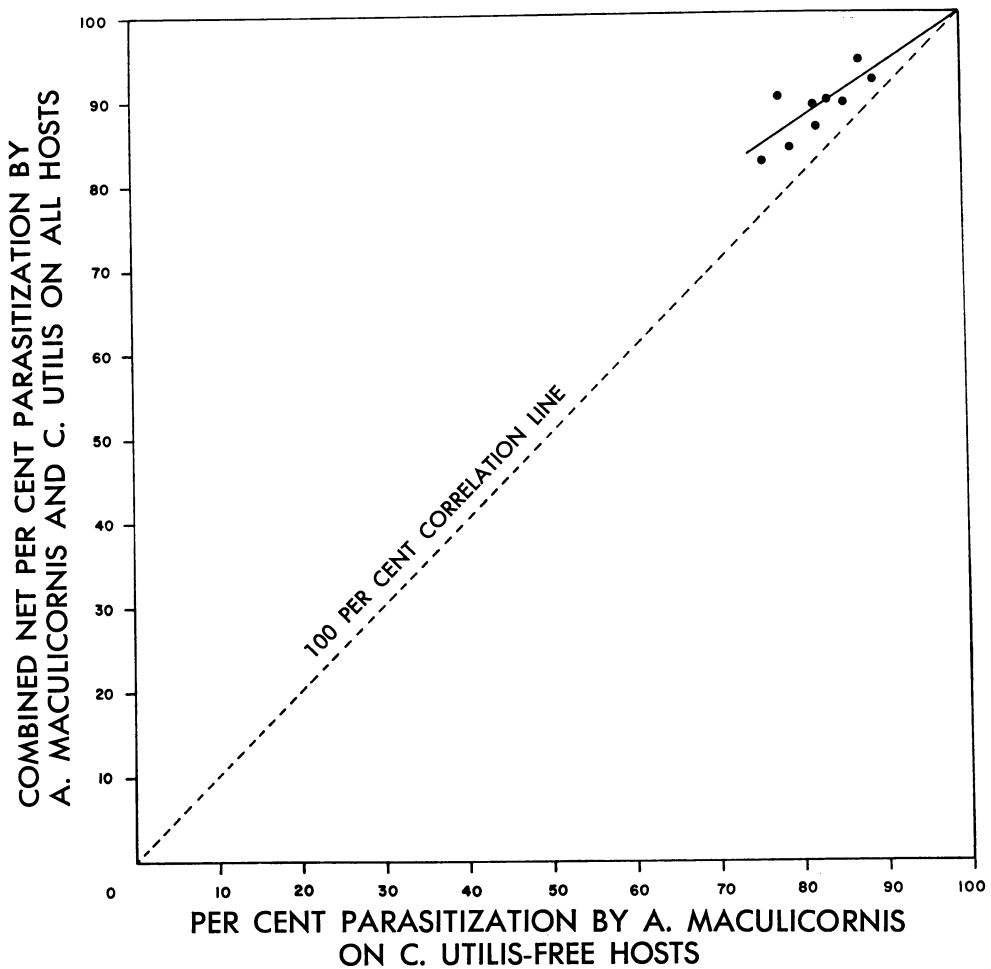
Fig. 5. Correlation between parasitization by *A. maculicornis* on *C. utilis*-free hosts and combined net parasitization by this species and by *C. utilis* on *P. oleae* at 9 locations—spring, 1964.

These results were then added, to estimate the total indicated parasitization by *A. maculicornis*.

From the estimates in table 4 we see that of 300 initially acceptable female hosts of the fall generation of 1962 that had not died from other causes, accumulated total-generation parasitization by *A. maculicornis* alone would have been 87.7 per cent—leaving only 12.3 per cent not destroyed by *A. maculicornis*. By April, *C. utilis* had not emerged. *C. utilis* numbers had declined because of accumulative destruction by *A. maculicornis*, which had parasitized hosts that *C. utilis* had previously para-

sitized, destroying both hosts and *C. utilis*. There was also some mortality of *C. utilis* caused by other factors, perhaps. Hence our most complete record of parasitization of the host generation by *C. utilis* was reached in November (here, 1962). Our data for *C. utilis* show it parasitizing 37.2 per cent (or 112) of the 300 available hosts. The potential of *A. maculicornis* for destroying these same individuals parasitized by *C. utilis*, in the conceived absence of the latter, is 87.7 per cent: thus, 98 of the 112 individuals parasitized by *C. utilis*, or 32.6 per cent of the 300 initial hosts. This leaves only
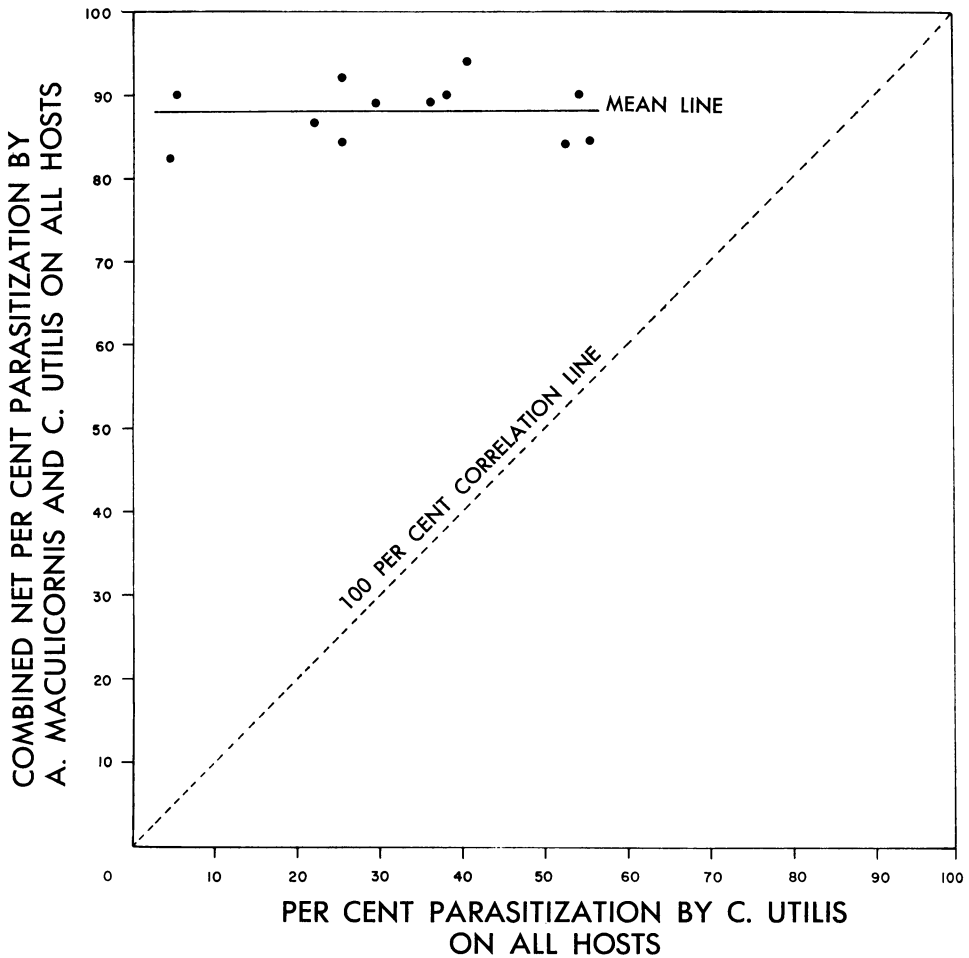
Fig. 6. Absence of correlation between parasitization by *C. utilis* and combined net parasitiza-
tion by this species and by *A. maculicornis* on *P. oleae* at 12 locations—spring, 1964.

14 hosts (or 4.7 per cent) as the addi-
tional or indispensable indicated mor-
tality due to *C. utilis* parasitization.
Therefore, the total indicated parasiti-
zation of hosts was 92.4 per cent (87.7
+ 4.7). This is 15.0 points higher than
the combined time-point net parasitiza-
tion by the two species for April, 1963
as shown in table 1; and it is a much
more realistic appraisal of the degree of
control actually experienced as shown
by the records of scale-damaged fruits
as seen in table 5.

For the fall host brood of 1963, there
were 35 estimated survivors out of the
initial 300, or 11.7 per cent remaining

after parasitization by *A. maculicornis*
acting alone (table 4). The total-gen-
eration mortality from *A. maculicornis*
was thus 88.3 per cent (265 hosts) in
contrast to the highest single time-point
parasitization on this generation by
this species of 82.3 per cent (table 1,
April, 1964). The former of these two
figures, 88.3 per cent, represents the ca-
pacity of *A. maculicornis* to kill hosts
in the absence of *C. utilis*. When this
percentage is applied to the recorded
maximum, or cumulative host parasiti-
zation, by *C. utilis* in December, 1963
it means that out of the 37.1 per cent
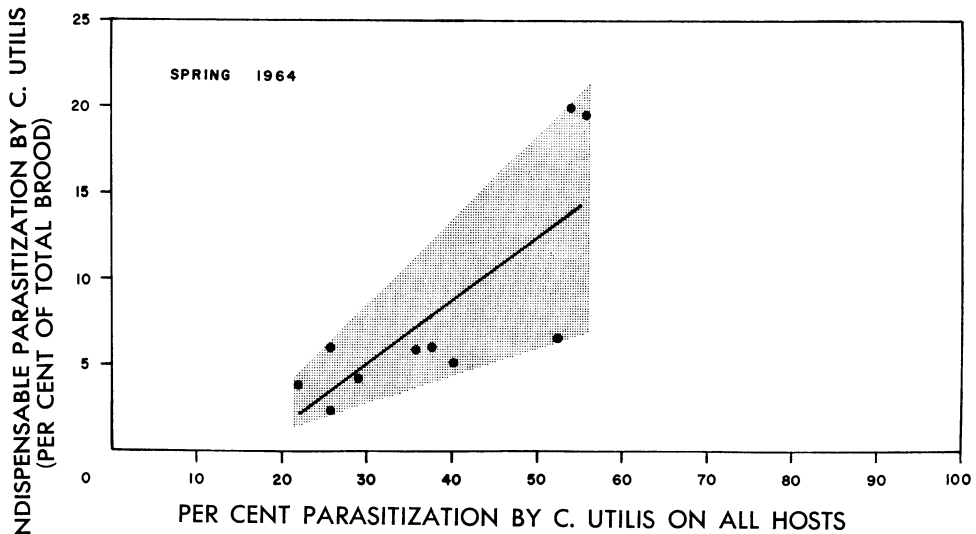of the total initial population of 300

Fig. 7. Correlation between total parasitization by *C. utilis* and the indispensable parasitization
by this species on *P. oleae* at 10 locations—spring, 1964.

(that is, out of 111 hosts) that were parasitized by *C. utilis,* 88.3 per cent (or 98 hosts) would have been destroyed by *A. maculicornis* if *C. utilis* had not been present. These 98 hosts equal 32.7 per cent of the initial brood of 300. Therefore, 37.1 –32.7 leaves only 4.4 per cent which is the indispensable cumulative host mortality caused by *C. utilis.* This gives a cumulative host net parasitization, from the two species, of 92.7 per cent (88.3 + 4.4)—in this case only 3.7 points higher than the total effective net parasitization by the two species in April, 1964, alone (table 1). Hence, when the parasitization by *A. maculicornis* in April is very high, there is not opportunity for the previously occurring parasitization by *C. utilis* to make so much difference in the final mortality, whether the latter is high or low.

An important point, however, is that a small portion of eggs may have been deposited by the host females before enough of the April parasitization by *A. maculicornis* has occurred to curtail host oviposition. The parasitization in April is not 100 per cent effective, while that occurring in March or earlier is.

Hence, a cumulative host mortality that reaches 90 to 95 per cent by mid-April is superior in control effect to a parasitization level of the same intensity which is not attained until May or early June.

We are unable to account for the superior searching success of *A. maculicornis* in April, 1964, for previously unparasitized hosts (82.3 per cent), as contrasted with its searching success in April, 1963 (66.1 per cent; see table 1). It is certainly not a simple result of better performance in a higher density of hosts, for the susceptible host densities on a per-twig basis were nearly the same for the two years. It is possible that the period in late March and April was more favorable climatically to *A. maculicornis* survival, searching and reproduction in 1964, in contrast to 1963, or that the exact time of the sample for 1964 coincided with a time when the reproduction sequence had progressed slightly further than it had in 1963.

To complete somewhat a composite, perhaps representative, picture of *total-generation* mortalty, we may introduce and add to these data earlier records of scale mortalities due to causes other

TABLE 4

ESTIMATES OF CUMULATIVE HOST-BROOD MORTALITY (OF FEMALES APPROACHING MATURITY) DUE TO *APHYTIS MACULICORNIS* AND *COCCOPHAGOIDES UTILIS*: FALL- AND SPRING-GENERATION HOSTS OF 1962 AND 1963 AT THE DUNCAN GROVE, HERNDON, CALIFORNIA*

Broods and dates of estimates	Percentage of hosts killed by *A. maculicornis*†	Cumulative kill by *A. maculicornis*		Remainder after *A. maculicornis* kill		Full-brood parasitization by *C. utilis*		Combined kill by the 2 species	Survivors	Indispensable full-brood kill by *C. utilis*		Indispensable full-brood kill by *A. maculicornis*	
		no.	*per cent*	*no.*	*per cent*	*no.*	*per cent*	*per cent*	*no.*	*no.*	*per cent*	*no.*	*per cent*
Fall, 1962:													
Initial lot........	....	:	.....	300	100.0								
October, 1962.....	all of 15.4%	46	15.4	254	84.6								
November, 1962..	½ of 42.9%	55	33.7	199	66.3	112§	37.2§						
February, 1963..	all of 34.5%	69	56.7	130	43.3								
March, 1963	½ of 30.0%	20	63.3	110	36.7								
April, 1963........	all of 66.1%	73	87.7	37	12.3								
Final brood results.	....	263	87.7	37	12.3	112	37.2	92.4	23‖	14	4.7	166	55.2
Fall, 1963:													
Initial lot........	....	:	.....	300	100.0								
October, 1963.....	all of 11.1%	21	7.0	279	93.0								
November, 1963..	½ of 21.3%	30	17.0	249	83.0	111§	37.1§						
February, 1964..	all of 14.0%	35	28.7	214	71.3								
March, 1964......	½ of 17.4%	19	34.3	197	65.7								
April, 1964........	all of 82.3%	162	88.3	35	11.7								
Final brood results.	....	265	88.3	35	11.7	111	37.1	92.7	22‖	13	4.4	167	55.6
Spring, 1962:													
Initial lot........	....	:	.....	300†	100.0								
July, 1962........	all of 5.0%	15	5.0	285	95.0								
August, 1962	all of 8.5%	24	13.0	261	87.0	198§	66.1§						
Final brood results.	....	39	13.0	261	87.0	198	66.1	70.5	89	172	57.5¶	13	4.4
Spring, 1963:													
Initial lot........	....	:	.....	300†	100.0								
July, 1963........	all of 2.9%	9	3.0	291	97.0								
August, 1963	all of 8.9%	20	9.7	271	90.3	156§	52.1§						
Final brood results.	....	29	9.7	271	90.3	156	52.1	56.8	130	141	47.1	15	5.0

* The figures in table 4 were derived in the following manner:

The total number of hosts killed by *C. utilis*, here taken as a center, is given the value of 100 per cent.

Fall, 1962: The accumulated kill by *A. maculicornis* is 87.7 per cent which, when subtracted from 100 per cent leaves 12.3 per cent—the indispensable fraction of *C. utilis'* total parasitization. (The fraction is indispensable since *A. maculicornis*, acting alone, could have killed 87.7 per cent of those killed by *C. utilis*.)

C. utilis parasitized 112 hosts, of which 87.7 per cent equals 98, which, subtracted from 112, leaves 14 as the number of hosts which *C. utilis* indispensably parasitized. This latter figure equals 4.7 per cent of the initial population of 300 individuals.

For 1963: Figures for 1963 are derived in the same manner as are those for 1962.

† Method of arriving at estimates shown in this column is described on page 299.

‡ The mortality between the egg stage and the mature female, independent of parasitization, in this spring generation is heavy—often 50 to 70 per cent (Huffaker, Kennett, and Finney, 1962). Hence the amount of parasitization required to depress population growth is not so great.

§ At peak. Method of estimating *C. utilis* full-brood parasitization is explained on page 301.

¶ Most years the proportion of *C. utilis* parasitization in midsummer that is indispensable would be greater than in 1963 and 1964.

|| It is probable that 80 per cent or more of the "survivors" here listed would not lay their full quota of eggs, as by May they are also normally killed by subsequent *A. maculicornis* attack.

than parasites (Huffaker, Kennett, and Finney, 1962, pp. 562 and 596). According to these earlier records, about 40 per cent of the fall-produced scale eggs failed to produce young settled stages (large crawler losses). Also, about 50 per cent of the early settled stages at five locations in 1956 died from weather adversity, malnutrition or other nonparasite causes. This means that we may consider that the 300 older females taken as our host population base in table 4 were those remaining of a larger population of 1,000 female-producing eggs, and the total female generation host mortalities would have been, as given in table 6, 97.7 per cent instead of 92.4 per cent in 1963; and 97.8 per cent rather than 92.7 per cent in 1964. The breakdown of this composite host mortality at the Duncan Grove would be, for 1963: 26.3 per cent parasitization caused by *A. maculicornis*, 1.4 per cent indispensable parasitization by *C. utilis*, and 40 per cent host-population losses in the egg and crawler stages; and 30 per cent in the early settled stages, from causes other than parasitism. The figures for 1964 would be 26.5 per cent mortality caused by *A. maculicornis*, 1.3 per cent indispensable parasitization by *C. utilis*; and 40.0 per cent losses in the presettled stages and 30.0 per cent losses in the early settled stages, as in 1963.

In considering whether the intensity of mortality from the action of a parasite or predator, under a given pattern of weather or climate and the general conditioning environment, is sufficient to control a given pest species at an economic level, the impact of mortality from other causes has a decisive bearing. Chamberlain (1941) showed that in places where the mortality of the wheat jointworm, *Harmolita tritici* (Fitch), from weather and other factors, is consistently high, a relatively low parasitization is all that is required to prevent outbreaks. Huffaker (in press) demonstrates how this general relationship between the action of density-indepen-

TABLE 5

TIME-POINT PARASITIZATION AND DEGREE OF CONTROL OF
PARLATORIA OLEAE BY *APHYTIS MACULICORNIS* AND *COCCOPHAGOIDES
UTILIS* AT THE DUNCAN GROVE, HERNDON, CALIFORNIA
(1956–1964)

Year	Month	Mature female scales in sample	Mature female scales per twig*	Parasitization			Commercial fruit cullage
				A. maculicornis	*C. utilis*	Combined net	
		no.	*average†*	*per cent*	*per cent*	*per cent*	*per cent*
1956	April	19	0.5	79.2		79.2	
	Aug.	9	0.2	0.0		0.0	5.4
1957	April	48	1.0	42.6		42.6	
	Aug.	72	0.8	0.0		0.0	4.4
1958	April	313	3.3	37.2		37.2	
	Aug.	190	1.9	3.1		3.1	27.4
1959	April	177	3.7	100.0		100.0	
	Aug.	22	0.4‡	0.0		0.0	7.4‡
1960	April	4	0.1	75.0	0.0	75.0	
	Aug.	15	0.3	0.0	35.9	35.9	0.4
1961	April	42	0.7	40.5	59.5	100.0	
	Aug.	19	1.6	0.0	42.1	42.1	0.5
1962	April	38	0.8	40.0†	50.0	90.0†	
	Aug.	42	0.9	2.4	78.5	80.9	0.0
1963	April	9	0.2	55.6	44.4	100.0	
	Aug.	3	0.1	0.0	33.3	33.3	0.0
1964	April	15	0.3	60.0	40.0	100.0	
	Aug.	4	0.1	0.0	75.0	75.0	0.0

* Sample size was varied considerably over the years—from a minimum of 12 twigs in the August 1961 sample to a maximum of 96 when densities were expected to be low.
† Estimated—see text, p. 313.
‡ To nearest tenth.

dent factors and a regulating density-dependent factor, applies in a special laboratory example, wherein competition for food, rather than attack by a parasite, was the regulating agent.

If we view the data of table 6 realistically, considering the demonstrated ability of both parasites—but particularly that of *A. maculicornis* in 1963 and 1964—we see a tremendous potential of compensation in the killing power of these two parasites, assuming as we do that the *A. maculicornis* fe-

males possessed enough eggs to have parasitized many more hosts than they did. To be sure, there is also a passive element of compensating action in the nonparasite-caused losses in the host egg, crawler, and early settled stages. If none of the individual hosts had died in the egg or crawler stages, the total-generation mortality in the early settled stages would have been 50 per cent rather than 30 per cent; and the absence of half of the 40 per cent losses in the egg and crawler stages

would have been made up for by this increase in losses in the early settled stages. By the same token, as Morris (1957) and Huffaker and Messenger (1964) have pointed out, although the quantitative mortality impact of a given factor may be relatively great, the apparent importance may in fact be a spurious one.

Significantly, since *A. maculicornis* demonstrated the power of killing about 88 per cent of the 1962 fall generation, acting just before egg deposition by the female hosts (table 4), we can reasonably assume that if losses from prior-acting, nonparasite causes had not occurred, *A. maculicornis* action would have compensated by destroying a nearly equal percentage of these individuals. Furthermore, had *A. maculicornis* not acted with this efficiency, a much greater amount of the action of *C. utilis* would have been meaningful. We see, then, that this latter parasite, too, stands in a rear-guard position to compensate, to an extent commensurate with its searching efficiency as a population, for diminished scale mortality from other previously occurring losses. Hence, if we conceive of a similar situation in which all eggs hatched and all scales lived to the time of attack by *C. utilis* and *A. maculicornis*, 92.4 per cent would still have died in the 1962 generation, and 92.7 per cent in the 1963 generation (table 4) rather than the 97.7 per cent and 97.8 per cent shown in table 6.

However, even such small differences in the indispensable loss in a given generation caused by nonparasite causes may be very important in natural control. When *A. maculicornis* was present alone, variations in such losses, and in scale fecundity, were tremendously important during years or seasons when *A. maculicornis* was reduced in effectiveness. Now that *C. utilis* also is effective, and more consistently so than is *A. maculicornis*, especially in the summer, a greater reliability of compensat-

TABLE 6
COMPOSITE OF TOTAL FALL-GENERATION MORTALITY AT THE DUNCAN GROVE (1962–1963)*

Stage of losses and causes of losses	Mortality	
	1963	1964
	per cent	per cent
Eggs and crawlers (non-parasite caused)	40.0†	40.0†
Early settled stages (non-parasite caused)	30.0‡	30.0‡
Aphytis maculicornis-caused losses in later stages	26.3§	26.5‖
Indispensable losses caused by *Coccophagoides utilis* in later stages	1.4¶	1.3**
Total-generation losses	97.7	97.8

* This presentation of the data gives a more nearly accurate picture of the direct causes of death of the total generation of scales than does table 4, but it *de-emphasizes* the role of the parasites, and gives a spurious picture of the *importance* of the respective factors in the natural control of this insect, unless viewed properly. See pages 26–27 of text.

† Estimated losses from 1,000 initial individuals. See p. 305.

‡ Estimated losses; 30 per cent of 1,000 initial individuals, or 50 per cent of remaining 600. See p. 305.

§ 87.7 per cent of 300 remaining (table 4, fall, 1962, final brood results, cumulative kill), or 26.3 per cent of initial 1,-000 individuals (*i.e.*, 263 individuals killed).

‖ 88.3 per cent of 300 remaining (table 4, fall, 1963, final brood results, cumulative kill), or 26.3 per cent of initial 1,-000 individuals (*i.e.*, 265 individuals killed).

¶ 14 individuals indispensably killed (table 4, fall, 1962, final brood results), or 1.4 per cent of the initial 1,000 individuals.

** 13 individuals indispensably killed (table 4, fall, 1963, final brood results), or 1.3 per cent of 1,000.

ing power in overall performance exists.

We see, then, that *A. maculicornis* rather solidly dominated control of the fall generation of hosts, in spite of the fact that *C. utilis* nearly equalled or even markedly exceeded *A. maculicornis* in levels of total parasitization, month by month, except in April (table 1). In that crucial month, parasitization by *A. maculicornis* is dominant. The April figures for 1963 (table 1) were 44.1 per cent and 11.3 per cent for the indispensable parasitization by *A. maculicornis* and *C. utilis*, respectively; and for 1964, 50.7 per cent and 6.7 per cent, respectively.

DOMINANCE OF *Coccophagoides utilis* ON THE
SPRING-PRODUCED GENERATION OF SCALES

Table 1 shows the parasitization of the spring generation of scales at the Duncan Grove almost in its entirety during July and August, when processes are much increased in tempo, the peak period being August. We may now contrast this summer activity with the parasitization of the fall generation of scales, during winter and spring.

A. maculicornis had reached high levels of parasitization (66.1 per cent and 82.3 per cent) on *C. utilis*-free hosts in April of 1963 and 1964, respectively (table 1). By contrast, in August of 1962 and 1963, both relatively favorable summers for *A. maculicornis,* this species attained maximal parasitizations of only 8.5 per cent and 8.9 per cent, respectively on *C. utilis*-free hosts. On the other hand, *C. utilis* attained fair levels of parasitization in August, as is customary, during both these years, but not as high as the levels which *A. maculicornis* normally attains on *C. utilis*-free hosts by April or May following favorable summers.

During the summer periods of 1962 and 1963, *A. maculicornis* was so ineffective that 87.0 per cent (100.0 –13.0) and 90.3 per cent (100.0–9.7) of all the parasitization by *C. utilis* was indispensable (table 4—columns 4 and 6). On the other hand, for the fall generations of 1962 and 1963, only an estimated 12.3 per cent and 11.7 per cent, respectively, of all the parasitization by *C. utilis* was indispensable (table 4).[4] The total cumulative host mortality resulting from these latter indispensable fractions was only 4.7 per cent and 4.4 per cent, respectively.

Considering the summer period of activity in table 4 in more detail, each year all the parasitization by *A. maculicornis* in July is taken to be distinct from that in August. This is a conservative estimate, because the life cycle of

this parasite spans little less than a month at that time of year. On the other hand, *C. utilis* does not develop that fast and new parasitizations in August are simply added to those in July. For this reason, we used the monthly peak value alone to represent the total cumulative parasitization by *C. utilis* in table 4.

As seen in table 4, of the total parasitization of the spring generation by *C. utilis* in 1962, 87.0 per cent was indispensable. Of the individuals reaching the third stage, the indispensable total cumulative parasitization was 57.5 per cent. For the spring generation of 1963, the proportion of all the destruction by *C. utilis* that was indispensable was 90.3 per cent, and the comparable indispensable total cumulative parasitization was 47.1 per cent.

In both 1962 and 1963, the parasitization of the spring generation by the two species combined was much lower than for the fall generation either year. However, the amount of impact provided by *C. utilis* is a very important feature of the reliability of control (see section on "Comparisons of Control with *A. maculicornis* Present and *C. utilis* Present and Absent," p. 309).

Considering still the spring generation of hosts during the summer period of activity, we have in table 7 much more limited data for a variety of groves that were not studied in detail. Reinforced by other records over a period of years showing that *A. maculicornis* is very ineffective at this time, these data strongly indicate a notable supplementing action by *C. utilis*. Table 7 shows results for the summer periods for five years for the Duncan Grove; for four years for the Oberti-H Grove, and for two years each for the Clovis, Lucca, Kirkpatrick and Sunland groves. The number of scales was in most cases

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[4] See footnote to table 4 for explanation of how these figures are derived.

very low, partly because of excessively heavy parasitization by *A. maculicornis* during the preceding spring periods, and also because most of the groves were not under intensive study and large samples were not taken.

Except for the unusually high figure for *A. maculicornis* parasitization (based on 10 scales) at the Clovis Grove, this species was a negligible factor. By contrast, *C. utilis* attained a substantial parasitization, varying from 20 per cent at the Clovis Grove to 67.7 per cent at the Duncan Grove, the latter based on a good sample; or 92.3 per cent at the Lucca Grove, but again based on a limited sample (only 13 scales). Nearly all the parasitism by *C. utilis* was indispensable.

There is little need to consider *A. maculicornis* in the correlation between parasitization of the spring generation of scales (summer activity) by *A. maculicornis* and *C. utilis* and the com-

bined net parasitization or control effect. The effect of *A. maculicornis* at this season has long been known to be nearly negligible. However, the degree to which it does survive the summer is critical in relation to its resurgence and effectiveness on the fall generation of scales during the next spring. In figure 8 we have indicated the 1963 summer results in 11 groves having both *C. utilis* and *A. maculicornis*, plotting the percentage of parasitization by *C. utilis* against the combined net parasitization by both species. The departures from the 100 per cent correlation line show, of course, the amount of parasitization by *A. maculicornis*. Only at the Clovis Grove was there an appreciable departure. The correlation in summer between *C. utilis* action and the net parasitization by the two species combined is thus direct, obvious, and very little confused by the negligible action of *A. maculicornis*. (Cf. figs. 2 to 7.)

COMPARISONS OF CONTROL WITH *Aphytis maculicornis* PRESENT AND *Coccophagoides utilis* PRESENT AND ABSENT

Results at Ten Locations in 1964

The high control potential of *A. maculicornis* and *C. utilis*, in places where both species are well established, and the fact that *C. utilis* is now becoming much more widely established, gives much promise of a general applicability to the entire olive industry. *A. maculicornis* has for a decade been generally established and has often been effective on the overwintered host females during the spring period in areas where insecticide interference has been minimal (Huffaker, Kennett, and Finney, 1962). The data previously discussed (table 2, p. 293) show that each of these two parasites possesses considerable capacity to make up for poor performance of the other on the overwintered host females. In the 1964 data that capacity

was greater for *A. maculicornis*. Since *C. utilis* has only recently been established, however, and in some places is increasing in effectiveness, its capacity in this respect may become more pronounced. The addition of *C. utilis* offers greater reliability of control of the overwintered host scales than when *A. maculicornis* alone is present. This is particularly so during years when *A. maculicornis* is very slow to recover from the adverse effects of a severely hot summer or from the effects of insecticides drifting into the groves.

The consistency of control during the spring period under the action of the two parasites is illustrated by the data of table 2. The time-point parasitization of the two species combined, from late April to early May, at the ten locations

TABLE 7

TIME-POINT PARASITIZATION OF SPRING-GENERATION FEMALES OF *PARLATORIA OLEAE* BY *APHYTIS MACULICORNIS* AND *COCCOPHAGOIDES UTILIS* IN GROVES WHERE *C. UTILIS* IS WELL ESTABLISHED*

(August, 1960–1964)

Grove	Year	Female scales	Parasitization by A. maculicornis	Parasitization by C. utilis	Combined net parasitization	Apparent time-point values							
						Dispensable kill by:				Indispensable kill by:			
						A. maculicornis		C. utilis		A. maculicornis		C. utilis	
		no.	per cent	per cent	per cent	no.	per cent	no.	per cent	no.	per cent	no.	per cent
Duncan	1960	89	0.0	35.9	35.9	0	0.0	0	0.0	..	..	32	35.9
	1961	19	0.0	42.1	42.1	0	0.0	0	0.0	..	..	8	42.1
	1962	319	2.8	67.7	70.5	6	1.9	6	1.9	3	0.9	210	65.8
	1963	168	4.2	51.8	56.0	4	2.4	4	2.4	3	1.8	83	49.4
	1964	4	0.0	75.0	75.0	0	0.0	0	0.0	0	0.0	3	75.0
Oberti	1960	30	0.0	43.3	43.3	0	0.0	0	0.0	..	..	13	43.3
	1961	142	0.0	34.5	34.5	0	0.0	0	0.0	..	..	49	34.5
	1962	10	0.0	38.1	38.1	0	0.0	0	0.0	..	..	8	38.1
	1964	3	0.0	66.6	66.6	0	0.0	0	0.0	0	0.0	2	66.6
Clovis	1963	10	30.0	20.0	50.0	0+	0.0+	0+	0.0+	3–	30.0–	2–	20.0–
	1964	26	3.8	26.9	30.7	0	0.0	0.4	1.4	1	0.0	6.6	25.5
Lucea	1963	13	0.0	92.3	92.3	0	0.0	0	0.0	..	..	12	92.3
	1964	15	0.0	66.6	66.6	0	0.0	0	0.0	0	0.0	10	66.6
Kirkpatrick	1963	9	0.0	33.3	33.3	0	0.0	0	0.0	..	..	3	33.3
	1964	13	0.0	38.5	38.5	0	0.0	0	0.0	0	0.0	5	38.5
Sunland	1963	56	1.8	21.4	23.2	0+	0.0+	0+	0.0+	1	1.8	12–	21.4
	1964	15	0.0	86.6	86.6	0	0.0	0	0.0	0	0.0	13	86.6

* Because of the high degree of control, many sample lots contained only few scales in spite of the fact that as many as 1,680 leaves and associated woody parts were included in the samples.
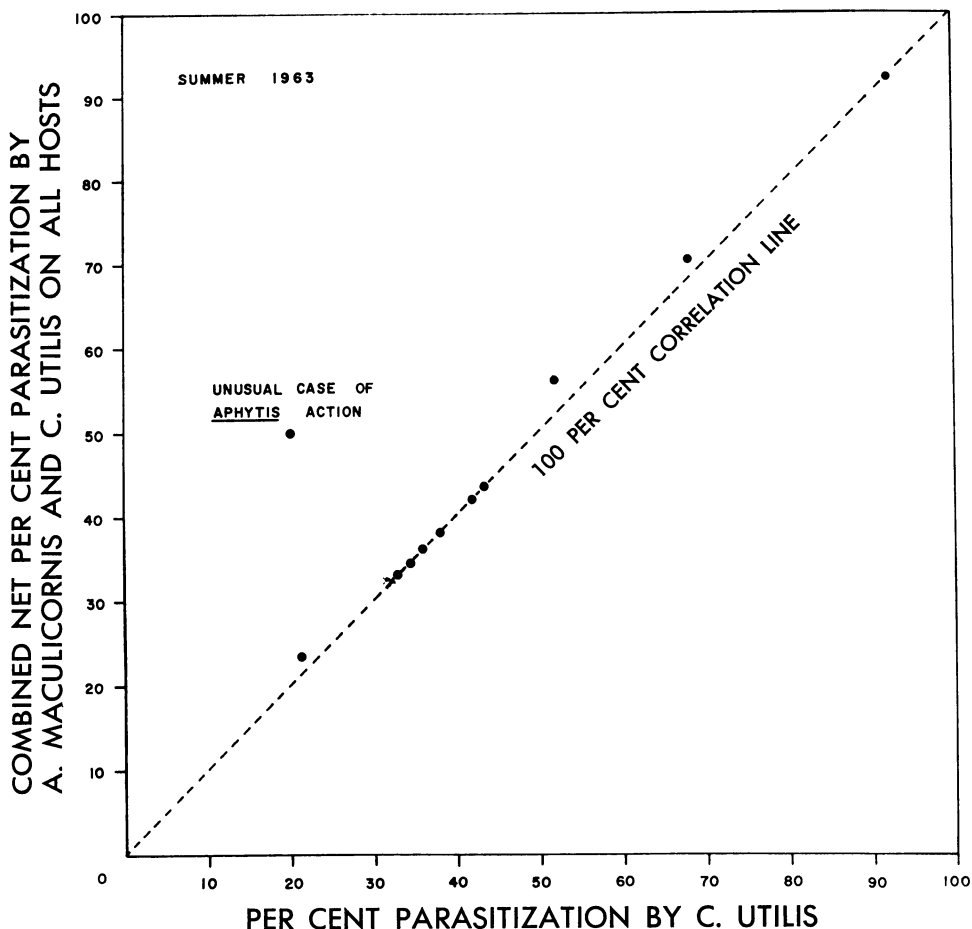
Fig. 8. Correlation between parasitization by *C. utilis* and combined net parasitization by this species and by *A. maculicornis* on *P. oleae* at 11 locations—summer, 1963.

where both species were active, averaged 88.2 per cent, with total-generation parasitization of females that would have reached maturity being *perhaps* as high as 92 to 95 per cent. In those groves where *C. utilis* was well established, the lowest critical period, or time-point, parasitization for the two species combined was 82.5 per cent, and the highest was 94.2 per cent. The lowest performance was at a location where *A. maculicornis* achieved a parasitization of only 56.8 per cent and *C. utilis* had not yet reached a very high level of effectiveness. The next lowest performance (with a parasitization level for the two species combined at

84.2 per cent) was at a location where parasitization by *A. maculicornis* was only 28.9 per cent on all scales and only 64.7 per cent on *C. utilis*-free scales. During many other spring periods at many similar locations *A. maculicornis* has performed as poorly if not more so (Huffaker, Kennett, and Finney, 1962).

Consequently, although *C. utilis* has not yet usually achieved a total parasitization greater than 50 to 60 per cent, such parasitization gives a great element of assurance against breakdown of biological control during seasons when *A. maculicornis* does poorly during its most favorable period (the spring). Also, the value of adding *C.*

utilis is further increased by the fact that all the female scales of the fall generation parasitized by this species die before they produce *any* eggs, while some eggs may be produced by females that are parasitized late by *A. maculicornis.*

The parasitization of the spring generation of female scales, which reaches a peak in midsummer, shows even more pointedly the importance of *C. utilis* as an additional safeguard against breakdown of control, or in obtaining full control where previously *A. maculicornis* was seldom adequate. Usually, only *C. utilis* is responsible for much parasitization of hosts at this season, although the developing young scales may suffer as high as 70 per cent mortality from other causes. Thus, one of the two yearly host generations is almost safe against attacks by *A. maculicornis. C. utilis* then steps in and effectively reduces the increase in host density that normally occurs in late spring and early summer when *A. maculicornis* alone is present.

Severely hot summer weather also has adverse effects on the spring generation of young scales. Therefore, even in the absence (formerly) of *C. utilis,* the bounce-back in scale densities of the spring generation in summer was only sporadically severe. Phenomenal upsurges in scale populations occurred particularly in the summers of 1958 and 1962, years during which the spring and early summer periods of young scale production and establishment were less hot and dry. During 1958, *C. utilis* was not yet effective in any grove, and an upsurge in scale populations occurred in all the groves observed. In 1962, on the contrary, the upsurge occurred in all groves observed except the two where *C. utilis* had become effective. These were the Duncan and Oberti Groves where this species was first established. The consistency of the combined control effect is illustrated by the long-term data from these two groves (tables 5 and 8).

The Duncan Grove

This grove is a crucial one for analysis of the effect on the overall degree of commercial control of the olive scale when *C. utilis* is introduced. Records from this grove also clearly demonstrate the supplemental and/or competitive interrelationships between this species and *A. maculicornis.* Here we have the most continuous long-term records of results before *C. utilis* was brought in, and here *A. maculicornis,* used alone, gave adequate control only during certain years. While variable effects from insecticidal drifts may well have been an explanation of the relatively low early-May parasitization by *A. maculicornis* from 1956 to 1958 inclusive, the introduction of *C. utilis* in 1957 appears to have materially improved the control (table 5).

Records at the Duncan Grove are continuous from 1956 through 1964, except that data for April, 1962, were not obtained. Judging by the records for January, 1962, however, and on the basis that *A. maculicornis* parasitization nearly always increases to at least 40 per cent by late April from a low (approximately 3 per cent) level in January, and that *C. utilis* does not exhibit a population increase between these months, we conservatively *estimated* the figures for April to be 40.0 per cent parasitization by *A. maculicornis* and 50.0 per cent by *C. utilis.* This gives a net time-point parasitization of 90 per cent for the two species combined in April, 1962. This would be a lower parasitization than what actually occurred in any other spring since *C. utilis* first became effective in 1961.

The sample size for determining the percentage of parasitization has been much too small on many occasions; but because of good performance, the recorded parasitization record has been consistently high since establishment of *C. utilis,* even though there were few hosts in the samples. It will be noted also that the time-point peak parasitiza-

tion record for April has been 100 per cent each year since *C. utilis* has been established, except in 1962, when we had no actual record for April but made a very conservative estimate for the *A. maculicornis* contribution (See page 312). But even before *C. utilis* was established, *A. maculicornis* was low in only two years—in 1957 at 42.6 per cent on 48 female scales, and in 1958, at 37.2 per cent, on 313 female scales (table 5). These were years following known insecticidal disturbances. These data are comparatively representative of densities of the host and of the parasites over the period of years, since the foliage and twig sample size was adequately maintained so as to ensure a reliable measure of scale density. Since, however, densities per twig have declined to so low a level under the excellent biological control, the number of hosts obtained to measure the percentage of parasitization has often been exceedingly small, although the sample size (48 twigs) was double that used originally at a number of locations (Huffaker, Kennett, and Finney, 1962).

Incidentally, the parasitization data for this grove shown in table 1 were obtained by intensive *selective* sampling for twigs containing higher densities of scales—and from different trees than those presented here for the nine-year sequence. It is possible that parasitization of scales in the *selected,* much higher-density samples may have been somewhat higher than that in the present trees, but our data indicate the opposite—that the parasites achieved the higher parasitization in the lower density of scales. This could be due to a more favorable ratio of searching parasites to available hosts if, in fact, parasites tend to drift from higher density locations, where most parasites are produced, to other parts of the trees or orchard where scales are scarce. However, the present parasitization record is undoubtedly not reliable for such comparative purposes.

Data for the spring generation of scales for this grove (summer season of activity) show that the parasitization was exclusively by *C. utilis* after that species became well-established, except in 1962, when *A. maculicornis* parasitized 2.4 per cent of the mature females (table 5). The lower combined net parasitization for the two species during the summer, as contrasted to the spring activity, illustrates the lack of efficient performance by *A. maculicornis* which characterizes that period. Since *C. utilis* usually achieves a parasitization of not more than 50 to 60 per cent, the combined net parasitization in the summer is about the same from year to year. However, in 1962 *C. utilis* did parasitize 78.5 per cent of the 42 female scales in the sample.

Our purpose here is to relate the increase in reliability of control to the new factor, *C. utilis.* The commercial test is cullage of fruits at marketing. This test, however, is to some extent not directly related to density of scales; cullage levels may also vary with picking time and weather or other factors as they affect ripening of fruits and their discoloration by the scales. Varietal differences are also striking, but the trees in the Duncan Grove are all of the Manzanillo variety. The cullage level may also be related to some extent to the density of overwintered mature female scales in the spring period, but it is more commonly directly related to the density as shown for the summer period. It should be noted that the fairly high cullage level (7.4 per cent) for 1959 is associated with a low density of scales (0.4 per twig). In addition to the stated explanations, this grove was treated with oil that summer (the only time during the study) to control black scale, *Saissetia oleae* (Bern.), and the low density of *P. oleae* is partly a reflection of insecticidal kill of this scale as well, whereas some of the fruits were already degraded by the scales before their death. Also, the number of *A. maculicornis* adults per twig, and per avail-

able host, in the spring of 1959, was much higher, and the parasite achieved 100 per cent destruction of the then much-reduced density of mature female scales in April. This is a case in which the month-to-month parasitization (not presented in this paper), from the fall of 1958 into and through March of 1959, had materially lowered the density of still-living scales reaching the mature state in April, 1959 and on which the parasitization record at that time is based. The third year, 1958–1959, was the first year of good biological control. This control had been accomplished by *A. maculicornis* alone during a period of years when the host densities on comparison trees that had been treated with DDT to remove the *A. maculicornis* (as a check method of analysis) increased some 400-fold (Huffaker, Kennett, and Finney, 1962, p. 621, table 23).

An important point derived from table 5 is that the degree of biological control, as measured by the less sensitive but only practical test, the scaly fruits, has been uniformly excellent during the five years (1960–1964) since *C. utilis* became well established, whereas before, the grove was under only marginally satisfactory biological control most years, and entirely inadequate control during one of the four years.

It is significant that during the spring period, only *A. maculicornis* has capacity to truly compensate for the degree of lesser effectiveness of the other parasite on the overwintered female hosts. This is because the *A. maculicornis* emerge as adults in this period and can search out any unparasitized and acceptable hosts, and parasitize them. The principal parasitization by *C. utilis* occurs in summer, and adults do not emerge until the host females are producing their next generation of young. This is perhaps the main reason why the percentage of total parasitization of overwintered female scales in the spring period is often high, while neither of the parasites alone, now that

C. utilis is effective, attains the very high degree of parasitization that *A. maculicornis* often attained alone (particularly following favorable years or at favorable locations) prior to the establishment of *C. utilis*. For example, in the Duncan Grove only in 1958 and 1962 were summer conditions conducive to survival of an appreciable number of *A. maculicornis*—that is, at 3.1 per cent and 2.4 per cent parasitization, respectively. During the spring following 1958, a favorable year, *A maculicornis* had parasitized all the scales in the sample by early May (table 5). Likewise, in the spring following the favorable summer of 1962, *A. maculicornis* parasitized all the still unparasitized scales and some of those already parasitized by *C. utilis*—those which had not yet reached an unacceptable stage of mummification.

On the basis of many other records over the state, the summer of 1963 also was favorable for survival of *A. maculicornis*, and in the Duncan Grove in the spring of 1964, it again achieved a very high degree of parasitization of still-unparasitized scales—that is, those still available which it had not previously killed or which were not already parasitized by *C. utilis*. It also parasitized some of those already parasitized by *C. utilis*. This very high spring performance by *A. maculicornis* at this location (which is often marginal due to summer weather stress on this parasite) occurred during three of the nine years of this study. During two of the other six years, *A. maculicornis* achieved a fair degree of parasitization, that is, 79.2 per cent and 75.0 per cent.

The Oberti Grove

Although the records for the Oberti Grove (table 8) cover a period of eight years, the record of only one of these years can be used as being fully representative of the level of biological control achieved by *A. maculicornis* alone. In 1957 biological control had just been

TABLE 8

TIME-POINT PARASITIZATION RECORD AND DEGREE OF CONTROL OF
PARLATORIA OLEAE BY *APHYTIS MACULICORNIS* AND *COCCOPHAGOIDES*
UTILIS AT THE OBERTI GROVE, MADERA, CALIFORNIA
(1957–1964)

Year and month	Mature female scales in samples*	Mature female scales per twig	Parasitization			Commercial fruit cullage
			A. maculicornis	*C. utilis*	Combined net	
	no.	av.	per cent	per cent	per cent	per cent
1957†						
March............	1,856	30.9	6.1	....	6.1	....
August..........	376	6.3	0.0	....	0.0	22.2
1958‡						
April............	1,186	19.8	5.6	....	5.6	....
August..........	697	11.6	26.7‡	....	26.7	60.2
1959						
April............	204	3.4	79.4	....	79.4	....
August..........	23	0.38	0.0	....	0.0	4.4
1960						
April............	39	0.65	89.7	5.1	94.8	....
August..........	30	0.50	0.0	43.3	43.3	0.2
1961						
April............	22	0.37	50.0	40.9	90.9	....
August..........	...	....	....	....	....	0.5
1962						
January..........	119	2.5	5.9	29.4	35.3	...
August..........	21	0.44	0.0	38.1	38.1	0.6
1963						
May.............	13	0.27	61.5	38.5	100.0	...
August..........	1	0.02	....§	....§	....§	0.4
1964						
May.............	19	0.39	52.6	36.8	89.4	...
August..........	4	0.08	0.0	25.0	25.0	0.3

* Sample size was 60 twigs from 1957–1961 inclusive, and 48 twigs from 1962–1964, inclusive.
† First year under biological control.
‡ Extraordinary summer survival of *A. maculicornis* possibly associated with industrial sprinkling operations adjacent to test groves.
§ Since there was only one scale in the sample, no percentage figure is listed.

initiated in the grove, and the parasites were not able to exert control during that year or the next. However, because of the remarkable survival of *A. maculicornis* during the summer of 1958 this parasite achieved a phenomenal month-by-month destruction of scales during the fall and early spring months—reaching a time-point peak of 79.4 per cent parasitization in April on a then much-reduced density of mature female scales. The cullage level that year was only 4.4 per cent, in contrast to 22.2 per cent the first year after cessation of insecticidal treatments and 60.2 per cent the second year.

Since the effective establishment of *C. utilis* in 1960, the level of culled fruits has remained at about one-half of 1 per cent or less (table 8). It will

be noted that there is no spring sample for 1962, but there is one for January of that year. With the normal rapid increase in activity of *A. maculicornis* between January and late April, it can be assumed that the scale density would have been reduced by April by some 50 per cent and the time-point parasitization of *C. utilis*-free hosts would have reached a level of perhaps 70 to 90 per cent. The low combined net parasitization by the two species for this January date cannot be taken, therefore, to indicate a failure of control. The densities of scales remained low thereafter. The low level of culled fruits and the densities of scales in August confirm this interpretation, as does our whole experience for twelve years' work with *A. maculicornis*.

UNPARASITIZED MATURE FEMALE *PARLATORIA OLEAE* AT BEGINNING AND
END OF AN EXPERIMENT USING DDT TREATMENTS AS A CHECK-METHOD
OF APPRAISING THE ROLES OF *APHYTIS MACULICORNIS* AND
COCCOPHAGOIDES UTILIS
(Duncan and Oberti groves)

Grove	Condition of test	Unparasitized mature female scales per twig	
		Beginning: January, 1962	Ending: May, 1964
		average	*average*
Duncan	No treatments, both parasites fully active	0.38	0.00
	Treatments against *C. utilis* only	0.10	2.52
	Treatments against *A. maculicornis* only	0.06	16.10
	Treatments against both parasites	0.23	107.54*
Oberti	No treatments, both parasites fully active	1.60	0.04
	Treatments against *C. utilis* only	0.02	0.92
	Treatments against *A. maculicornis* only	0.50	7.35
	Treatments against both parasites	0.38	149.33†

* Ratio of increase 488:1.
† Ratio of increase 393:1.

DDT Check Method of Evaluation

A further general indication of the greater reliability of biological control by the combined action of the two parasites acting together, over *A. maculicornis* alone, or *C. utilis* alone, is presented in table 9. This table presents the significant initial and end results from an experiment using DDT as a check method of interfering: (1) more with *A. maculicornis*; (2) more with *C. utilis*; and (3) with both species; compared to (4) plots where both species were left undisturbed. We had hoped that by properly correlating the applications to the active and inactive periods of the two species, we could effectively interfere with one species and not the other in given trees in the same grove. However, we were not able to do this very well.

In the treatments for removal of *C. utilis* alone there was substantial evidence that *A. maculicornis* was also interfered with, as is perhaps inevitable. *A. maculicornis* is somewhat more susceptible to treatments of any kind than is *C. utilis* which has long periods in its yearly sequence when treatments harm it very little. This latter characteristic is of value in environments that are sometimes blanketed from the sky on a vast scale by insecticides being applied to nearby crops; it also has its practical aspect in integrating this biological control with necessary occasional insecticidal control of other pests on olives.

However, there was also evidence (from material not included in this paper) that *C. utilis*, too, was impeded by the treatments designed to remove only *A. maculicornis*. For example, during the summers of 1962 and 1963, parasitization by *C. utilis* in the untreated trees in the Oberti Grove was 38.1 per cent, whereas in the trees treated for removal of *A. maculicornis* only, *C. utilis* achieved only 2.0 per cent parasitization. Again, in the Duncan Grove, the depressed status of this species in summer (doubtless a carry-

over effect from spring treatments for
A. maculicornis removal) was less se-
vere but still substantial. Here, the 1962
summer parasitization by *C. utilis* was
only 6.3 per cent, in contrast to 78.5
per cent in the untreated trees; and,
again, in 1963, it was 7.7 per cent in
contrast to 33.3 per cent.

Since this species parasitizes young
scales in the fall and these survive into
the spring, the treatments designed for
removal of *A. maculicornis* only, inter-
fered with the spring parasitization by
C. utilis to a somewhat lesser extent,
but still appreciably so. For example,
from untabulated data the spring para-
sitizations by *C. utilis* in the Oberti
Grove in 1962 and 1963 were 32.8 per
cent and 10.3 per cent, respectively, for
the treated trees; and 38.5 per cent and
36.8 per cent, respectively, for the un-
treated trees. For the Duncan Grove
in 1962 and 1963, respectively, the fig-
ures were 12.7 per cent and 1.3 per cent
parasitization by *C. utilis* in the treated
trees, and 44.4 per cent and 40.0 per
cent parasitization by this species in
the untreated trees. The reduced *per-
centage* of parasitization may be due in
part to increase in scale/parasite den-
sity ratios, which the parasites cannot
make up for under the impediments. It
seems obvious that a substantial impedi-
ment occurred. Also, the exact timing of
emergence of overwintering parasites
and the breakdown stage of the DDT
residues, are variables about which we
have no detailed data, and these may
have materially affected parasite ac-
tivity.

Recognizing the shortcomings of
the method, we do nonetheless, gain
something from the results. Table 9
shows that in the untreated biological-
control trees, where both parasites were
active, there was a further marked de-
crease in scale densities during the test
years below that occurring at the initia-
tion of the tests in both groves. The
trees chosen for this group were those
initially having, by prior determina-
tion, the highest densities of scales, al-

though all the trees had comparatively
low densities. Hence the scale densities
in the test trees were, if anything, less
favorable to control by the parasites.

It is also seen in table 9 that final
scale densities were next lowest, and
not markedly high, in the trees treated
to impede *C. utilis* but not *A. maculi-
cornis*. Densities were, however, mark-
edly higher in the trees where treat-
ments were designed to interfere with
A. maculicornis but not with *C. utilis,*
while in the trees treated to curtail ef-
fective action of both species, densities
were about 108 and 149 unparasitized
female scales remaining per twig in the
Duncan and Oberti groves, respec-
tively. This is a 400 to 500-fold increase
over initial densities, and much higher
still relative to the concurrent densities
in the trees in which both parasites
were left fully active, that is, 0.0 and
0.04 unparasitized female scales at the
Duncan and Oberti groves, respectively.

Perhaps we have not properly ap-
praised the relative amounts of inter-
ference by the test materials in these
tests, but the results seem to confirm
our other data and conclusions that *A.
maculicornis* working alone is a better
parasite than *C. utilis* alone. Further
experience with *C. utilis* may lead to a
different conclusion. However, it seems
obvious from all considerations that the
parasites operate well together, each
supplementing the other to give a more
reliable and higher degree of control
than either is likely to achieve alone.

Additional Short-Term Records of Joint Action by *A. maculicornis* and *C. utilis*

In addition to the more specific data
presented here, comparative evidence
from some 20 or more additional groves
or plots where *C. utilis* is well estab-
lished, even though only for the past
three years, indicates a higher level and
greater uniformity of control from
grove to grove, and area to area, than
has been experienced with *A. maculi-*

cornis alone. The critical comparison time has not arrived, for in 1963 and 1964 *A. maculicornis* has had favorable preceding summer periods, and *A. maculicornis* operating alone performed better in 1964 than it usually has. Hence, the best general test will come one year after *A. maculicornis* is again under the stress of a severely hot summer.

Test block areas in a much expanded program of biological control have now been initiated in all major areas where the scale, *Parlatoria oleae,* is a pest on olives. Extensive releases of *C. utilis* have been made, and *A. maculicornis* is already present or will soon move into these areas on its own. Establishment of *C. utilis* is irregular—poor in some places but very good in others—in some of the cases the reasons being obvious, in others not. We feel that with continued effort this parasite will become generally established and will be a potent, even vital addition to the program. The results from the many 1-acre to 3-acre trial blocks, combined with results from approximately 1,000 to 1,500 commercial acres now generally under biological control, should make it possible to predict with what success the entire olive-growing industry might be able to use this method of control.

USE OF K-VALUES TO IDENTIFY THE KEY-FACTOR FOR CHANGE

We found Varley and Gradwell's (1958) technique, an extension of Haldane's (1949) method, useful in identifying the impact of various mortality factors on host population change. This method permits a "key-factor" judgment.

Data are available for analyzing the influences of different kinds of mortality factors on such change from two olive groves from 1956 through 1960. Assuming that mortality caused by *A. maculicornis* (Huffaker, Kennett, and Finney, 1962), is the principal reason for observed differences in actual egg production by female olive scales that reach the mature stage, we may thus concentrate on the mortality, rather than on the natality, in analyzing population change.

In fact, k-values for the "reduction in actual egg production" as based on an assumed mean maximum of 40 eggs per parent female survivor, gave rather uniform values for the present data except for one instance (p. 324). In addition, more extensive data obtained from a grove having higher densities gave no significant difference in average fecundity of unparasitized females, comparing those of the spring and fall generations in the same grove. The mean number of eggs per female was 22 to 23 in both cases. Mean fecundity is normally near 25.

These k-values representing unrealized natality, rather than mortality, are not presented in figures 9 and 10, because we considered it poor procedure to combine reduction in *natality,* based on a hypothetical yardstick of expectation, with actual *mortality.* However, it is recognized that if the expected value could have any real meaning (i.e., if departure from such a yardstick performance could be assigned with reliability to any known cause) then the total population repressive impact (reduced natality plus mortality) would be estimated by total K as so calculated. In our case we do not consider this procedure justified.

Thus, in our usage, total mortality $K = k_1 + k_2 + k_3 + k_4 \ldots$ where the k-value for each mortality is the difference between the logarithms of the numbers per unit of area before and after its action.

Following Varley and Gradwell's suggestion, we also used common loga-

rithms. Our data had been recorded giving the actual egg population, the mean population representing the early settled stage (first- and second-settled stages), the immature third-stage female and the mature third-stage female. Males were disregarded by excluding half the eggs and half the early settled stages, and by observation in later censuses, as the sex could then be determined. Results indicate that populations of this scale are in fact half male and half female (Huffaker, Kennett, and Finney, 1962). Since the males emerge long before the females mature, and are subject to a lower intensity and shorter period of mortality, and since the females are of prime concern, we used only the females.

The component k-values of total K are: k_1 = mortality during the period from the total egg population to peak population level representing the average for first- and second-stages, which overlap in time. [Mortality in these stages (when existing host densities are relatively low, as here) is caused almost entirely by chance loss of crawlers searching for suitable places to settle, and also by the action of rain, heat, wind, and aridity, primarily on crawlers and the first settled stage]; k_2 = mortality from the previous peak level to the peak level of immature third-stage development, losses caused mainly by heat, wind and aridity; k_3 = mortality caused by *A. maculicornis* in third-stage scales from the point of peak immature third-stage development to death; while k_4 = mortality in these same third-stage females from causes other than *A. maculicornis*. Thus, the mortality caused by *A. maculicornis* and that caused by other factors are separated.

Statistically, the populations on which the calculations are based are in some cases inadequate. This may account for the erratic course of change with respect to some of the curves (figs. 9 and 10). Nevertheless, change in total K is seen to be simulated (particularly

for the Hills Valley population) with significant closeness by k_3—*A. maculicornis* attack. This was, therefore, the *key-factor for change* at that location. There are two generations of the olive scale each year. The graphs of figures 9 and 10 plot k-values for both generations. However, *A. maculicornis* is effective only on the overwintered females of the fall-produced generation.

Taking just the Hills Valley grove, the total K-value is seen to reflect very well the action of *A. maculicornis*; total K for the fall generation is high as is *A. maculicornis* attack (k_3) and total K for the spring generation is low, while *A. maculicornis* attack (k_3) is very low indeed. It has already been shown (Huffaker, Kennett and Finney, 1962) that population increases were clearly associated with low *A. maculicornis* attack on the spring-generation females (summer parasitism), while marked population reductions were clearly associated with high *A. maculicornis* attack on the overwintered females of the fall generation. The present technique permits closer comparisons.

Crawler and earliest-settled-stage mortality (k_1) was unusually high in the spring generation of 1956. It held at a fairly high level in the fall generation that year, and in the spring generation of 1957. It was extremely low in the fall generation, 1957, and then remained nearly constant in later generations. Thus, there is little correlation, either positive or negative, with total K and other components. Mortality of late early settled stages (mainly second stages) and early third stages (k_2) was low for the spring generation of 1956. It then rose to one of its higher levels, and subsequently declined, varying considerably with no close conformity to trends in total K or to the key-factor, k_3, *A. maculicornis* attack.

If we consider the Herndon Grove, we see (fig. 10) that *A. maculicornis* parasitization of the 1956 fall-generation scales (spring activity, 1957), and

the 1957 fall generation of scales (1958 spring period of activity), was rather low. Thus, the impact of *A. maculicornis* activity on those generations did not dominate the total K value, as it did for the fall generation of 1958 at Herndon, and for the corresponding periods for every year at the Hills Valley Grove.

We have already alluded to the fact that at the Herndon Grove during those years *A. maculicornis* was not giving satisfactory biological control. Whether the documented near-annihilation of the parasite during the previous summer periods was due mostly to weather severity or to drift of insecticides is not known. All the k_3 values (*A. maculicornis* action) on the spring generation of scales were very low, as was true at Hills Valley.

The overall effect is that *A. maculicornis* was not the key-factor for change at Herndon; nor was any other component factor of total K. During the latter period shown on the graph, *A. maculicornis* did dominate the one major upsurge in total K and its subsequent decline.

An interesting feature of this grove is that k_1 (crawler and early-settled-stage mortality) varied in a manner exactly contrary to the usual action of *A. maculicornis*. Weather appears to be the explanation. The stress of hot summer weather on *A. maculicornis* depresses spring-generation k_3 values, while fall and spring favorability permits high k_3 values on the fall generation of scales. The early summer severity of the weather acts on the crawlers and early settled stages of host spring generation, causing high k_1 values, while the fall weather is not so severe on the fall generation (Huffaker, Kennett and Finney, 1962).

The heat of summer weather, and the summer period as a whole, is a bit more extreme at the Herndon location. Crawlers and early settled stages of the scale are especially affected by this severity in early summer, as is *A. mac-*

ulicornis. This may account for the near-annihilation of the parasite each summer at Herndon, whereas its survival has been better year after year at Hills Valley.

It is seen from these comparisons that *A. maculicornis* attack on the mature females was the key-factor for change only at Hills Valley.

It has also been shown (Huffaker, Kennett, and Finney, 1962) that *A. maculicornis* is also the principal controlling factor for population *size*, this being the other side of the population coin. Thus, we see that *A. maculicornis* appears to be a key-factor for population change under some conditions, and that it is also the primary control factor within the existing regime of climate and cultural practices.

Data are being collected for fuller analysis of the action of both *A. maculicornis* and *C. utilis* attack; the results for *C. utilis* are as yet too limited to permit making conclusions.

The K-values plotted in figures 9 and 10 depict the intensity of mortality from various factors acting on the different stages of olive scales, and show as well the changes in such intensities from generation to generation.

The key-factor for change in population density is expected to be the one which parallels most closely the total generation mortality. Yet, it is essential to compare the pattern of such a key-factor with the changes in *density* of the population. Otherwise, the reader may assume that direct consequent effects on population density or on relative changes in density exist which are not shown in figures 9 and 10. Density itself is in no sense expressed in K-value graphs expressing mortality impact.

Also, the question arises as to what stage of the insect's development should be used as the gauge for comparisons of density, generation to generation. In our case, the early-settled stage is economicaly critical for the eventual harvest of sound olive fruits. However, the densities of this stage were less ac-
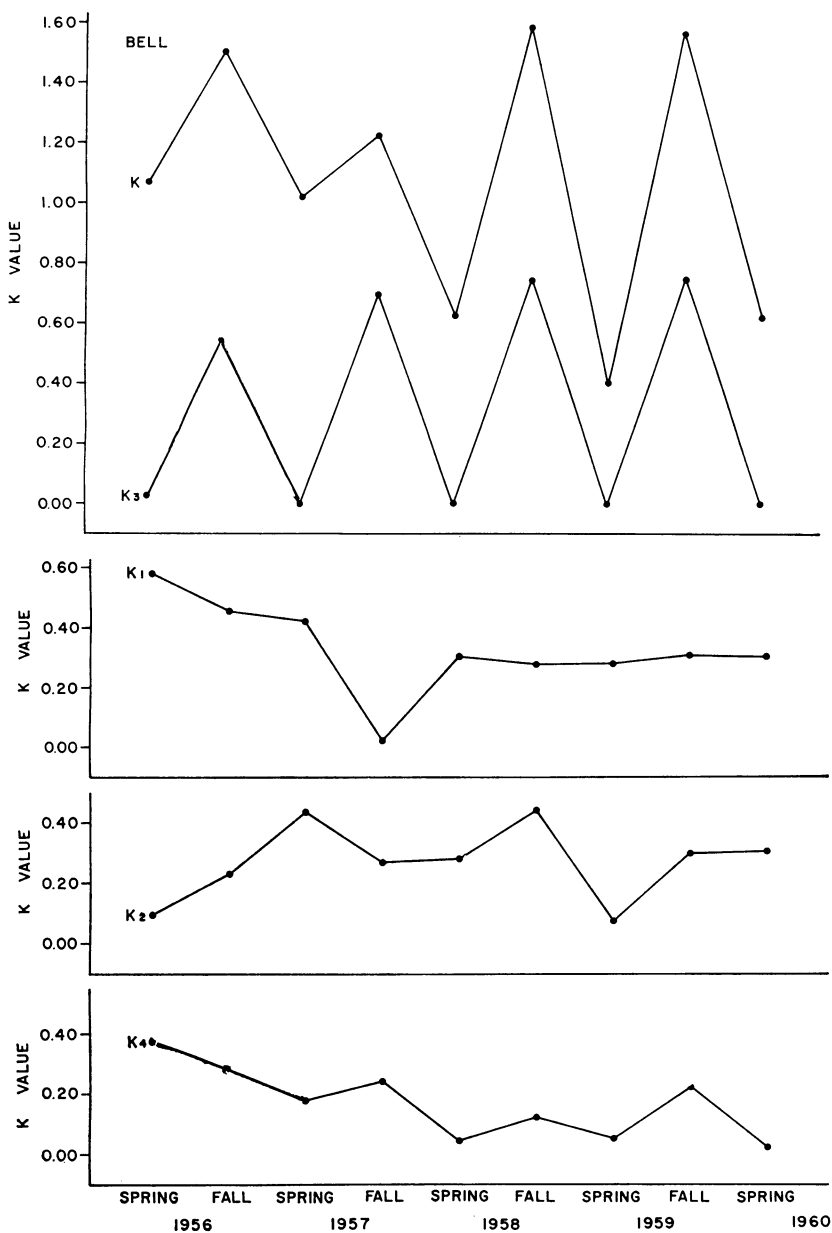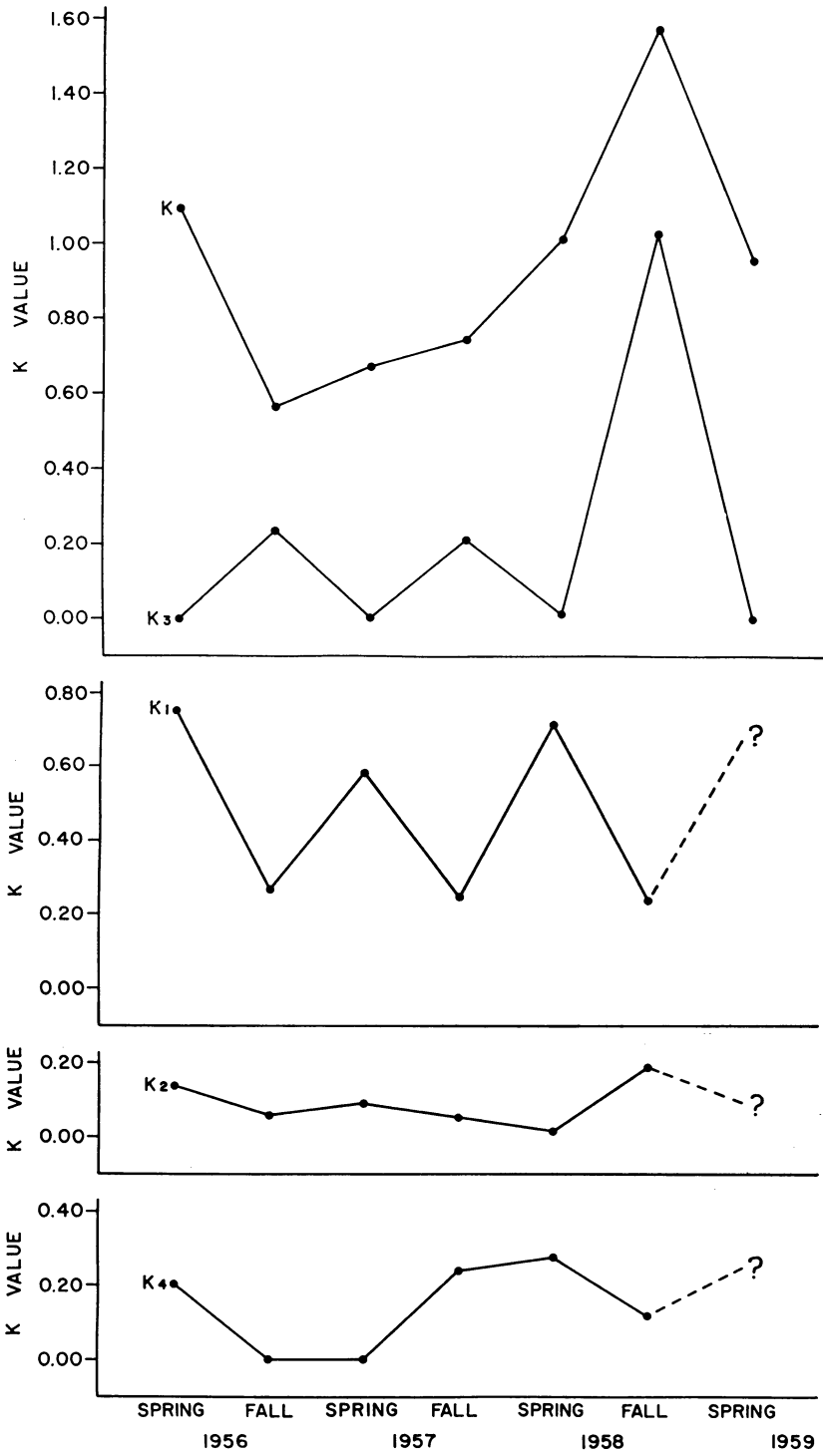
Fig. 9. K-values for various mortality-causing factors for detecting the key-factor for change in spring and fall generations of *P. oleae*—Hills Valley, California.

curately appraised than was the egg stage. There was also a substantial loss of crawlers from various causes between the time that total mortality of the parent generation of females culminated, and the time of census of this stage. The egg population is of course

the actual brood beginning. Here the only variations in egg production per surviving female occur between the time of total K-value measurement and the census of the stage.

Thus, although we plotted the changes in density from each respec-

Fig. 10. K-values for various mortality-causing factors for detecting the key-factor for change in spring and fall generations of *P. oleae*—Herndon, California.
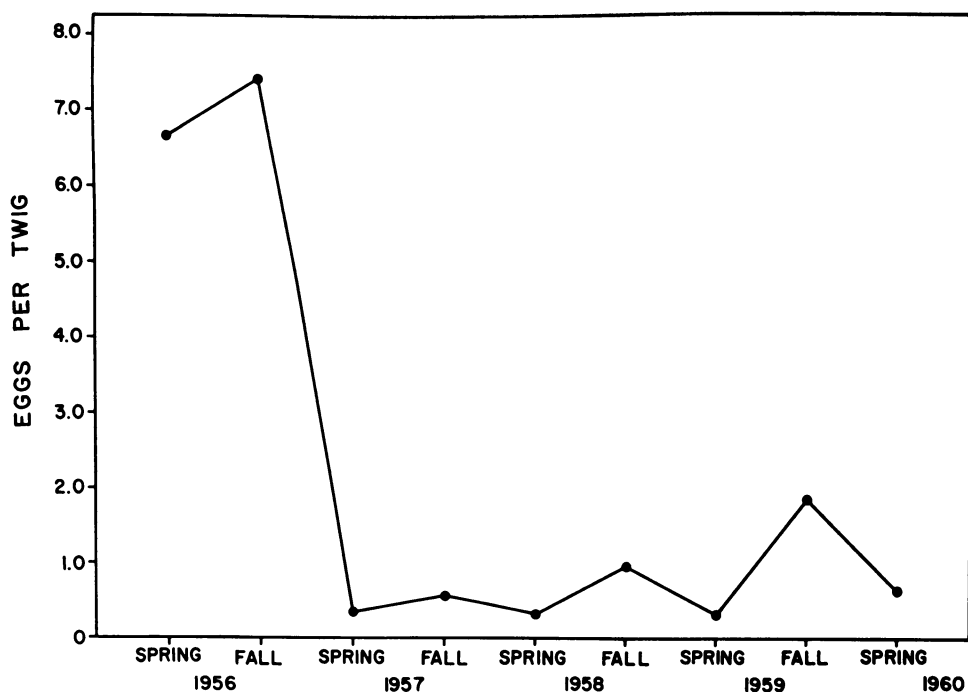
Fig. 11. Egg densities of *P. oleae* for spring and fall generations—
Hills Valley Grove, 1956–1960.

tive stage to the same stage of each subsequent generation, we present here only the data for the egg stage, figures 11 and 12. In figure 11 we show the densities as such, while in figure 12, the bar graphs show percentage change in density, either increase or decrease, between the generations.

Comparing figure 11 with figure 10, we see that general density patterns are similar to patterns expected from the total mortality impact just preceding each density, and also that k_3, *A. maculicornis* attack, is the most similar in pattern to the egg density pattern. It should be noted here that the data for other stages gave the same sequence of spring to fall alternation in patterns of change, but the degrees of change did not conform quite so closely to total K of the previous, or parent, generation, or to k_3, *A. maculicornis* attack. It is obvious that the farther removed from the parental adult survivors is the stage used as the criterion for generation-to-

generation change, the greater will be the departure from conformity in pattern to total K, and thus to a given factor most closely conforming to total K.

Now considering percentage change in egg density, generation to generation, rather than density as such, we note a striking, although not perfect correspondence with total K-values, and a corresponding conformity with k_3, *A. maculicornis* attack.

Keeping in mind that if the total generation mortality is about 92 per cent, the population will neither increase nor decrease (see p. 291), we understand why it is that the percentage increase in numbers of eggs from one generation to the next is so much greater with only a small decrease in the corresponding total mortality of the producing females.

For example, taking here the data for the increase in egg-density phase of figure 12, that is, spring to fall changes, there was a rather high total K in the

spring of 1956 (figure 9), in spite of the low *A. maculicornis* attack. Also, densities were already high since biological control had not yet been established. The percentage increase in egg density (figure 12) was then only 8 per cent. Total K was somewhat less in the following spring, 1957, and the corresponding change in egg density from the spring to the fall of 1957 was 60 per cent. Again, total K for the spring of 1958 was still less, and the corresponding increase in egg density from the spring to fall of 1958 was 197 per cent. Also, the lowest total K-value of all, representing a further sharp drop, was in the spring of 1959, and the corresponding increase in egg density was 472 per cent (see figures 9 and 12).

Considering now the decrease phases, which as previously shown, are invariably associated with high previous *A. maculicornis* attack—as are the increase phases associated with low previous *A. maculicornis* attack—we see that in terms of percentage, the decreases also correspond to total K-values, and likewise to *A. maculicornis* attack, but to a less close degree. Here, it is obvious that decrease cannot exceed 100 per cent, while of course, increase may. Here we submit that *A. maculicornis* attack on the fall generation of 1956 was probably considerably higher than indicated by our data. (The sample was taken too early; this fault was corrected in later sampling.) If this assumption is true, the total K-value at that time would have been higher than at any other time, and this would account for the very striking subsequent reduction in egg density. Total mortality (K) must have been higher, otherwise a 95 per cent subsequent decrease in egg density would not have been likely to result. The lowest total K-value of the decrease phase was on the fall generation of 1957 (fig. 9), and the decline in subsequent egg density was the lowest observed, at 43 per cent. The two other total K-values for the decrease

phase were almost identical, as were the k_3 values, *A. maculicornis* attack, and the corresponding subsequent decreases in egg density were equal at 66 per cent each.

For the first drop in egg density, either there was an inadequacy in the sampling, resulting in nonrepresentative estimates of total mortality (K), or of the populations involved; or else the egg production by the producing females was lower than normal. Otherwise, a decrease of 95 per cent (fig. 12) in egg density could not have occurred. We know that the samples were inadequate, particularly at the low densities attained at the end of the decline period. However, the data do show that the peak in progeny per apparent surviving female was unusually low at only 3, and every successive sample also showed supporting evidence of very low populations. We believe that additional *A. maculicornis* action subsequent to the time of the sample from which total K of the parent generation was determined, sharply reduced the number of eggs laid by the females classed as survivors. That year, the progress of egg deposition was retarded for the date of the sample (roughly the same each year). Had a slightly later measure of *A. maculicornis* attack been taken, the effect of k_3, and consequently total K, on the parent females may have been higher—thus bringing total K into closer agreement with the observed 95 per cent decrease in the egg density between the two generations.

We cannot rule out the possibility of unusually low inherent natality independent of *A. maculicornis* attack, but it is the only time we have had an indication pointing to this possibility; because of the alternative explanation, it cannot be considered a probability. We have already considered the question of using k-values for the "reduction in actual egg production" (p. 318).
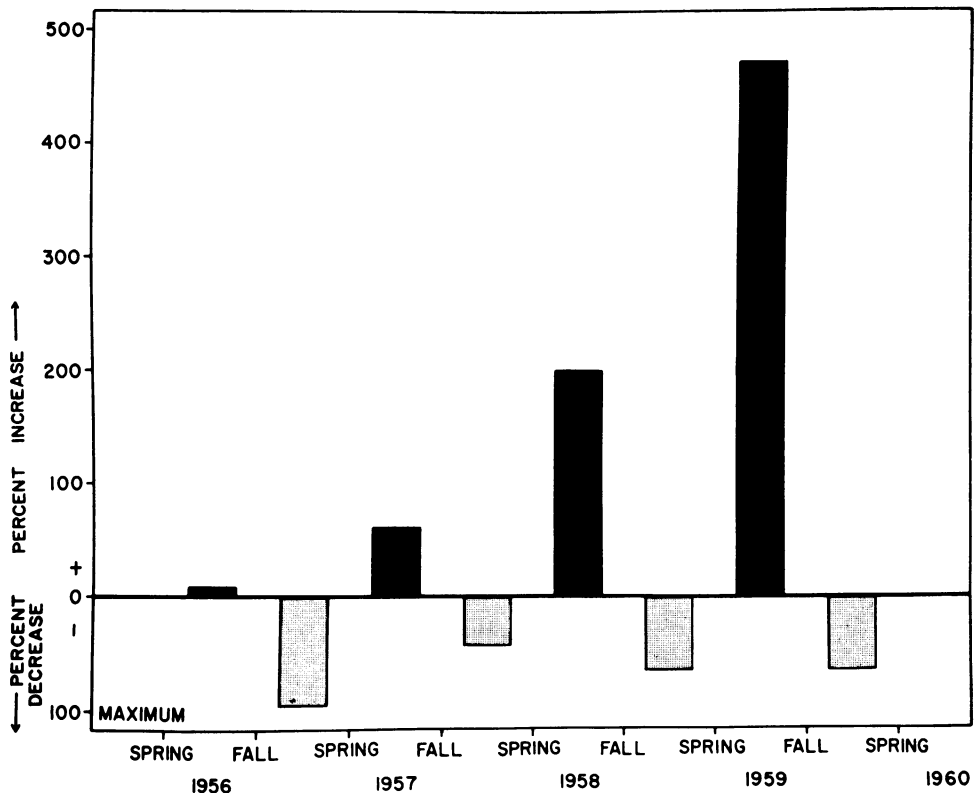
Fig. 12. Percentage change in egg densities of *P. oleae*, generation to generation—
Hills Valley Grove, 1956–1960.

DENSITY-DEPENDENT OR NONDENSITY-DEPENDENT
ACTION OF *A. maculicornis*

Much controversy exists in the literature relative to the question of whether entomophagous parasites and predators, even those admittedly effective as control agents, act in a density-dependent way—that is, whether they cause a proportional increase in deaths with increase in host or prey density. Biological control has been demonstrated on many occasions (DeBach, 1964), but clear proof that the biotic enemies involved have acted in a density-dependent way has often been left to inference. The works of Morris (1959) and Neilson and Morris (1964),

however, are notable exceptions.

Applying this inference to control of olive scale by *A. maculicornis*, and omitting consideration of *C. utilis*, all we can say now is that its action in the broad overall sense appears to be density-dependent. Certainly the parasite's efficiency is very high during the spring period some time after it is first introduced into high-density situations. An apparently confusing aspect is that its efficiency is also very high in the spring during especially favorable years, even after host densities have greatly declined.[5] This is probably to be explained

[5] However, in one such study as yet incomplete, wherein the percentage of parasitization was plotted against density of acceptable female hosts, a strong positive regression was obtained. The data were plotted tree by tree, for 20 trees. Sample size was greater than was necessary to obtain 99 per cent confidence. From each tree 100 twigs were taken, each having about 20 pairs of leaves and associated stem segments. Unless the correlation was due to common association with some unknown factor, or unless a chance event had occurred against odds of less than 1:100, *A. maculicornis* performed in a true density-dependent way, according to definition.

by the fact that each summer the host density rebounds enough so that high searching success by *A. maculicornis* is again possible the following spring, at which time numerical increase of the parasite is extremely rapid (fig. 1).

There is an unproved implication here that even if the weather stress did not intervene during the summer, *A. maculicornis* would then still operate less efficiently, because of the lower host density; or else the parasite would reduce the host density still further, to such a point that reduced parasitization would result at some later time. The intervention by the weather pattern prevents the enacting of this alleged process, and clear proof or disproof thus is not readily obtainable.

Regardless of this reduced efficiency during the summer, *A. maculicornis* gradually or sharply reduces infestations after it is introduced into groves (Huffaker, Kennett, and Finney, 1962). This is effective biological control. It may be inferred that if the effectiveness of *A. maculicornis* did not in general decline at some much lower host density, or if some other density-dependent component of total stress on the scales did not decline sufficiently, continued decimation of the host to the point of actual annihilation would occur. We cannot think of any other kind of density-dependent element of total stress on the host in this situation that could possibly relax in its effects after such low densities are attained suffici-

ently to account for the survival of the scales, tree by tree, branch by branch, in olive groves, assuming here an undiminished intensity of attack by *A. maculicornis*. In fact, intraspecific competition of the olive scales for food at such low densities is almost nonexistent. The scope for relaxation of such competition in this realm of density seems far too limited for it to serve this role. Intraspecific competition for shelters would appear to have long since almost completely relaxed.

Thus, since complete annihiliation of the host does not occur, this appears to mean that the parasite's action is relaxed at least at very low host densities. Several sets of data suggest this relationship, but they are inconclusive, possibly because of the many interrelated and confusing variables involved. An intensive effort is currently being made to collect conclusive data at very low host densities. Until such data are at hand, there seems little reason to discuss these variables and the complexities involved.

(The work of van den Bosch (in press) strongly suggests a true density-dependent action of the parasite *Aphidius smithi* Sharma and Rao, on the pea aphid, *Acyrthosiphon pisum* (Harris), and at the same time, shows how other variables, both biotic and abiotic, may either complicate or enhance detection of a true density-dependent action by such a parasite.)

THE QUESTION OF COMPETITIVE RELATIONS AND THE USE OF MULTIPLE INTRODUCTIONS

A last question here is that of competitive displacement, or interference by one of these parasites with the other. If *A. maculicornis* were inherently capable of completely excluding or annihilating *C. utilis,* the latter would not have become established. Competitive pressure by *A. maculicornis* on *C. utilis* in groves where the host species is already at a low population level, is, how-

ever, a possible reason why it is so difficult to get *C. utilis* well established in some groves. We feel, nevertheless, that once *C. utilis* is well distributed in the groves, its position will be improved and it will not be under such severe stress from competition with *A. maculicornis*. The readiness with which it has often been established, and the vacant niche it occupies, seem to us to

be assurance against its exclusion by *A. maculicornis* (see page 285, and also Kennett, Huffaker, and Finney, 1966).

On the other hand, this same reasoning does not apply when we consider whether *C. utilis* may ever displace *A. maculicornis*. The evidence given earlier in this paper indicates that *A. maculicornis* will remain the dominant factor during the spring period of activity, if not the dominant factor overall. *C. utilis* will dominate the summer activity and also serve as a strong reliability factor during the spring period.

This brings up the renewed polemic interest in the question of whether it is wise to carefully preselect the particular species of enemy to be introduced against a given pest species and to introduce only the single species judged superior in overall performance. The common practice for many years has been to introduce as broad a complex of suitable species as possible. The present data detail the pattern and reasons for the improved control of olive scale being achieved since both *A. maculicornis* and *C. utilis* have become established, in contrast to the conditions prevailing when *A. maculicornis* alone was present. This example thus adds to the empirical evidence favoring multiple introductions. Of course, a great weight of such evidence relating to specific examples cannot entirely refute the possibility that a lesser degree of control may be achieved as a result of introducing two or more enemy species rather than the best one alone.

We enter this discussion fully realizing that the record of biological control is too sketchy, and the mathematical or theoretical solutions thus far presented are too limited in applicability to real situations, to serve as any final answer to the important questions raised.

The senior author has for a good many years had some reservations, on theoretical grounds, against the concept that multiple introductions must necessarily result in improved control. He has felt, however, that, in general, Smith's (1929) deductive arguments in favor of making multiple introductions, combined with the weight of the empirical evidence, justify the common practice. The hypothetical models Smith employed admittedly lack some degree of general applicability or realism.

Early contrasting positions on this subject have been reviewed in papers by Pemberton and Willard (1918), Smith (1929), Turnbull and Chant (1961), van den Bosch *et al.* (1964), and Doutt and DeBach (1964). These latter two support the practice of making multiple introductions. Doutt and DeBach, however, accept the idea that under certain circumstances a given additional enemy *could* bring about a deterioration in the overall degree of biological control achieved.

The deductive conclusions of Nicholson (1933) in this respect were not considered in the paper by Turnbull and Chant (1961), nor in that by Doutt and DeBach (1964) nor in van den Bosch *et al.*'s (1964) work. G. C. Varley, however (personal communication), considers that Nicholson proved it unsound to make such multiple introductions indiscriminately. While some caution is justified, the way in which Turnbull and Chant reopened this question has caused administrative officials to hesitate in making *any* introductions, if even moderately effective natural enemies are already present, or if funds available do not permit an *exhaustive* investigation to attempt to establish just which single species of enemy should be introduced first. Such an attitude is the last thing we need at present in our period of renewed vitality and great promise of expanding success, using orthodox methods of biological control but emphasizing more enlightened ecological approaches. Success will certainly turn on intelligent ecological programs of evaluation, pest management, and integrated practices. Moreover, as Turnbull and Chant (1961, p. 743) remind us, it may not be

possible, within the limits of our present ecological knowledge and the urgency of practical limits of our present solutions, to make the extended studies necessary to assure the best preselection. Indeed, it may *never* be possible to make such exhaustive pre-investigations.

Conceptually—on some uniform, small island, for example—a given pest species may be under good control by a host-specific entomophagous parasite. A euryphagous enemy might be introduced which normally would pay very little attention to the given pest species, but which, given an unusual concurrence of events, might develop extremely high numbers from its attacks on more preferred, alternate host (or prey) species. At such times, after decimating its preferred host population, it might then exert a near-annihilative pressure on the given pest species, thus causing the complete annihiliation of the efficient host-specific enemy by eliminating its food supply. The pest species would then be free of the operation of this efficient enemy and could outbreak. Or, on the other hand, the efficient enemy might be only partially eliminated; thus, the pest species would be free to increase for a prolonged period, until this effective enemy again attained a controlling status.

In uniform simple environments, or microcosms, situations were visualized by Nicholson (1933) wherein the combined effect from two or more primary enemy species could be less than that from one good one. This author considered: (1933, p. 154) "When a new specific parasite species is introduced to attack a host species that is already attacked by specific parasites, the density of the host at the stage attacked by the introduced parasite is increased"; and again: "When a new specific parasite species is introduced to attack a host species already attacked by specific parasites, the initial and final steady densities of the host may be either increased or decreased." He adds (p.

155): "More detailed investigation shows that the introduction of a new parasite may either increase or decrease the density of the host species at any stage of its life cycle, other than that attacked by the introduced parasite." Nicholson then described situations in which such increases or decreases would occur.

On theoretical grounds Nicholson has shown, for example, that an earlier-acting parasite has adequate advantage over a later-acting parasite: it may, once established, continue to exist with a later-acting parasite even though it possesses, within certain definite limits, a lower power of discovery than the later-acting parasite that is comparable in other respects. The later-acting parasite having the higher power of discovery will presumably be the regulating agent. According to these theoretical determinations such an earlier-acting parasite inserts itself into the food chain in a way that causes an increase in the densities of both the host species and the later-acting, regulating parasite species. If this has any practical meaning in nature, it is that under such conditions, the existence of a *series* of enemies means that the control exerted will be less than that exerted by the most efficient enemy operating alone. Thus, this view is compatible with Watt's (1965) and Zwölfer's (1963) interpretations (see p. 331).

Yet, Nicholson himself has stated that the later-acting of two host-specific enemy species must have the higher power of discovery, for if the prior-acting species has the greater ability in this respect, the later-acting species cannot survive at all. Now, it also appears to us that if we conceive that the later-acting enemy species, having the higher power of discovery, is present first and constantly holds the host species at the respective theoretical low density consistent with that searching power, the host density would be too low for the earlier-acting enemy species to become established at all. In varying

environments of localized near-annihilation from time to time, a poorer searching enemy would often be locally confronted with this problem of establishment. Under natural fluctuating situations, severe pressures arise from lag effects in the numerical response of enemy species. The great numbers of enemy individuals that finally result exert an intense, prolonged pressure on the host or prey population. It is questionable whether the parasite with lower discovery powers could survive—other things being equal—even though it acts on an earlier stage in the life cycle of the host and could perhaps survive, in spite of its inferior power of discovery, if environmental conditions remained stable.

Nicholson (unpublished mss.) also stated, "It will be noticed that the limits of the permissible powers of discovery [permissible of conceptual coexistence] for any given natural enemy do not permit of more than a very moderate modification of the power of discovery,"... and that "... comparatively small modifications of the power of discovery of a natural enemy would cause the extermination of one or more species [of a series acting on the same host]". He also stated, "For a permanent state of equilibrium it is necessary that the concentrations of the host and the two [or more] natural enemies should be exactly maintained from generation to generation."

Here Nicholson was dealing with steady-state densities, which are not representative of field situations. He was also assuming that the "area of discovery" of the parasite species is a constant—an unreal assumption. Furthermore, he was considering for each theoretical situation a given *constant* set of conditions, a microcosm as it were. In such microcosms there is a limited theoretical range (1933 p. 153) in the parasite's power of discovery, if it is to coexist with a pre-existing parasite of a given power of discovery. We suspect that in such microcosms the areas of discovery of any two such competing parasites would seldom be so delicately balanced as to permit them to jointly have a steady state of coexistence with the host. Furthermore, Nicholson here projects what would happen *if* the parasites (host-specific) concerned *could* coexist in the given microcosm. It is our belief that the species which can survive at the lowest density would inevitably completely displace the others in any such uniform microcosm, provided the host species is assumed to be under control by such enemies, other things being equal.[6]

In complex field situations it seems unlikely that many pairs of potential competitors, those acting as essentially primary parasites of the same host species, would have searching capacities so overlapping within the delicate range envisioned over any appreciable geographically diverse terrain so that they would coexist in such a way as to give a lesser degree of overall control than if only the better species were present.

It appears to us that in these more natural situations the species with the capacity to control the host at the lowest density where operating alone would dominate the situation although it may not completely displace the other. Its advantage at low host densities would tend to prevent an earlier-acting species of lesser searching power from interfering with it at those places where it is in fact superior.

In field situations we are not introducing parasites into a single simple environment of unchanging conditions, as Smith (1929) and van den Bosch *et al.* (1964) stressed. Usually we wish to achieve biological control of a pest species over an extensive geographic range with varying conditions and also with pronounced changes occurring over a period of time at any given place. We

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[6] The case of coexistence reported by Utida (1953) is a special one, and cannot be discussed here.

are therefore dealing with a mosaic of environmental conditions in both time and space. It seems evident that the chances of improved, more reliable overall control are greater when a complex of enemy species is present, since collectively they possess a greater adaptability to contrasting conditions in space and changing conditions in time. (See also Silvestri, 1932; Smith, 1937; and Flanders, 1965). Furthermore, as Huffaker (1957) stated, relatively small, subtle features of the general climate, or even the biotic modifications expressed in the microenvironmental "climates," may be of paramount importance.

Nicholson's general views and their consequences for practices in biological control contrast somewhat with the academic questions of the steady-state conditions referred to. He has stated (personal conversations) that as former Chief of the Entomology Division of the Australian Council for Scientific and Industrial Research Organization, he never used these theoretical conclusions to deny the introduction of a complex of enemy species; rather, he favored the introduction of all enemies which possess suitable biological properties.

Turnbull and Chant (1961) also used a simplified model by which they purport to dispose of Smith's (1929) general position. One objection to their treatment is their confusing discussion of Smith's use of "niche" and "prolificacy." Also, in their model they assume that parasite A is "superior" to parasite B extrinsically (outside the host) and intrinsically "inferior" to parasite B (when both attack the same individual). Furthermore, they assume that parasite B has a rate of increase which is less than that of the host, and "thus B has no chance of controlling the host by itself." Here it is an extreme fallacy

to assume that in many natural situations a parasite *must* have an intrinsic rate of increase greater than that of the host in order to control it. However, a high rate of increase is necessary for the parasite to gain a controlling status quickly. But once it attains this, and has decimated the host population, even if helped along by impact of food shortage for the host, or by other stresses, it may maintain control, if not interrupted by other unfavorable factors. This may be so even when the parasite's intrinsic rate of increase is much less than that of the host. At equilibria positions, differences in inherent searching powers, rather than intrinsic powers of increase, are of paramount importance. Strangely, Turnbull and Chant attempted to pool these two parameters by saying that "prolificacy" is restricted if hosts in which to lay the eggs are not found.[7] It also seems obvious that if Turnbull and Chant's inferior parasite is to exterminate the superior parasite, it can only do so if it also exterminates the host. Other aspects of their model are also unrealistic, as they state.

In our case history, *A. maculicornis* does need, however, a high intrinsic power of increase, because it does not maintain efficient engagement during the summer period, when the host population increases under the relaxed parasitic pressure. Hence *A. maculicornis* must quickly re-establish a good ratio of searching parasites to hosts before the female hosts mature and lay their eggs. This it does.

Ullyett (1947) considered that "catastrophic" factors such as disease might cause such a seasonal or periodic annihilation of given stages of a host species, creating an even-brooded condition, that a specific enemy requiring an uneven-brooded host condition would be prevented from maintaining control. It is interesting that a comparable ex-

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[7] In the present example of biological control of olive scale by *A. maculicornis* and *C. utilis*, the data support the view that the performance efficiency of *A. maculicornis* in the spring period is primarily dependent on its searching efficiency, and only slightly if at all on its not having available enough eggs to parasitize more hosts (assuming they could have been found).

ample is at hand from studies in Fiji on the biological control of the hispid beetle *Promecotheca reichei* Baly. According to Taylor (1937), this native Fijian insect had been under good control by its own native enemies (particularly *Elasmus hispidarum* Ferr. and *Oligosita utilis* Kow.) prior to the inadvertent establishment of the mite *Pediculoides ventricosus* Newp. The attack of this predatory mite created an unfavorable even-brooded condition in the host and the formerly efficient enemies could no longer control it. Through the later introduction of an exotic parasite from Java, *Pleurotropis parvulus* Ferr., which attacks all the larval stages and the pupal stages, a very high degree of biological control— even better than before—has been reestablished. However, this detrimental action by *P. ventricosos* is not a fair empirical indictment of past practices in biological control, since it is an enemy of a much broader host range than those commonly introduced for control of specific pests; in this case, in fact, it invaded on its own, rather than being introduced for use in any program of control.

Turnbull and Chant (1961) further state: "The more species of agents that attack the pest, the sooner competition will start and the more severe will be its effects"; and: "... a single efficient organism introduced without competition would appear likely to serve our purposes best." We believe, on the contrary, that usually the additive compensatory potentials inherent in the presence of a complex of species will more than offset any possible disadvantage from such competition. Turnbull and Chant propose that all candidate species for introduction be thoroughly appraised ecologically before introductions are made and that only the "ideal" one be introduced. Aside from the fact that the best parasite in one aspect of the ecological mosaic may certainly be different from the best one(s) for other patches of the environment, it is not

even *possible* to preselect with much certainty the best ecological entity for use in the new environment. There is also the question of financing the introduction of a species.

We can, should, and do attempt to select the better *primary* parasites, by giving emphasis to enemies in environments climatically comparable to the region where the introduction is desired and by considering the parasite's efficiency and role at low host densities. Turnbull and Chant omit the point that the fauna and flora in two such climatically equivalent regions may be vastly different. Such biotic factors may be as important as physical factors in determining the success of a given enemy.

Both Watt (1965) and Zwölfer (1963) support Turnbull and Chant's (1961) view that a single efficient enemy species will do a better job of control if it is not hampered, in effect, by competition with other enemy species—that is, if other attacking species are not introduced. These authors inferred a cause and effect relationship from an observed association between the number of attacking species associated with related host or prey species, and the relative abundance and degree of stability exhibited by the populations of the host or prey species concerned. Comparisons were thus made between totally different sets of biological and ecophysical systems.

Zwölfer (1963) discusses the host-parasite complexes of several species of European moths: *Choristoneura murinana, Coleophora deuratella, Paraswammerdamia caesiella, P. lutarea, Hydroecia petasitis* and *H. micacea.* He found that each of these species is attacked by "one or two (scarcely three) biologically specialized and well synchronized parasite species." He notes that in the *Choristoneura murinana* and *Coleophora deuratella* complexes these well-adapted parasites are confronted with heavy competition by other parasites, whereas in the *Para-*

swammerdamia spp. and *Hydroecia* spp. complexes, the well-adapted parasites operate with little interference by competing parasites. He infers that the greater instability and lack of natural control as exhibited by the *Choristoneura* and *Coleophora* species are due to the interference of the presumed otherwise capable parasites by this host of competing parasites. He likewise infers that the greater control and stability of the other host species referred to are a result of the fact that their capable parasites operate pretty nearly alone.

In using such observations for such a purpose, only strictly comparable situations may be employed. Even though the observations in each case were limited to representatives of specific taxonomic groups, the fact that different species of prey, different species of enemies, and different meteorological regimes and community relationships, in general, were involved, prohibits the inferences drawn.

On the other hand, in the history of biological control of insect pests and weeds there exist *more nearly* suitable empirical data to suggest or support the principle Watt challenged. In this case, there are a great many species of pests, each of which has been a separate subject for biological control attempts (DeBach, 1964). Over and over again, all over the world, enemy species have been introduced, often only one or two at a time, with regard to effective local releases against the same host or prey species. At each respective place, these "experiments" have been conducted under conditions of climate and ecosystem relations in general which can be considered far more nearly the same at the times when enemies "a", "b", "c", "d" *et cetera* were respectively introduced, than those conditions which obtained in comparisons of entirely different species of host or prey species, as were made by Watt and Zwölfer.

While the gross record of deliberate introductions of enemies to control given pests (running into the thou-

sands of introductions) is largely undocumented as to the degrees of control achieved by the first introduced enemy alone vs. the first two vs. the first three or four, *et cetera*, two facts seem abundantly clear from experience alone: (1) introduction of additional enemies has invariably improved upon the degree of overall control or else it has made little difference, and (2) unless we can make the highly unlikely assumption that in *all* cases the first parasite was an inferior one and that later one(s) added could have done a better job if introduced alone, the suggestion of Watt is disproved that the more enemies a species has, the poorer and more unstable will be the degree of control. For in this record of biological control we have had a sequence (in time it is true, with some variation in weather *et cetera*), involving a suitable comparison of the action on the same host species in the same communities of enemy "a" alone vs. enemies "a" and "b" vs. enemies "a", "b" and "c" *et cetera*.

We strongly suspect, in fact, that *cause and effect* possibly involved in the association observed by Watt (1965) and Zwölfer (1963) may have been reversed in their inference of a "principle". We feel that in the case where evolution has produced a really outstanding host-specific enemy, one that reliably controls its host at a low density, there is a much reduced chance that additional host-specific enemies will have evolved in association with the given host species. In fact, many such previously existing inferior species may have lost their positions. Host species that do not possess such a really efficient enemy, then, but which are controlled occasionally by complete exhaustion of their food supply, for example, will be more abundant (although more unstable in one sense), subject to outbreaks, and will have had greater opportunity to have evolved a complex of species of somewhat more fugitive nature, perhaps, merely as by-products of their greater abundance (except at pe-

riods following drastic catastrophe resulting from disease or famine). Stenophagous enemies can more readily serve as such fugitive, rear-guard agents of control, but less reliable ones.

Monophagous species will generally exhibit a definite superiority over other species in utilizing the host or prey species under certain conditions to which such enemies have superior adaptation. Regarding enemy species that are monophagous for all practical purposes in the habitat concerned, it is difficult to see how an introduced inferior species could so interfere with a really superior established, enemy species that the two of them combined would cause an increase in the host or prey population above that experienced under the action of the superior one alone. Under fluctuating and oscillating conditions in nature conceptual steady-state possibilities are not realized. The inferior enemy species would be under especially severe pressure to survive at the lowest positions of the fluctuations in host densities while the superior species would be fully capable of maintaining itself. The superior enemy would then tend continuously to displace the inferior one at all times and places where the superiority exists. It is difficult to see how it could possibly be caused to so reduce its intensity of action on the host as to permit the increase in the host population necessary for the support of the additional introduced enemy species. Also, the superior enemy species would seem to assert itself and the host species would be reduced by it to a level inimical to the inferior enemy species, even if the superior species were the later introduction.

If, of course, a really unused niche exists and there is not complete or even strong interspecific competition between the two introduced enemy species, as is so in the present case of olive scale and our two host-specific[8] parasites, *A. maculicornis* and *C. utilis,* the unused niche may be filled by a generally inferior enemy species. Note here, however, that such a "generally inferior" enemy (considering year-after-year performance and all microhabitat situations) is in fact the superior one relative to its own specific niche. Where diversity in time and space creates such distinct, if overlapping possibilities, the total potential of control would seem to be better met if many enemy species, each superior in its own niche, were available.

Arthur, Stainer, and Turnbull (1964) indicate that it was unwise to introduce into Canada the ichneumonid parasite *Temelucha interruptor* (Grav.) against the pine-shoot moth, *Rhyacionia buoliana* (Schiff.). They showed that this parasite is, however, ecologically more of a hyperparasite on the more effective primary parasite, *Orgilus obscurator* (Nees), than it is a primary parasite of the pine-shoot moth itself. But they did not show by field studies that this "harmful" parasite, *Temelucha interruptor,* is in fact sufficiently abundant in the field to actually depress the overall influence of *Orgilus obscurator* on pine-shoot moth populations. Nor did they demonstrate that the latter is capable of controlling the shoot moth even if *T. interruptor* were not present. This work by Arthur, Stainer, and Turnbull does not constitute an empirical example of a harmful effect from introducing a complex of species rather than just one. Arthur, Stainer and Turnbull (1964), however, introduce a very excellent ecological tool in appraising the degree of "ecological" hyperparasitism *vs.* primary parasitism.

It is certainly unwise to introduce purely secondary parasites; and the nearer to this status, ecologically, a second parasite is found to be, the more harmful its potential effect on overall control, other things being equal. With a parasite farther from this status, the

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[8] They are host-specific for all practical purposes in this habitat.

harmful tendency could be more than offset by the greater overall advantage in having two parasite rather than one for action under changing conidtions, or to supplement one another in areas where one or the other is less adapted.

In the final analysis, while we should use caution and common sense, it is patently unfeasible to make long-term, complete ecological studies on all possible candidates to select the "ideal" species before making any introductions. Such studies, even if they could be financed, would not guarantee against the exceedingly rare mishap; nor can the solution to the problem brook a delay of 25 years. The record of experience weighs overwhelmingly in favor of introducing a complex of primary enemies and is itself the best

proof of whether or not it is *ecologically* or *economically* a sound procedure (see especially Doutt and DeBach, 1964). We should, however, consider more critically the ecological tendency, rather than the purely inherent capacity under forced conditions, of a given candidate species to serve as a secondary, in contrast to primary, parasite of a specific host. It becomes immediately clear, however, that the moment we start excluding a given parasite of both primary and secondary parasitic capacities, under situations where it operates at different efficiency in different environments, and relative to more than one pest species complex, we bring in many conflicting interests that may greatly complicate the problem of whether or not to make an introduction.

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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.